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What Makes an Image Memorable? Effects of Encoding on the Mechanism of Recognition

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What Makes an Image Memorable?
Effects of Encoding on the Mechanism of Recognition

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Abstract

Memory is undoubtedly one of the most important processes of human cognition. A long line of research suggests that recognition relies on the assessment of two explicit memory phenomena: familiarity and recollection. Researchers who support the Dual Process Signal Detection (DPSD) model of recognition memory link the FN400 component (a negative ERP deflection peaking around 400 ms at frontal electrodes) with familiarity; however, it is currently unclear whether the FN400 reflects familiarity or implicit memory. Three event-related potentials (ERP) studies were conducted to determine whether implicit memory plays a role in setting up encoding strategies, and how these encoding strategies influence recognition.

Experiment 1 consisted of two phases; an encoding/study phase and recognition/test phase. During the encoding phase, participants viewed pictures of common objects and later during a recognition test phase they made remembered/not-remembered judgments about previously seen (old) pictures and new pictures. ERP analysis of the encoding phase compared subsequently-remembered and subsequently-not-remembered stimuli and revealed marginally significant subsequent memory effects for the FN400 and LPC components. Because participants first saw the pictures during the encoding phase, the FN400 effect during this phase suggested that it was driven by conceptual fluency. Additionally, the fluency ERP (a positive ERP deflection during the time window ~200 - 400 ms) during the encoding phase significantly distinguished subsequently-remembered stimuli from subsequently-not-remembered stimuli, indicating that processing during encoding determined the stimuli to-be-remembered during the recognition test. During the

recognition test, the FN400 component correlated with the behavioral indicators of recollection and appeared to benefit from repetition.

Experiment 2 was similar to Experiment 1 except that participants saw meaningless novel stimuli (fractals). ERP results from recognition indicate that the FN400 effect did not capture repetition-based familiarity, however, the fluency ERP appeared to gain from the repetition of the stimuli. These results suggest that the FN400 potentials were driven by conceptual implicit memory during encoding, whereas during recognition, the behavioural indicators of recognition linked with the perceptual implicit memory, suggesting that explicit memory is not the only source of familiarity and the neural correlates of perceptual (fluency ERP) and conceptual (the FN400 component) implicit memory can influence decisions made by explicit memory.

Experiment 3 manipulated perceptual fluency, conceptual fluency, and repetition-driven familiarity. Participants viewed primed and unprimed, blurred and clear images of common objects that were presented once, twice or three times. Based on recognition performance, ERPs were back-sorted into their corresponding conditions. Fluency and FN400 components correlated with the behavioral indicators of recognition. Additionally, a conceptual implicit priming effect was significant over anterior and right frontal electrodes and perceptual implicit priming was significant at the occipital electrodes.

Conclusion: Collectively, the behavioural and ERP results add support the idea that the FN400 is “multiply determined” and may reflect familiarity (explicit memory driven) or conceptual fluency (implicit memory) depending on the task and stimulus, revealing that performance on recognition is not explicit memory driven. The *Discrepancy Attribution*

Hypothesis may provide a better understanding of the heuristics of familiarity, however, further research is needed to better examine the processes that underlie recognition.

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1 Chapter: Introduction

Memory performance is not a unitary ability; rather it is the product of multiple blends of processes that are specific to different circumstances. Encoding refers to the memory process that binds our everyday life experiences into memory traces, and retrieval is the process of retrieving this encoded information (Dudai et al., 2015). These memory processes, encoding and retrieval, can be explicit or implicit (Roediger & McDermott, 1993; Roediger et al., 1990). Explicit memory typically refers to conscious voluntary recollection of prior experiences, whereas implicit memory involves an unconscious, unintentional involuntary retrieval of information, such that people may not be aware of using memory at all (Jacoby, 1984). Conducting a memory experiment generally involves an encoding phase usually denoted as ‘study’ that is followed by a recognition phase referred to as ‘test’. During encoding/study phase, participants study memory items whereas during recognition/test phase, participants are tested on their study items. One way to investigate these memory processes is to examine the underlying neural mechanisms by using a variety of noninvasive neuroimaging techniques. In particular, event-related potential (ERP) techniques have been very useful in revealing cognitive mechanisms and their neural substrates during memory tasks (Luck, 2014) The goal of this dissertation is to examine the neural processes engaged during memory encoding and recognition by using ERP techniques.

1.1 Event-related potentials (ERP) and Electroencephalogram (EEG)

It was reported by Hans Berger in 1929 that the electrical activity of the human brain could be recorded from the scalp using electrodes (Luck, 2014; Berger, 1929). Changes in brain activity are revealed by plotting the changes in voltage over time once the signal is amplified. This electrical activity is called the electroencephalogram or EEG (Cohen, 2017). EEG signal contains the neural responses linked to stimuli known as task-related-events (or simply events). These events can be extracted by means of a simple averaging technique that yield an ERP. With this simple averaging technique, task unrelated events are averaged out as they are temporally inconsistent. Whereas ERPs elicited by stimuli produce time-coherent data akin to time series data of voltage changes over time in the form of positive and negative deflections (Paller et al., 2017). The shape, polarity and timing of these deflections differ with the nature of the stimuli, cognitive task and response. In memory paradigms, EEG is usually recorded both at encoding and at test, while participants are busy doing a memory task. Different ERPs have been associated with memory processes during both stages. We discuss these ERPs in the following sections.

1.1.1 Encoding ERPs

In a standard ERP study of memory encoding, brain activity is recorded while participants process a given task. Later, at the testing phase, the participants are tested on the studied items randomly mixed with some new items. Based on the test, the encoding activity is sorted out as subsequently remembered (SR) or subsequently not remembered (SNR). The difference between SR and SNR ERPs is called the subsequent memory effect (SME) based on the assumption that SMEs are the neural substrates of successful memory formation (Wilding & Ranganath, 2011; Wagner & Paller, 2002). Therefore, these SMEs depend upon the type of stimuli (e.g. words or images) and the depth of processing (Wilding & Ranganath, 2011; Otten & Rugg, 2001a). Additionally, SMEs for recall are more pronounced than those for merely recognition processes due to the reason that recall refers to the retrieval of a memory item without any cue and therefore rely greatly on associative information (Johnson, 1995; Paller, 1995). In contrast, recognition refers to our ability to recognize an event based on a cue.

1.1.2 Recognition Memory Processing and Recognition ERPs

Most previous studies are based on the widely accepted assumption that recognition performance is based only on explicit memory processing, i.e. familiarity and recollection (Yonelinas et al., 2007; Parks & Yonelinas, 2007; Rugg & Curran, 2007; Curran et al., 2006). Recollection refers to a slow process of conscious awareness that involves the retrieval of contextual details and source information of a test item. Familiarity, on the other hand is a relatively fast-acting sense of knowing a test item that does not provide contextual details about the test item (Wixted, 2007; Parks & Yonelinas, 2007; Tsivilis et al., 2001). A substantial amount of neurophysiological evidence supports the idea that familiarity and recollection are produced by functionally distinct neural mechanisms (Murray et al., 2015; Curran & Hancock, 2007; Rugg & Curran, 2007; Parks & Yonelinas., 2007; Rugg & Yonelinas., 2003; Yonelinas, 2002; 1999).

A large line of research supports the *dual-process-signal-detection (DPSD)* theory, which is based on the idea that recognition performance uses only explicit memory processing, i.e. familiarity and recollection (Yonelinas et al., 2007; Parks & Yonelinas, 2007; Rugg & Curran, 2007; Smith & DeCoster, 2000). Based on this model, familiarity reflects, “shallow encoding” of the stimulus and entails only a quantitative basis for judgment. Conversely, recollection provides a qualitative account of the judgment and reflects “deep encoding” (Wilding & Ranganath,, 2011; Rugg et al., 1998). The shallowest level refers to the perceptual processing such as the physical and sensory characteristics of the stimulus, and the deepest level is the semantic processing such as comprehension and pattern recognition (Craik, 2010; Lockhart & Craik, 1972).

1.2 Dual-Process-Signal Detection Model

A substantial amount of neurophysiological evidence supports the DPSD model by distinguishing neural correlates of recollection and familiarity, suggesting that they are produced by functionally distinct neural mechanisms (Yonelinas ET AL., 2014; Rugg & Curran, 2007; Parks & Yonelinas., 2007; Curran et al., 2006; Rugg & Yonelinas., 2003; Yonelinas, 1999, 2002). For example, event-related potential (ERP) studies reveal neurophysiological indices of these two processes. There is almost a general consensus that the ERP component known as the late-parietal component (LPC) is linked to recollection-based recognition memory (Addante et al., 2012; Wilding & Rugg, 1996; Wilding, 2000; 1999; Sanquist et al., 1980). Initially, it was shown by Sanquist and colleagues (1980) and later replicated by Rugg (Rugg et al., 1995; 1994) that ERPs elicited by previously studied stimuli are more positive than ERPs elicited by new stimuli. This effect was found to be largest over left-parietal areas in a 500 - 800ms time window and was therefore called the left-parietal old-new effect (Curran & Cleary, 2003; Curran, 2000; Rugg & Allan, 2000; Rugg, 1994). Likewise, another ERP component, which is more negative for new/unfamiliar stimuli over mid-frontal regions between the 300-500 ms time window, and mostly referred to as FN400, has been linked to familiarity-driven recognition (Curran & Hancock, 2007; Rugg et al., 1998). The dual-process account assumes that there exists a dissociation between the mid-frontal and left-parietal effect, and that these two effects are temporally, spatially and functionally distinct because they are linked to different aspects of memory (Rugg & Curran, 2007; Curran et al., 2006; Rugg et al., 1998). For instance, the mid-frontal effect is linked to the type of memory when a memory item is recognized as being experienced somewhere in the past without any contextual details. This aspect of memory just gives a sense of familiarity. Whereas the left-parietal effect is associated with recollection; when a memory item is recognized vividly with all its contextual and temporal details. These ERP findings represent pivotal support for the DPSD model's assertion that the familiarity and recollection processes arise from distinct neural mechanisms (Sweeney-Reed et al., 2016; Frithsen & Miller, 2014; Rugg & Curran, 2007; Eichenbaum et al., 2007; Düzel et al., 1997).

1.3 Single-Process Model

In contrast to the DPSD model, there is the '*single-process'* model, which suggests that recognition is determined by the strength of a unitary process continuum, of which, familiarity and recollection lie at opposite ends of two hierarchical levels (Squire et al., 2007; Wixted, 2007; Squire et al., 1995). This idea is based on the assumption that recognition memory relies on a single, continuously varying process that results from the strength of a neural signal in response to a stimulus, which leads to either recollection or familiarity (Wixted, 2007; Wilding & Ranganath, 2011; Donaldson, 1996). The classic version of signal-detection theory, which is known as the equal-variance model, holds that the decision criterion of recognition stems from two equal-variance Gaussian distributions; one being targets and the other lures. A test item is considered "old" if it elicits a memory strength that exceeds the decision criterion or else it is "new" (Wixted, 2007). However, a relatively new version of the equal-variance model suggests that recognition relies on recollection and familiarity such that recollection is a threshold-like retrieval process whereas familiarity is a signal-detection process that is independent of recollection.

Additionally, familiarity is functionally associated with conceptual implicit memory; however, it is distinct from perceptual implicit memory (Yonelinas, 2002). Consequently, the signal-detection model assumes that recognition may not necessarily rely on the explicit representation of memory i.e. familiarity. It is possible that implicit memory supports recognition based on the context (Paller et al., 2012; Nessler et al., 2006; Schott et al., 2005; Tulving & Schacter, 1990). Relatively little is known about implicit memory's contribution to recognition memory despite the fact that it plays a crucial role in human behavior and cognition.

1.3.1 Implicit Memory and Recognition

Despite growing neurophysiological and behavioural evidence suggesting that implicit memory influences recognition (Park & Donaldson, 2016; Keane at el., 2006), it is still a challenging issue to determine when and where in the brain this influence occurs. Multiple studies have shown that priming affects explicit memory during recognition (Voss et al., 2012; Paller et al., 2007; Paller et al., 2007; Gabrieli, 1998; Gabrieli et al., 1995; Rugg et al., 1998; Rugg, 1985; Jacoby & Dallas, 1981). Priming effects are an exhibit of implicit memory that is driven by prior experience (Schacter & Buckner, 1998; (Roediger & McDermott, 1993; Roediger et al., 1990; Tulving & Schacter, 1990; Schacter, 1987), such that a prior experience with a certain stimulus may unconsciously facilitate the response to that stimulus or to a related stimulus in a certain way. In other words, priming enhances the "fluency" of processing, which is reflected in behavioural measures of memory (Voss et al., 2010; Schacter & Buckner, 1998; Rugg, 1985; Schacter, 1987). Priming induces fluency in multiple ways based on the stimulus type and the relationship between the priming stimulus and the test stimulus. Whittlesea

(1993) described fluency as an unconscious attribution process that that is capable of altering the perception about a stimulus and the time required to process (Whittlesea, 1993; Whittlesea et al., 1990). The types of priming effects have been categorized as perceptual fluency and conceptual fluency (Voss et al., 2012; Paller et al., 2007). Perceptual fluency arises from sensory processing and does not involve meaning, whereas conceptual fluency is driven from the meaning of the stimulus and it goes beyond the physical characteristics of the stimuli (Paller et al., 2007). However, in most cases, a stimulus may trigger perceptual fluency based on its physical features as well as conceptual fluency based on its meaning (Guo et al., 2015; Voss et al., 2010). Conceptual fluency and the FN400 share the same neuronal mechanism and therefore FN400 may reflect conceptual fluency and not familiarity (Paller et al., 2007; Yonelinas, 2002; Rajaram & Geraci, 2000; Whittlesea et al., 1990; Jacoby & Dallas, 1981). Below we describe both conceptual and perceptual fluency in more detail.

1.3.1.1 Conceptual Fluency

Conceptual fluency is the ease of conceptually driven processing (Gabrieli, 1998; Whittlesea, 1993). A stimulus that involuntarily triggers or initiates a concept may constitute the basis for conceptual fluency. Seeing a meaningful stimulus (a picture or word) may facilitate fluency or ease of processing when the same stimulus or a semantically related one is subsequently presented (Whittlesea, 1993). This process can happen in several different ways; however, the repeated exposure of a meaningful stimulus has been shown to be particularly effective for generating conceptual fluency (Janiszewski & Meyvis, 2001; Dallas & Jacoby, 1981).

Although the dual-process model holds that recognition memory is driven by explicit memory processing, there exists some neurophysiological evidence that goes against this notion, which suggests that conceptual fluency is an expression of implicit memory that contributes to recognition memory (Wang et al., 2015a; Rajaram & Geraci, 2000). For example, several studies challenged the idea that the FN400 component reflects familiarity as an expression of explicit memory. Instead, these studies suggested that the FN400 component is closely linked to the N400 component, which reflects conceptual implicit memory and that the observed FN400 and N400 effects reflect a shared underlying mechanism (Packard et al; 2017; Ortu et al., 2013; Paller et al., 2012). Specifically, these researchers claim that the meaningful stimuli such as namable pictures or words prompt the retrieval of concepts in semantic memory. Therefore, the experience of familiarity and conceptual implicit memory (referred to as conceptual fluency hereafter) co-varied such that, in many studies, the FN400 component captured conceptual fluency instead of familiarity (Voss et al., 2012; Paller et al., 2007).

Conversely, when familiarity and conceptual implicit memory are distinguishable, the FN400 component correlates with behavioural measures of conceptual implicit memory rather than familiarity (Voss et al., 2012; Paller et al., 2007). In a review paper, Paller and colleagues argued that familiarity and conceptual priming (a form of implicit memory) are tightly correlated. In addition, they argued that the FN400 effects may actually index conceptual priming rather than familiarity due to the reason that their respective neural signatures are difficult to disentangle (Paller et al., 2007; Voss et al., 2007).

1.3.1.2 Perceptual Fluency

Perceptual priming or perceptual fluency is generally considered to arise from sensory processing and refers to the ease of processing perceptual features of an item because of its prior presentation (Susser et al., 2015; Snodgrass et al., 1996). Snodgrass and colleagues (1996) argued that perceptual fluency uses the sensory match effect to influence recognition memory, which is based on the retrieval of stored information (Snodgrass et al., 1996; Snodgrass, 1972). In other words, perceptual fluency is a form of implicit memory that can influence the response to a stimulus based on its previous experience without the participant necessarily being aware of the previous exposure or the meaning of the stimulus (Voss & Paller, 2010; Paller et al., 2012). There is behavioural and electrophysiological evidence that suggests that perceptual fluency plays a crucial role in shaping recognition judgments (Bruett & Leynes, 2015; Leynes & Zish, 2012). However, according to the discrepancy attribution hypothesis, fluency is not inherent to the physical properties of a stimulus; instead, it is interpreted via top-down control processing (Whittlesea & Leboe, 2003; Whittlesea & Williams, 2001a, b). This notion is supported by other studies, which have shown that stimulus repetition becomes a source of perceptual fluency by affecting the semantic memory system (Nessler et al., 2006; Snodgrass et al., 1996; Conroy et al., 2005). In other words, Nessler and colleagues suggest that a part of the recognition-based familiarity of meaningful stimuli stems from the same neuronal circuits that also contribute to perceptual fluency.

Interestingly, perceptual fluency has been shown to have distinct neural correlates from explicit memory at encoding (Schott et al., 2005; 2002; Tulving & Schacter, 1990). Schott and colleagues (2002) observed that processes associated with perceptual fluency occurred earlier than those processes that were associated with explicit memory. Likewise, Nessler and colleagues (2006) conducted multiple experiments to examine the ERP indices of perceptual fluency and familiarity. By using a paradigm where participants recognized famous and non-famous faces, they found that perceptual fluency correlated with an early ERP effect (~200-400 ms) at centro-parietal electrodes, whereas familiarity correlated with the FN400 component (Nessler et al., 2006). Similar results have been observed in other studies (Kurilla & Gonsalves, 2012; Rugg et al., 2000; 1998). Particularly, Rugg and colleagues noted that an ERP component (280-400 ms) at parietal sites was distinct from the ERP pattern at frontal sites. Furthermore, regardless of the accuracy of the response, this component was more positive for the old stimuli as compared to new stimuli (Rugg et al., 1998). Hence, Rugg et al. (1998) suggested that this effect is the neural correlate of memory in the absence of conscious recognition, which is known as implicit memory. The evidence from Rugg et al. (1998) and other studies suggests that this early parietal fluency ERP effect is linked to perceptual fluency, which is a qualitatively different ERP effect from the FN400 effect (Leynes & Addante, 2016; Leynes & Zish, 2012; Kurilla & Gonsalves, 2012; Rugg et al., 1998).

1.4 Link between Encoding and Recognition Memory Processing

Relatively little is known about implicit memory's contribution to recognition memory even though it plays a crucial role in human behavior and cognition. On the other hand, it is also a question of great concern whether processes at encoding are linked to FN400 at recognition. ERP studies of encoding have shown that subsequently-remembered (SR) stimuli are more positive than subsequently-not-remembered (SNR) stimuli, usually around 400 ms and beyond. The effect was initially called 'difference due to subsequent memory (Dm), but was later called the subsequent memory effect (SME) (Duarte et al., 2004; Yovel & Paller, 2004; Friedman & Johnson, 2000). To our knowledge, studies of encoding have not attempted to examine the subsequent FN400 effect by sorting their trials based on recognition performance. Several studies have shown that the level of processing (i.e. shallow or deep) at the encoding phase can affect the retrieval outcome revealing that these processes are linked (Craik, 2002; Fabiani et al. 1990). Further, ERPs at the time of encoding/study have been found to be predictive of subsequent memory performance in certain cases (Paller et al., 2017; Bridge and Paller, 2012). In general, early ERP deflections have been associated with shallow stimulus-driven processes (Luck 2005). Moreover, the FN400 has been linked to shallow memory processes (Rugg et al, 1998). One could expect that the earlier SM ERPs and FN400 should have some common grounds (Chen et al., 2014). Furthermore, Griffin and colleagues have shown that ERP components that are typically linked with recognition were observed during encoding, and were predictive of some of the subsequent memory performance (Griffin et al., 2013). Thus, it is a question of great interest whether an SM ERP at study, in a similar time interval to that of the FN400 effect is predictive of the FN400 effect at test, with the understanding that ERPs during study and test reflect different processes (i.e. encoding and recognition).

A number of recognition studies have shown that conceptual implicit memory contaminates the neural measures of familiarity when familiarity and conceptual implicit processing co-occur (Paller et al., 2012; Voss et al., 2012; Voss & Paller, 2010a). Voss and Paller (2012) suggest that implicit memory (e.g. perceptual or conceptual) contributes to familiarity during recognition and that processing may get reflected in the FN400 component. If true, the FN400 may reflect multiple mechanisms involved in recognition

(Mecklinger et al., 2012; Zarella et al., 2005). Moreover, the FN400 may not reflect a process exclusive to the memory processes related to familiarity, rather this ERP component may also reflect conceptual fluency and/or familiarity depending upon the context (Bruett & Leynes, 2015; Lucas & Paller, 2013; Paller et al., 2007).

In sum, many studies suggest that the repetition of a stimulus appears to initiate several cognitive processes, including perceptual fluency, conceptual fluency, and/or familiarity. DPSD model posits that the FN400 component reflects familiarity, whereas univariate signal detection (UVSD) model suggests that this component is linked to conceptual implicit memory (Berry et al., 2008). Others appear to disagree by suggesting that the FN400 component is multiply determined and indexes an unknown combination of familiarity and implicit memory processes (Paller et al., 2017; Leynes & Bruett, 2017). The basic question that we asked in these studies is how and when familiarity or conceptual implicit memory influence recognition judgment and how do these processes modulate encoding. Three EEG experiments were conducted to test these hypotheses. All three experiments consisted of two phases, encoding (study) and recognition (test). In Experiment 1, images of common objects were used as stimuli, Experiment 2 used the meaningless fractals and Experiment 3 used a combination of primed and unprimed clear and blurred images of common objects. Participants were tested for their memory during a recognition test phase by making remembered and not-remembered judgments about the studied items.

2 Chapter: An ERP Study of Encoding and Recognition Memory for Pictures of Common Objects

2.1 Introduction

Encoding refers to the memory process that binds our everyday life experiences into memory traces, while retrieval is the process of retrieving this encoded information. These memory processes, encoding and retrieval, can be explicit or implicit. Explicit memory typically refers to conscious voluntary recollection, whereas implicit memory refers to unconscious, unintentional and involuntary recollection of prior experiences (Jacoby, 1984). It is interesting to note that most studies have tried to understand memory from a retrieval perspective; despite the fact that the processes that lead to encoding strongly influence the way information is retrieved (Craik & Lockhart, 1990; 1972).

A large line of research supports the *dual-process-signal-detection* (DPSD) theory, which is based on the widely accepted assumption that recognition performance is based only on explicit memory processing, i.e. familiarity and recollection (Yonelinas et al., 2014; Parks & Yonelinas, 2007; Rugg & Curran, 2007; Smith & DeCoster, 2000). Recollection is a slow deliberate process that involves the retrieval of contextual details and source information of the test item, whereas familiarity is a relatively fast-acting sense of knowing the test item that does not provide contextual details about the test item (Wixted, 2007; Parks & Yonelinas, 2007). Based on this theory, familiarity reflects "shallow encoding" of the stimulus and entails only a quantitative basis for judgment whereas recollection provides a qualitative account of the judgment and reflects "deep encoding" (Wilding & Ranganath,, 2011; Rugg et al., 1998).

Alternatively, in contrast to the DPSD model, there is the '*single-process'* model, which suggests that recognition is determined by the strength of a unitary process continuum, of which, familiarity and recollection lie at the two hierarchical levels (Squire et al., 2007; Wixted, 2007). This idea is based on the assumption that recognition memory relies on a single, continuously varying process that results from the strength of a neural signal in response to a stimulus, which leads to either recollection or familiarity (Wixted, 2007; Wilding & Ranganath, 2011; Donaldson, 1996). Consequently, the single-process model assumes that recognition may not necessarily rely on the explicit representation of an item i.e. familiarity and recollection. It is possible that implicit memory supports recognition based on the context (Paller & Voss, 2012; Nessler et al., 2006; Schott et al., 2005; Tulving & Schacter, 1990). Relatively little is known about implicit memory's contribution to recognition memory despite the fact that it plays a crucial role in human behavior and cognition.

A substantial amount of neurophysiological evidence supports the DPSD model by distinguishing distinct neural correlates of recollection and familiarity and suggesting that familiarity and recollection are produced by functionally distinct neural mechanisms (Murray et al., 2015; Rugg & Curran, 2007; Parks & Yonelinas., 2007; Curran et al., 2006; Rugg & Yonelinas., 2003; Yonelinas, 2002; 1999; Hockley & Consoli, 1999). In particular, event related potential (ERP) studies reveal neurophysiological indices of these two processes. There is almost a consensus that the ERP component known as the late-parietal component (LPC) is linked to recollection-based recognition memory (Wilding, 2000; Wilding & Rugg, 1996; Sanquist et al., 1980). Initially, it was shown by Sanquist and colleagues (1980) and later replicated by Rugg (Rugg et al., 1995; 1994) that ERPs elicited by previously studied stimuli are more positive than ERPs elicited by new stimuli. This effect was found to be largest over left-parietal areas in a 500 - 800 ms time window and was therefore called the left-parietal old-new effect (Curran, 2000; Rugg & Allan, 2000; Rugg, 1994). Likewise, another ERP component, which too is more positive for old/familiar than new/unfamiliar stimuli over mid-frontal regions between the 300-500 ms time window, and mostly referred to as FN400, has been linked to familiarity-driven recognition (Curran & Hancock, 2007; Rugg et al., 1998). Dual-process accounts assume that there exists a disassociation between the left-parietal and mid-frontal effects, indicating that these two effects are temporally, spatially and functionally distinct and linked to different aspects of memory (Rugg & Curran, 2007; Curran et al., 2006; Rugg et al., 1998). Thus, the LPC and FN400 have been used as pivotal support for the DPSD model and assertion that the familiarity and recollection processes arise from distinct neural mechanisms (Sweeney-Reed et al., 2016; Rugg & Curran, 2007; Düzel et al., 1997).

Despite much neurophysiological and behavioural support for the DPSD model, according to which the FN400 potentials reflect familiarity (Rugg & Hancock, 2007), it is still a challenging issue to validate the neural signature of familiarity, mostly because the nature of familiarity is disputed (Voss & Paller, 2012; Rugg & Curran, 2007; Whittlesea et al., 2001). Paller and colleagues (Paller et al., 2007; Voss & Paller, 2012) challenged the claim that the FN400 component reflects familiarity; instead, they suggested that the FN400 component is closely linked to the N400 component, which reflects implicit memory (Cheyette & Plaut, 2017). They showed that in circumstances when familiarity and implicit memory are distinguishable, the FN400 component correlates with a behavioural measure of implicit memory rather than familiarity (Paller et al., 2007; Voss & Paller, 2012).

In a review paper, Paller and colleagues (2007) argued that familiarity and implicit memory are tightly correlated, and the FN400 may index implicit memory rather than familiarity due to the reason that their respective neural signatures are difficult to disentangle (Paller et al., 2007; see also Voss et al., 2007). Implicit memory stems from different forms of fluency, such as perceptual fluency and conceptual fluency, based on stimulus properties (Voss et al., 2012; Paller et al., 2007). Therefore, it is important to explore the exact form of implicit memory that may contribute to the FN400 amplitudes (Voss et al., 2012).

Conceptual fluency stems from the meaning of an item and goes beyond the physical characteristics of the stimulus whereas perceptual fluency appears as the ease of sensory processing of a stimulus, driven by prior experience without having awareness of having experienced it before (Voss et al., 2012; Paller et al., 2007). Hence, it is plausible to assume that distinct neural measures are associated with these two forms of implicit memory (Paller et al., 2012). A number of recognition studies have shown that conceptual implicit memory contaminates the neural measures of familiarity when familiarity and conceptual implicit processing co-occur (Paller et al., 2012; Voss et al., 2012; Voss & Paller, 2010a). For instance, Voss and Paller (2012) conducted a series of experiments to identify the neural correlates of conceptual implicit memory and familiarity using semantic and non-semantic stimuli (Voss et al., 2011; 2010; Voss & Paller, 2007). The FN400 component was found to correlate with familiarity when familiarity co-varied with conceptual implicit memory. No FN400 was observed when conceptual fluency was disassociated from stimuli (Voss & Paller, 2007). Therefore it can be speculated that FN400 does not reflect a process exclusive to the memory process related to familiarity, rather this effect may also reflect conceptual fluency and/or familiarity depending upon the context (Bruett & Leynes, 2015; Lucas & Paller, 2013; Paller et al., 2007).

Although numerous studies have shown that the mid-frontal effect (FN400) reflects conceptual implicit memory, it remains to be seen whether and how perceptual fluency is linked to the FN400 effect (Paller et al., 2012; Voss et al., 2012). As mentioned earlier, implicit memory stems both from perceptual as well as conceptual fluency; therefore, the ERP correlates of these two forms of fluency should be examined separately. Perceptual fluency emerges from the sensory processing of the physical attributes of a stimulus mostly because of repetition (Schacter, 2008; Snodgrass et al., 1996). It has been widely documented now that perceptual implicit memory, or simply perceptual fluency, is linked with the early positive ERP peaking around ~300 ms at parietal sites (Bruett & Leynes, 2015; Leynes & Zish, 2012; Nessler, et al., 2005). This component is more positive for the new stimuli as compared to old stimuli and it a temporally and spatially dissociated from the FN400 effect (Leynes & Addante, 2016; Leynes & Zish, 2012; Kurilla & Gonsalves, 2012; Woolman et al., 2008). Depending upon different testing scenarios, implicit memory through perceptual or conceptual fluency, can contribute to familiarity (Lucas et al., 2012; Voss & Paller, 2012). Studies have shown that the perceptual features of a stimulus can affect the neural correlates of familiarity (Wang et al., 2015; Lucas & Paller, 2013). For example, the FN400 varied when perceptual features were manipulated while conceptual information was kept constant (Mecklinger et al., 2012). Additionally, repetition of a stimulus (i.e. oldness) may also increase the perceptual fluency of a stimulus, as well as increase responses due to familiarity and elicit the FN400 effect (Bruett & Leynes, 2015; Schacter et al., 2007). Therefore, it is necessary to examine the fluency ERP effect in conjunction with the FN400 ERP and its association with perceptual implicit memory.

Collectively, these studies suggest that implicit memory (e.g. perceptual or conceptual fluency) contributes to familiarity during recognition and that implicit memory / fluency may be reflected by the FN400 component (Mecklinger et al., 2014). A separate but related question of great concern is whether the processes at encoding are linked to the FN400 at recognition. Based on the performance from recognition test, subsequent memory encoding studies have shown that subsequently remembered (SR) ERPs are more positive than subsequently not remembered (SNR), usually around 500 ms and beyond, initially called ‘difference due to subsequent memory (Dm) and later became subsequent memory effect (SME) (Duarte et al., 2004; Yovel and Paller, 2004; Friedman and Johnson, 2000).

A very few recognition studies have attempted to examine the FN400 effect by back-sorting their trials based on recognition performance. ERPs at the time of encoding/study have been found to be predictive of the retrieval outcome revealing that these processes are linked (Craik & Lockhart, 2002; Fabiani et al. 1990). Furthermore, Griffin and colleagues have shown that the FN400 and old/new parietal components that are typically linked with recognition were also observed during encoding in a task that did not require explicit memory judgment (Griffin et al., 2013). In a simple encoding task, images of common objects were presented in random order and subjects were instructed to classify them as natural or man-made. Their task did not involve an explicit memory judgment during encoding. Some stimuli were presented twice and for other stimuli their exemplars were presented. This task was then followed by a surprise recognition task.

One could expect that the earlier SM ERPs and the FN400 ERP should be operating under common grounds (Chen et al., 2014). Thus, it is a question of great interest whether an SM ERP at study, similar time interval to that of the FN400 effect is predictive of the FN400 effect at test knowing that ERPs during study and test reflect different processes (i.e. encoding and recognition).

In order to investigate the hypothesis that the FN400 ERP reflects conceptual implicit memory whereas the fluency ERP reflects perceptual fluency, we used a paradigm that only allowed a shallow level of encoding (Fukuda et al., 2015). Given that the time and the attention that is taken to process a stimulus determines the depth of the processing, a shallow encoding task was used to decrease the likelihood of recollection during recognition (Craik & Rose, 2012; Craik, 2002; Rugg et al., 1998). Recognition performance relies on the depth of processing (Craik & Lockhart, 1990; 1972; Craik, 2002). Processing of a stimulus involves a hierarchy of analyses running from early sensory processing to later in-depth analysis of conceptual features. The time and the attention that is taken to process a stimulus determines the depth of the processing, where "depth" is the qualitative nature of the processing performed on the stimulus (Craik & Rose, 2012; Craik, 2002). The recruitment of different levels of memory-related tasks (shallow or deep / easy or hard) by different mechanisms is based on the idea that these levels of processing are part of a continuum (Anderson & Hanslmayr, 2014; Craik, 2002; Friedman & Johnson, 2000). Lockhart and colleagues used the term "domain of processing" to imply that processing proceeds through multiple stages in a hierarchical manner. Thus, the process when encountering a word is such that the phonology of the word would recruit the shallowest level of encoding whereas articulation, lexicon and conception to apprehend the word would employ higher/deeper levels respectively (Craik, 2010; Lockhart & Craik, 1990; 1972). Thus, the order of processing is somewhat hierarchical and strictly depends upon the task. Familiarity corresponds to a shallow level of processing whereas recollection captures higher/deeper levels of processing (Marzi, et al., 2010; Rugg et al., 1998).

The stimuli we used in this paradigm were pictures that possessed similar perceptual fluency and conceptual fluency (Brady et al., 2008). Pictures are better remembered than words (Grady et al., 1998). Therefore, given that there were a large number of trials for our participants to remember, we chose pictures of common objects as our stimuli. There were two phases in the study: the encoding phase and the recognition testing stage. In the first phase, participants passively viewed pictures and in the second phase, participants provided a recognition judgment indicating whether they remembered seeing the stimuli previously. As mentioned, shallow level of processing leads to implicit memory encoding (Craik, 2002) so we predicted that implicit memory would guide the behavior of participants when they were asked to remember the pictures. An FN400 might act as an index of conceptual memory if it were to be observed during the encoding phase since this would be the first time the participants would be encountering the images in the experiment (Leynes et al., 2017; Griffin et al., 2012).

During recognition, participants viewed pictures a second time along with some new pictures and it is assumed that the repetition of some of the pictures during the recognition test should distinguish old (old/new familiarity ERP effect) against new stimuli (DPSD model: Rugg & Curran, 2007; Yonlinas, 2000). Thus, if repetition-based familiarity is reflected by the FN400 component (DPSD model: Rugg & Curran, 2007; Yonlinas, 2000), then we expected more positive amplitudes for the FN400 components for remembered stimuli (Hit) during the recognition testing compared to the FN400 ERPs elicited by the new pictures. During encoding, however, if the FN400 component does reflect conceptual fluency, more conceptually fluent stimuli should be recognized more easily and therefore the FN400 amplitudes for SR stimuli should be more positive than SNR.

2.2 Methods

2.2.1 Participants

After consenting to procedures approved by Wilfrid Laurier University Research Ethics Board, 27 healthy participants (12 F, 14M, 1 other) participated voluntarily in the study. All participants were right-handed and had normal or corrected to normal vision. No participant reported having any psychiatric illnesses or brain trauma. None of the participants were on psychotropic medications. Analyses were conducted on all 27 participants who were between 19 to 31 years of age (mean age = 21 years). Participants signed informed consent forms prior to taking part in the study. They were granted course credits for their participation.

2.2.2 Stimuli and procedures

Stimuli were adapted from a published set of photographs (Brady et al., 2008). A MATLAB script was used to randomize the process of selection of these stimuli and stimuli were included from all categories. There were two phases in the experiment; the encoding task and the recollection or recognition task. During the encoding task, participants were sequentially presented with 800 pictures from a published set of photographs (Brady et al., 2008). There were short breaks every 8-minutes (every 100 pictures), which divided the encoding session into 8 blocks of 100 pictures each. Participants initiated each block by pressing a button on a response pad. However, for the rest of the trials within the block, participants were not in control. Each trial started with a 1 s pre-encoding period, where participants focused on a blank screen with a central fixation dot. Each picture was presented for 250 ms, followed by a 1s-encoding period, during which the computer screen remained blank (see Figure 2.1). Participants were told in advance that they would be tested for their memory of the photographs and to watch each item carefully in order to perform the recognition memory test.

After a short break, participants performed the recognition test during which 500 pictures (300 old, 200 new taken from the same database) were randomly presented. The ratio of old to new stimuli was a bit higher for two reasons: first, the performance on recognition test was retrospectively used to categorize the encoding trials and more old trials gave us more SR and SNR trials. Second, the number of CR trials is always higher than FA and a smaller number of new trials gave us almost an equal number of trials for Hits and Misses. During the recognition test, pictures were presented on the screen until a response was recorded. Participants were instructed to press ‘1’ on the response pad if they remembered seeing the picture or press ‘2’ if they didn’t remember seeing the picture.

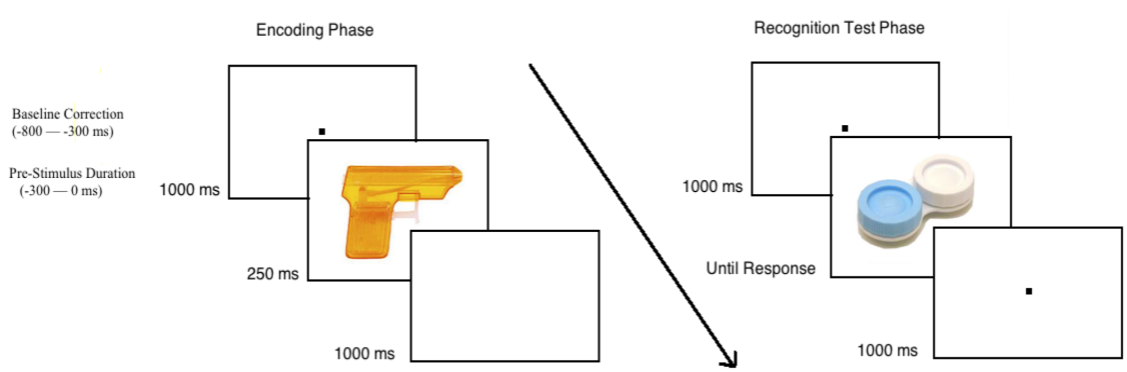


Figure 2.1. Schematic diagram of the timeline of a trial in the encoding and recognition test phases.

2.2.3 EEG data and Acquisition

EEG data were recorded from a 32-channel NeuroScan Quik-Cap (Compumedics, Charlotte, SC, USA) in a sound-attenuated, electrically shielded booth (Raymond EMC, Ottawa, ON, Canada) while participants performed the encoding and recognition tasks. Impedances were kept below 5kΩ.

An EEG cap was placed onto the participant's head such that electrodes fixed over the frontal lobes (Fp1, Fp2, F7, F3, Fz, F4, F8, FC3, FCz, FC4), temporal lobes (FT7, FT8, T7, T8, TP7, TP8), parietal lobes (CP3, CPz, CP4, P7, Pz, P4, P8), occipital lobes (O1, O2), and at the central position of the scalp (C3, Cz, C4). Electrode Cz was visually centered above the central vertex found halfway between the glabella and the external occipital protuberance medially and the preauricular points laterally. Electro-gel was used to improve conduction between the skin and the electrode surface. Surface electromyographic electrodes were positioned at the outer canthii of both eyes and above and below the left eye. EEG signals were initially referenced to mastoid electrodes (M1, M2), which were placed on the mastoid process behind each ear.

2.2.4 Behavioural Analyses

Performance in the recognition task was analyzed. Specifically, we investigated participants' task accuracy and response time. Each participant's hit, miss, correct-rejection and false alarm rates were calculated.

ERPs based on subsequently-remembered (SR) trials during the encoding task were compared to subsequently-not-remembered (SNR) trials based on the performance in the recognition test for each participant. Reaction times during the recognition task were analyzed using a one-way ANOVA with the within-subject factor as the subsequent memory effect (subsequently remembered/SR, not-remembered/SNR).

The perceptual sensitivity of the recognition task based on signal detection theory (SDT) was calculated by computing A′ for each participant. We used A′ as our main index of performance (Stanislaw & Todorov, 1999) because A′ is capable of distinguishing response bias from sensitivity. Usually in memory studies, where responses are mainly based on a yes/no paradigm, participants are highly responsive to suggestion or direction. In that case, recall or recognition is improved but the false alarm rate also increases. Therefore, it is important to measure response bias and sensitivity separately. A′ was computed in the following manner:

$$A' = \begin{cases} 0.5 + \dfrac{(H-F)(1+H-F)}{4H(1-F)} \ \ when\ H \geq F \\ 0.5 - \dfrac{(F-H)(1+F-H)}{4F(1-H)} \ \ when\ H < F \end{cases}$$

$$H = \frac{Hits}{Hits + Misses}$$

$$F = \frac{FalseAlarms}{(FalseAlarms\ +\ CorrectRejections)}$$

A′ can take any values between 0.5 and 1, with 1 being perfect performance, while 0.5 occurs when a participant completely failed to distinguish old from new stimuli.

2.2.5 Controlling for Fatigue

Our experiment was almost two hours long and could cause fatigue. We ran an analysis to establish that the spectral measures from our data came from brain activity that resulted from memory processes rather than fatigue. Most importantly, studies report that alpha oscillations (9-12 Hz) increase with fatigue and drowsiness (Tanaka et al., 2012; 1999). Therefore, it was important to ensure that the alpha we observed in our results was not a spurious effect stemming from fatigue. To explore that, we divided our data from the encoding task into 8 blocks and extracted and averaged the oscillatory measures for each block for all participants. Our results revealed that there was no significant difference in the oscillatory activity across time (Hits across time: $F(7, 192) = 1.8$, p = n.s; Oscillatory activity: $F(7, 192) = .52$, p = n.s).

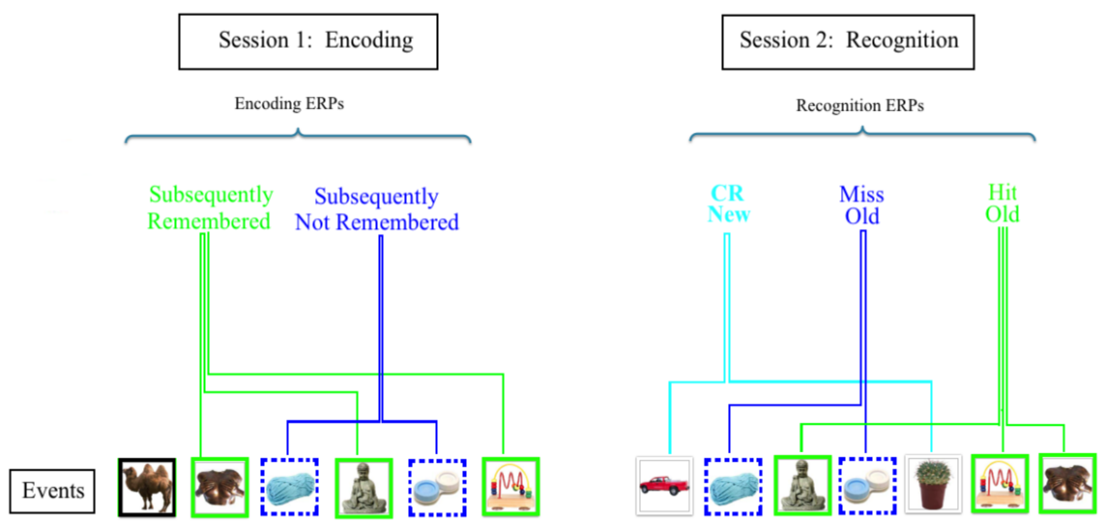


Figure 2.2. A schematic diagram of the encoding and recognition phases of the experiment. Based on the recognition performance, ERPs of subsequently remembered and subsequently not remembered stimuli were chosen for the encoding analysis.

2.3 ERP Preprocessing and Analyses

The EEG data preprocessing and analysis were performed using custom MATLAB (The Mathworks, Inc.) scripts operating in conjunction with the open-source EEGLAB toolbox (Delorme and Makeig 2004, http://sccn.ucsd.edu/eeglab). A four-step analysis approach was used to analyze our data, which is given as follows.

Step 1- Preprocessing: Continuous EEG signals were down-sampled to 250 Hz. Continuous data were filtered using a high-pass finite impulse response (FIR) at 1 Hz and then re-referenced to average reference (Winkler et al., 2015). The continuous data signals were then inspected and corrected for outliers, body movements and muscle and cardiac artifacts by using Artifact Subspace Reconstruction (ASR) (Bigdely-Shamlo et al., 2015).

Step 2- ICA: Next, an Adaptive Mixture ICA (AMICA) was applied separately to single subject datasets (Palmer et al., 2008). An ICA decomposition method has the ability to linearly un-mix EEG channel data into temporally independent component activities with a fixed spatial projection pattern (Onton & Makeig, 2011; Onton et al., 2006; Makeig et al., 2004a). The ICA decomposition method assumes EEG channel signal a linear mixture of the activities of brain and non-brain sources with almost independent time courses (Onton & Makeig, 2011). Therefore, ICA un-mixes the traditional channel data into a channel-weighted sum of temporally near-independent component activity with a fixed spatial projection pattern. Thus, ICA decomposition offers temporal and spatial resolution of separable and near-independent EEG source-level activities or more precisely independent components (IC). In short, an IC can be regarded as spatially coherent local field activity of a near-single cortical source of temporally near-independent time course and near-dipolar scalp projection (Delorme et al., 2012; Onton et al., 2006; Makeig et al., 2004; 1996) as opposed to the traditional scalp channel signal analysis where several cortical sources contribute to the same channel. ICA decomposes channel data into as many as the number of channels. For instance, we used a 32-channel cap; therefore ICA decomposition of our channel data yielded 32 independent components for each subject. This way, with the ICA decomposition method, it is easier to un-mix brain cortical signals from the noisy non-brain source activities. Thus, all 64 ICs were inspected for their spectral, temporal and spatial properties to identify brain activity components from non-brain activities such as eye-blinks, cardiac and muscle artifacts, lateral eye movements and line noises etc. ICs associated to non-brain activities were excluded from further analyses.

Step 3 – Epoching and IC processing: Next, we calculated a single equivalent dipole model for the scalp topography of each IC, to further exclude ICs that could not be attributed to any cortical sources. For this purpose, we used DIPFIT toolbox of EEGLAB (Oostenveld, Delrome, & Makeig., 2003). For the source modeling, each participant's electrode locations were registered to an MNI (Montreal Neurological Institute) template head model, which uses a Boundary Element Method (BEM) to calculate an electrical forward solution. This way, the equivalent dipole for the scalp projection pattern of each remaining IC was estimated and was fit to its scalp map. The data were then sliced into segments of three seconds (from 1 s before to 2 s after task stimulus onsets) (Makeig, 1993).

Step 4 – ERP Analysis: For ERP analysis, the epoched signals were then low-pass filtered at 30 Hz. All trials above 5 μV voltage potential from baseline were rejected. On average, 11% of the trials per participant were rejected. Trials were referenced to a 200 ms pre-stimulus baseline. For encoding ERPs, epochs were grouped into subsequently remembered items (SR) and subsequently not remembered items (SNR), based on the participants' performance during the recognition task (see Figure 2.2; Encoding).

After a short delay, participants were tested with these "old" pictures randomly intermixed with "new" pictures during the recognition test. participants had to discriminate whether each picture presented was old or new. Based on the performance of each participant during the recognition test, the studied pictures in the encoding task were categorized as remembered and not-remembered items for analysis and the difference between the neural activities for the remembered and not-remembered stimuli was called a subsequent memory effect (SME) (Paller et al., 2002; 2001; Rugg & Allan, 2000). ERPs at the recognition test were averaged separately for the recognized/remembered (Hit) items correctly identified as new (correct rejection, CR) responses, and items that were incorrectly identified as new (miss) (see Figure 2.2; Session 2).

In general, we focused on three effects; the fluency ERP, which is an early parietal effect (200-400 ms) that has been associated with perceptual fluency of stimuli (Paller et al., 2007; Rugg & Curran, 2007); the FN400 effect, an ERP component during the 300–500 ms time interval at some of the mid-frontal electrode sites such as F3, Fz, and F4 (Voss et al., 2012); and the LPC-effect, a late parietal component ERP elicited during the 500–800 ms time interval at left-parietal electrodes (Leynes & Zish, 2012; Paller et al., 2007; Rugg & Curran, 2007; Curran & Hancock, 2007; Curran, 2000;).

For our statistical analysis, we ran several levels of analyses to identify whether fluency, the FN400, and the LPC ERPs contributed to recollection based on recognition judgments. In our first analysis, we ran a global analysis for all three effects by computing averages at frontal (F3, Fz, F4), frontal-central (FC3, FCz, FC4), central (C3, Cz, C4) central-parietal (CP3, CPz, CP4), and parietal electrodes (P3, Pz, P4) (Leynes et al, 2017; Bruett & Leynes 2015; Leynes & Zish, 2012). Next, we focused more on a local analysis specific to the above stated three effects, i.e a fluency ERP effect at central-parietal (CP3, CPz, CP4) and parietal electrodes (P7, P3, Pz, P4, P8), the FN400 effect at mid-frontal electrodes and fronto-central electrodes (F3, Fz, F4; and FC3, FCz, FC4) and the LPC effect at left-parietal electrodes (P7, P3, Pz).

For the encoding phase, an ANOVA with within-subjects factors of condition (Subsequently-Remembered/SR, Subsequently-not-remembered/ SNR), electrode location as anterior to posterior (AP; with 5 levels - frontal, fronto-central, central, centro-parietal, and parietal), and laterality (LCR; 3 levels - left/center/right) was conducted (Leynes et al., 2017). Likewise, another ANOVA with the factors of response types (Hit, Miss, CR), electrode location and laterality (LCR) was used to analyze the recognition data.

Prior studies have shown that the FN400 and parietal components are distinct, with the FN400 maximal over anterior sites, and the fluency and LPC ERPs maximal over posterior locations. Topographic visualizations were prepared with the EEGLAB Matlab toolbox (Delorme & Makeig, 2004). All significant effects were corrected for non-sphericity by using Greenhouse–Geisser corrections and corrected degrees of freedom are reported wherever appropriate.

2.4 Results

2.4.1 Behavioural Results

Our results showed that participants, in general, were capable of discriminating old from new pictures, as indicated by an average A′ of 0.74 (SD: +/− .09; range 0.56 to 0.88). The average response time (RT) for all types differed, $F(3,14075)=46.50$, $p<0.001$. Pairwise comparisons indicated that participants recognized hit items faster than all other responses. However, none of the other responses were different among themselves ($p > 0.05$).

On average, participants performed the recognition task accurately. They successfully rejected 78.65% of the new photographs but failed to reject 21.3% of the new items. For the old items, participants recognized 50.22% of the old stimuli objects and failed to recognize the remaining 49.78% of the stimuli. It is clear from Table 2.1 that we had large standard deviations for both the accuracies and RTs. Two participants were excluded from the analysis due to excessive amount of ocular artifacts and muscular artifacts as well as their performance were below chance.

Table 2.1

Accuracy (percentage) and response time (ms) values, reported along with their standard errors across participants in parentheses.

Condition	Accuracy	Response Time (ms)
Hits (old)	50.22 (16.59)	971.8 (794.85)
Misses (old)	49.78 (16.58)	1158.57 (856.37)
Correct Rejection (new)	78.65 (13.4)	1148.29 (980.08)
False alarms (new)	21.3 (13.28)	1120.18 (903.72)

2.4.2 ERP Results

2.4.2.1 Encoding Task

SME analysis: A visual inspection of the ERPs indicated the presence of an overall subsequent memory effect for SR when compared to SNR stimuli. In accordance with previous studies (Fellner et al., 2013; Schnieder et al., 2016), our results revealed significant subsequent memory effects (SME) for early latencies. Significant effects from the analysis of the ERP amplitudes from the encoding and recognition phases are presented in Table 2.2. Figure. 2.3 and 2.4 display the grand-averaged ERPs with topographic maps for SNR vs SR and Hit, Miss, and CR stimuli, respectively. The detailed results that follow present the focused ERP analyses.

Fluency ERP (200 – 400 ms): Our three-way repeated-measures ANOVA (condition x anteriority/ posteriority x laterality) did not reveal a significant main effect of condition although significant interactions of condition X anterior/posterior (AP) location and condition X laterality (left/center/right (LCR)) location were observed (Table 2.2). These AP and LCR interactions were explored with post hoc analyses that examined effects at parietal electrodes (P7, P3, Pz, P4, P8). ERPs elicited by SNR were more positive than SR during the encoding phase, revealing a fluency ERP effect. The analysis of right-parietal electrode effects did not reveal any significant old/new differences, whereas the analysis of left parietal and occipital ERPs revealed significant SR/SNR differences (Fluency ERP at P3: $t(24) = 2.98$, $p = 0.007$; O2: $t(24) = 2.89$, $p = 0.008$), indicating that SR stimuli elicited less positive ERPs than the SNR stimuli.

FN400 (300 – 500 MS): Our 3-way repeated-measures ANOVA revealed only a significant main effect of condition at the encoding stage, limited to the mid-frontal electrodes. Additionally, a two-way repeated-measures ANOVA with the factors SME and electrode sites (fronto-polar/mid-frontal electrodes , FP1, FP2, F3, Fz, F4) conducted for the FN400 time interval revealed a significant main effect of SME [$F(1,24) = 4.79$, $p = 0.04$, $\eta_2 = 0.17$], reflecting less positive amplitudes for SR stimuli than SNR. This effect was confirmed by separate t-tests for SR and SNR ERPs, which revealed that the FN400 amplitudes were more positive for the subsequent hits when compared to subsequent misses [Fz: $t(24) = 3.05$, $p = 0.006$; FCz: $t(24) = 3.07$, $p < 0.005$]. The topographic map for the FN400 effect appeared to be bilaterally distributed over mid-frontal locations and appears to be less negative for the SR stimuli, contributing to the marginal significance of this interaction (see Table 2.2).

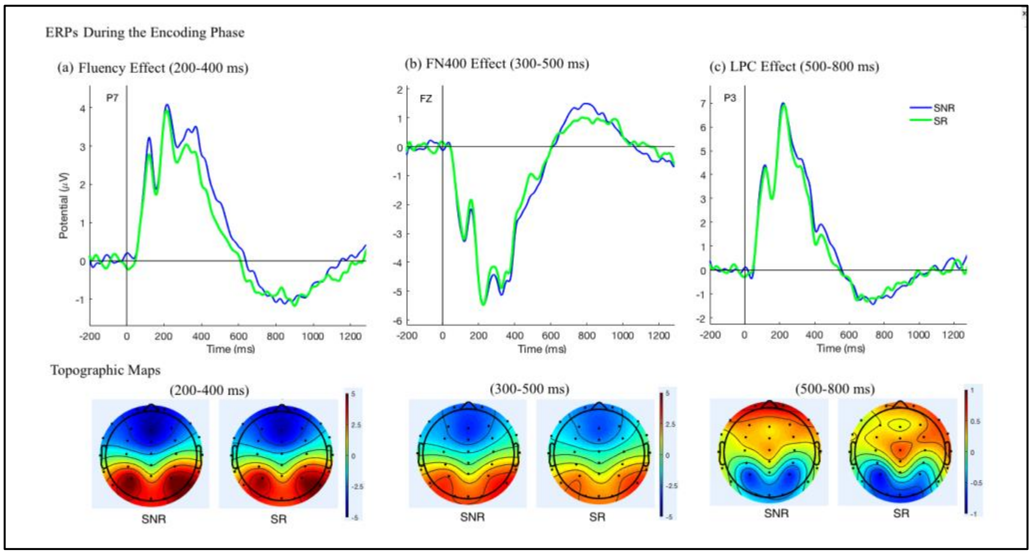


Figure 2.3. Grand-average ERPs at the left-parietal, mid-frontal electrodes (top panel) elicited by SR and SNR pictures averaged across all participants. Topographic maps depict the time course of fluency (200-400 ms), FN400 (300-500 ms), and LPC effects during the encoding phase. Small circles represent electrode locations as viewed from above.

Table 2.2

Significant effects from the analysis of ERP amplitudes for encoding phase and recognition test.

	Encoding						Recognition (Hit / Miss)						Recognition (Hit/ CR)					
	Fluency (200 - 400 ms)		FN400 (300 - 500 ms)		LPC (500 - 800 ms)		Fluency (200 - 400 ms)		FN400 (300 - 500 ms)		LPC (500 - 800 ms)		Fluency (200 - 400 ms)		FN400 (300 - 500 ms)		LPC (500 - 800 ms)	
	t(24)						t(24)						t(24)					
P7	-2.479	p = 0.021	-	-	-	-	-2.592	p = 0.016	-	-	-3.442	p = 0.002	-	-	-	-	-	-
P3	-2.979	p = 0.007	-	-	-	-	-3.038	p = 0.006	-	-	-	-	-	-	-	-	3.458	p = 0.002
Pz	-	-	-	-	-	-	-	-	-	-	3.567	p = 0.002	-	-	-	-	3.016	p = 0.006
P4	-	-	-	-	-	-	-3.062	p = 0.005	-	-	-	-	-2.574	p = 0.017	-	-		-
P8	-	-	-	-	-	-	-3.737	p = 0.001	-	-	-3.542	p = 0.002	-2.989	p = 0.006	-	-	-2.629	p = 0.015
CPz	-	-	-	-	-	-	-	-	-	-	4.028	p < 0.001	-	-	-	-	3.896	p = 0.001
CP3	-2.124	p = 0.044	-	-	-	-	-	-	-	-	5.833	p < 0.001	-	-	-	-	6.639	p < 0.001
C3	2.027	p = 0.054	-	-	-	-	-	-	-	-	6.471	p < 0.001	-	-	-	-		-
Cz	-	-	2.841	p = 0.009	-	-	-	-	2.579	p = 0.016	4.613	p < 0.001	-	-	-	-	4.143	p < 0.001
C4	-	-	-	-	-	-	-	-	-	-	3.624	p = 0.001	-	-	-	-	-	-
FP1	-	-	-	-	2.082	p = 0.048	-	-	3.896	p = 0.001	-		-	-	2.428	p = 0.023	-	-
FP2	-	-	-	-	-	-	-	-	3.864	p = 0.001	-	-	-	-	2.732	p = 0.012	-	-
F3	-	-	2.15	p = 0.042	-	-	-	-	3.723	p = 0.001	2.659	p = 0.014	-	-	2.244	p = 0.034	-	-
Fz	-	-	3.05	p = 0.006	-	-	-	-	3.997	p = 0.001	3.13	p = 0.005	-	-	2.629	p = 0.015	-	-
F4	-	-	2.329	p = 0.029	-	-	-	-	2.3	p = 0.03	-	-	-	-			-	-
FCz	-	-	3.067	p = 0.005	-	-	-	-	4.034	p < 0.001	4.903	p < 0.001	-	-	2.428	p = 0.023	-	-
FC3	-	-	3.653	p = 0.001	-	-	-	-	3.855	p = 0.001	3.925	p = 0.001	-	-	2.348	p = 0.027	-	-
FC4	-	-	2.406	p = 0.024	-	-	-	-	0.852	p = 0.403	3.061	p = 0.005	-	-			-	-

Late positive component (500 – 800 ms): The three-way ANOVA did not reveal a significant LPC main effect of condition, although a significant two-way interaction was observed between SME and laterality (left/center/right), revealing that SNR stimuli elicited more positive amplitudes only at the left-frontopolar electrode (FP1). This effect was confirmed by a paired sample t-test ($t(24) = 2.08$, $p = 0.05$).

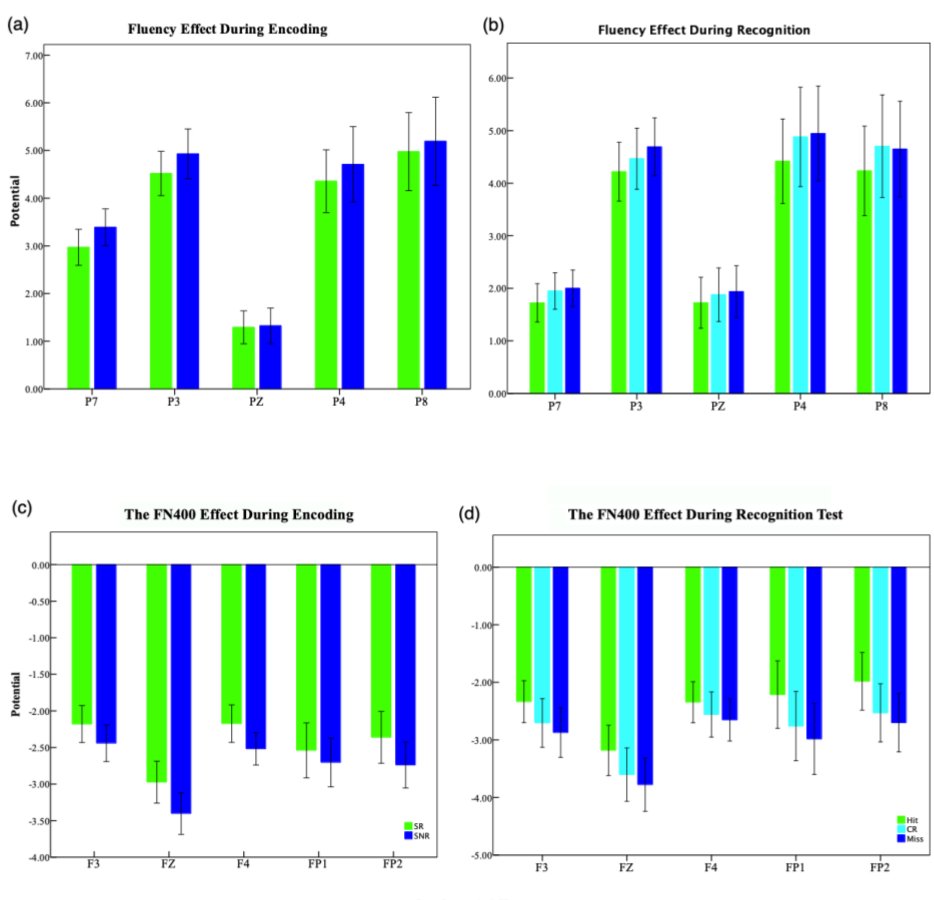
2.4.2.2 Recognition Task

Fluency ERP Effect (200–400 ms): Our three-way repeated-measures ANOVA did not reveal any significant differences in the amplitudes for the fluency ERP, however, an interaction between the fluency SME and Anterior/Posterior location was observed. The topographic map of the fluency ERP was very similar to the pattern observed in the encoding phase as can be seen from Figure 2.4b and 2.5, bottom panels. Paired samples t-tests revealed that correctly identifying new 'CR' stimuli and 'Miss' ERPs were more positive than ‘Hit’ ERPs and that the effect was maximal at right parietal electrodes [P8: $t(24) = 2.99$, $p = 0.008$; P4: $t(24) = 2.57$, $p = 0.02$] (see Table 2.2).

FN400 (300–500 ms): In our 3-way repeated-measures ANOVA we did not observe a significant main effect for the FN400 that could discriminate correctly identified items (old/hit) from correctly identified new (CR) stimuli. However, an omnibus two-way analysis of response-type and fronto-polar/mid-frontal electrodes (FP1, FP2, F3, Fz, F4) sites for the FN400 time interval yielded a significant main effect of response type [$F(2.21, 52.95) = 4.1$, $p = 0.02$, $\eta_2 = 0.15$], reflecting that more positive ERPs were elicited by Hit than Miss and CR stimuli. This effect was confirmed by separate t-tests, which revealed that FN400 amplitudes were more positive for Hits such that Hit > CR > Miss [Fz: $t(24) = 2.63$, $p = 0.006$; F3: $t(24) = 2.43$, $p = 0.03$; FP2: $t(24) = 2.73$, $p = 01$; FP1: $t(24) = 2.43$, $p = 0. 02$] consistent with prior findings (Rugg & Curran., 2007) (see Figure 2.4d). Moreover, the topography of the FN400 effect was very similar to the pattern observed in the encoding phase as can be seen from Figure 2.5, bottom panels.

Late positive component (500–800 ms): Our three-way repeated-measures ANOVA revealed a marginally significant main effect for the three response types during the late positive component interval [$F(1.89, 45.39) = 3.03$, $p = 0.06$, $\eta_2 = 0.11$]. Significant interactions between amplitude differences for LPC amplitudes - laterality and anterior/posterior sites were also observed (See Table 2.2; also Figure 2.5c). A paired t-test comparison between old (Hit) and new (CR) stimuli revealed a significant difference between the amplitudes at left-parietal sites and central sites where Old ERPs elicited more positive amplitudes than new stimuli [P3: $t(24) = 3.46$, $p = 0.002$; Pz: $t(24) = 3.02$, $p = 0.006$; CPz: $t(24) = 3.90$, $p = 0.001$; CP3: $t(24) = 6.64$, $p < 0.001$; Cz: $t(24) = 4.14$, $p <$

0.001] consistent with prior findings (Paller et al., 2007; Rugg & Curran, 2007). There was also a significant decrease at P8 and T8 in the voltage potentials for the old (hit) ERP amplitudes when compared to new (CR) ERPs [P8: $t(24) = -2.63$, $p = 0.02$; T8: $t(24) = -4.86$, $p < 0.001$]. It is important to note that the topographic map of the LPC effect was very different from the pattern observed in the encoding phase (see Figure. 2.3 and 2.5, bottom panels). The LPC topography pattern for SR stimuli observed during the encoding phase was more central and towards right-frontal sites, whereas the same topographic map observed during the recognition phase was mostly centered at the central-parietal and parietal electrodes.



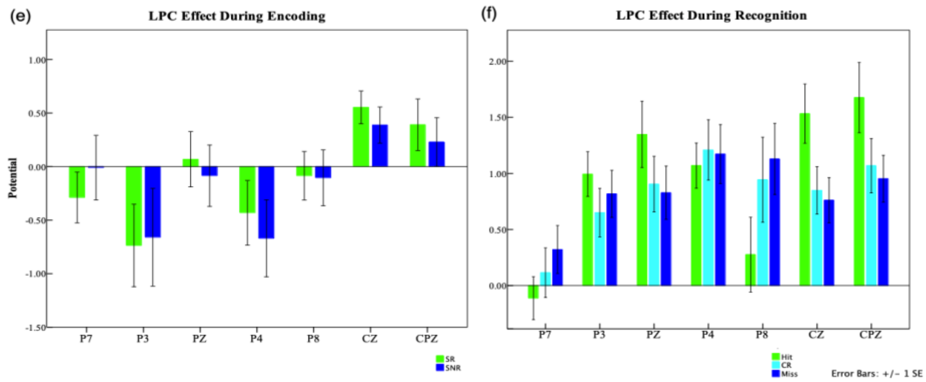


Figure 2.4. Mean ERP amplitudes for subsequent- fluency ERP, FN400, and LPC effects elicited by SNR and SR stimuli (a), (c), and (e) respectively during the encoding study phase. Panels (Nee) (d) and (e) depict the mean ERP amplitudes for fluency ERP, FN400, and LPC effects elicited by Hit, Miss, and CR stimuli during the recognition phase.

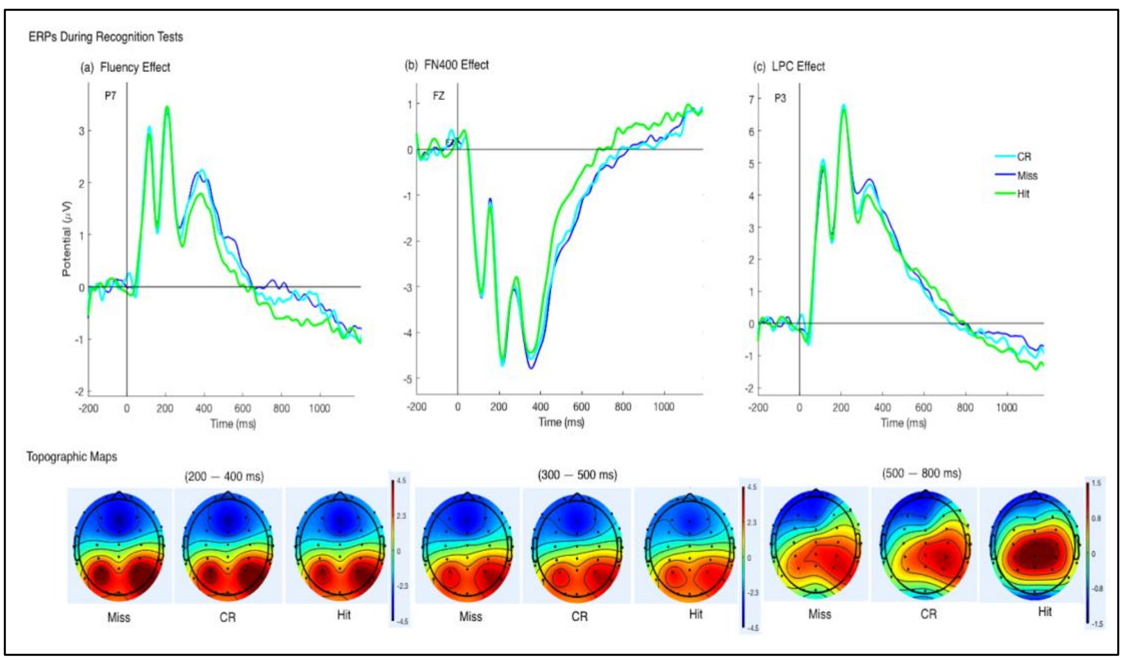


Figure 2.5. Grand-average ERPs at the left-parietal, mid-frontal electrodes (top panel) elicited by Hit, Miss, and CR stimuli, averaged across all participants. Topographic maps (bottom panel)

depict the time course of fluency ERP (200-400 ms), FN400 (300-500 ms), and LPC effects during the recognition test. Small circles represent electrode locations as viewed from above.

2.5 Discussion

The present study investigated the disputed nature of the FN400 component in regards to familiarity (an exhibit of explicit memory) and conceptual fluency (implicit memory). Additionally, we examined the claim of Griffin et al (2013) that FN400 and old/new parietal effects (which are linked to recognition at test) could also be observed during encoding (Griffin et al., 2013). Our results showed that the FN400 component was observed during recognition revealing that Hit items were more positive than Miss and CR (see Table 2.2) and that relative to the FN400 effect observed during encoding, the FN400 during the recognition phase was more positive. Additionally, SR items were more positive than SNR items during encoding.

As mentioned earlier, advocates of the DPSD model assume that familiarity occurs when a prior exposure to a stimulus creates a sense of feeling-familiar during the second exposure and that the participant is aware of the repetition (Rugg & Curran, 2007; Nessler et al., 2005). Our FN400 results from the recognition test indicate that, relative to the FN400 observed during the encoding phase, the FN400 became more positive due to repetition (the second presentation); not only were Hit (old items) more positive than CR (new items) but the difference between Hits and Miss was larger for the second presentation during the recognition phase. We hypothesized that during encoding, since this was the first time participants would see the pictures, the presence of an FN400-like ERP (similar to the one observed during recognition) would suggest that this ERP component is at least in part driven by conceptual fluency. The fact that the FN400 during recognition was more positive than during the encoding phase suggests that the FN400 component reflects both repetition-based familiarity during recognition, as well as conceptual fluency.

As can be seen in Figure 2.5, the FN400 potentials gained from repetition (see Figure 2.5, Table 2.2; Recognition (Hit/Miss)). That is, the FN400 amplitudes in the recognition phase were significantly more positive than the amplitudes in the encoding phase. However, the finding that Hit > CR > Miss is difficult to explain. The FN400 effect at fronto-polar electrodes showed a Hit > CR > Miss pattern, whereas at the mid-frontal electrode (FZ), the effect discriminated old from new stimuli such that Hit > CR, Miss (see Table 2.2, Figure 2.5). If the FN400 component reflected familiarity driven by repetition, then one would expect that Miss (old) items would be more positive than CR (new) items (Rugg et al, 1998), but this was not the case. Also, the FN400 effect produced during recognition was very similar, in terms of ERP latency, time window and scalp location, to the one we observed during the encoding phase. Based on these results, it is plausible that the FN400 component reflected two neural processes. During encoding, the FN400 effect reflected conceptual implicit memory, whereas during the recognition phase it reflected a conceptual fluency effect as well as a repetition effect.

Additionally, a fluency ERP difference was observed both during encoding and recognition, During encoding, SR were less positive than SNR whereas during recognition Hits were the less positive than all the other responses. Fluency, in general, refers to the ease of processing (Jacoby & Dallas, 1989). Those stimuli which are fluently processed use less neuronal sources and therefore elicit less positive ERPs (Whittlesea & Williams, 2001a; Jacoby & Dallas, 1981). Thus, it is plausible to assume that during recognition those stimuli which were conceptually more-fluent + old were less negative than both stimuli that were fluent + new (CR) and less-fluent + old (Miss).

Collectively, in line with UVSD studies, our ERP results suggest that the mechanisms that underlie the FN400 were "multiply determined" during recognition whereas during encoding the FN400 potentials were primarily reflective of conceptual fluency (Paller et al, 2012; Voss et al., 2010a; Voss & Paller, 2007).

Furthermore, findings from other recognition studies have shown that conceptual implicit memory contaminates the neural measures of familiarity when familiarity and conceptual implicit processing co-occur (Voss & Paller, 2017; Voss et al., 2012; Voss & Paller, 2010).

Advocates of the UVSD model have shown evidence that recognition judgments are influenced by perceptual and/or conceptual implicit memory (Bruett & Leynes, 2015; Lucas and Paller, 2013; Oppenheimer, 2008). In contrast, according to the DPSD model, the FN400 component is an "old/new" mid-frontal effect that reflects familiarity based on recent exposure to a stimulus (Rugg & Curran, 2007). However, the presence of the FN400 component during the encoding phase, before any previous exposure to the stimuli, suggests that the FN400 component in our experiment may have indexed conceptual fluency (implicit memory) derived from a participant's semantic memory regarding the stimulus (Voss & Paller, 2010; 2007). There is a possibility that familiarity itself stems from conceptual attributions from previous experiences (Jacoby & Dallas, 1981). According to the level of processing framework, bottom-up processes during encoding influence the next level of processing (Meeuwissen et al., 2011). For instance, a visual analysis of a picture would determine which neural mechanism triggers the concept attached to that visual stimulus (Craik, 2002). Therefore, for a participant who has never heard of Buddha, bottom-up stimulus-driven processes would activate structural processing that would focus on the physical qualities of the Buddha. This structural processing of the physical features is perhaps reflected in the fluency ERP. On the other hand, a participant who was aware of Buddha may have bypassed the middle stage of structural processing by moving up to the processing of the concept/meaning of Buddha. This processing may have activated the neural sources responsible for the implicit memory processing, which would have been eventually reflected in the FN400 amplitudes (Lucas & Paller, 2013; Voss et al., 2012; Paller).

Another interesting finding from this experiment was the fluency ERP effect during encoding. We found that the SNR ERP amplitudes were more positive than SR amplitudes. A similar effect was observed during encoding in other studies (Wang et al., 2015; Bruett & Leynes., 2015; Woollams et al., 2008). Rugg (1998) suggested that the fluency ERP component is the neural correlate of the familiarity with old/new items without recollection (implicit memory) (Rugg et al., 1998). However, in our experiment this effect appeared during the encoding stage as well as during recognition.

It is particularly of interest to note that perceptual fluency has been defined as the ease of perception due to *repetition* (Snodgrass et al, 1996). In other words, perceptual fluency arises from the sensory processing of the physical attributes of a stimulus and refers to the ease of perception of an item because of repeated exposure to those physical attributes (Snodgrass et al., 1996). Given that perceptual fluency uses the sensory match effect to influence recognition memory based on the retrieval of stored information (Nittono et al., 2007; Snodgrass et al., 1996), it is possible that the perceptual fluency effect that we observed during encoding (first exposure) arose from long-term stored information. The sensory match effect refers to the earliest interactions between sensory information and stored memory traces (Waldhauser et al., 2016; Snodgrass et al., 1996; Tulving, 1995). There are studies that support this view as they consider perceptual fluency to be a part of the semantic memory system and suggest that fluency stems from long-term stored information rather than repetition over the short-term (Nessler et al., 2005; Tulving, 1995; Mandler, 1980). This view is based on multiple studies that Nessler and colleagues (2005) conducted to examine the ERP indices of perceptual fluency and familiarity. By using a paradigm where participants recognized famous and non-famous faces, they found that perceptual fluency correlated with an early positive ERP (~300-450 ms) at centro-parietal electrodes, whereas pre-experimental familiarity correlated with the FN400 component (Nessler et al., 2005). Similar results have been observed in other studies (Kurilla & Gonsalves, 2012; Woolman et al., 2008; Rugg et al., 1998). Therefore, our current study is in line with previous work suggesting that different forms of fluency (perceptual or conceptual) may contribute to recognition memory (Lucas & Paller, 2013). These two fluencies are linked to two different ERP components such that perceptual fluency is associated to a positive component peaking around ~300 ms post stimulus at parietal sites (Voss & Paller, 2010; Nessler et al., 2005) whereas conceptual fluency is linked to FN400 (Voss et al., 2012).

It is important to note that the fluency ERP (200-400 ms at parietal electrodes) produced amplitudes that were less negative for Hit trials as compared to the other response types. Voss and Paller (2010) reported similar results and argued that perceptually more fluent stimuli use less cortical resources to process stimuli, hence elicit less positive ERP amplitudes. Others have also suggested that more fluent or easily perceived stimuli use fewer neurocognitive resources for processing as compared to less fluent stimuli which require more resources to process and therefore elicit larger ERP amplitudes (Leynes et al., 2015; 2012). Moreover, studies have shown that processing more fluent or easily perceived stimuli weakens subsequent recognition performance (Guo et al., 2015; Beskin & Mulligan, 2013). Perhaps the reason for this impaired memory performance is that perceptually more fluent stimuli require less neural resources to be active (Guo et al., 2015; Paller & Wagner, 2002). This idea is similar to the *level of processing framework* (Craik et al, 2002; 1972), which suggests that memory traces are the byproduct of the cognitive processes that are carried out during the time of encoding. Thus, shallow encoding would yield relatively low memory performance as compared to a deeper level of processing.

Although we assumed that our stimuli were equally fluent based on Brady et al's study (2008), some pictures may have been more fluent for some participants than others. In support of this post hoc supposition, our behavioural results showed that some of the stimuli were remembered more by the participants than other stimuli. This indicates that some pictures may have carried more conceptual fluency than others. For instance, 25 out of 27 participants remembered the picture of Buddha or a nude female figurine; however, only two were able to remember a yarn of wool or a case of contact lenses (see Figure 2.6b).

Note that the fluency ERP effect at the encoding stage was observed only at left-parietal electrodes (P7, P3) where the SNR ERPs were more positive when compared to SR ERPs. Interestingly, the fluency ERP at the recognition test phase was observed at right-parietal electrodes (P8, P4), where Hits were less positive than the other response types i.e.

correctly identified new stimuli and Miss stimuli, respectively. We are not aware of any reason for this laterality shift; on the contrary, similar results from previous studies indicate that viewing a novel to-be-remembered stimulus produces a visual perceptual learning effect, which is right-lateralized at the parietal cortex (Voss & Paller, 2010; Schott et al., 2006). This perceptual learning effect leaves a memory trace that allows more fluent processing of the same item if encountered again. During a second encounter, a participant may unconsciously be able to discriminate old from new because of the "implicit recognition" effect as described by Voss and Paller (2010). This phenomenon is observed particularly in a two-alternative forced-choice paradigm. Therefore, consistent with previous observations (Leynes et al., 2017; Voss & Paller, 2013; Voss & Paller, 2010; 2007), the fluency ERP effect during recognition seems to reflect implicit memory driven by perceptual fluency. Regardless of the repetition and behavioural indices, old stimuli produced the least negative amplitudes than all others again suggesting that old items used less neuronal resources as a result of their enhanced fluency (Voss & Paller, 2012).

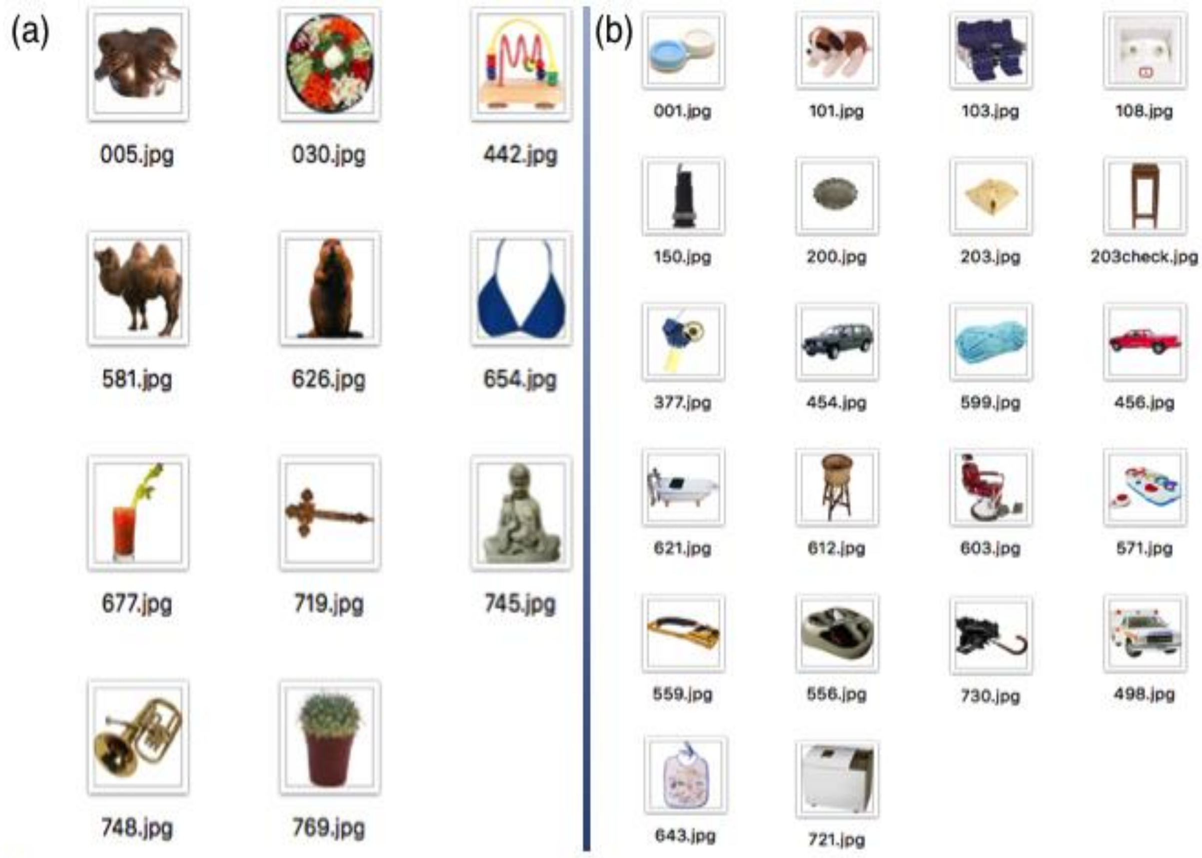


Figure 2.6. A list of the picture used in the study: (a) contains pictures that were remembered more by participants; (b) contains the pictures, which were remembered by less than five participants.

We did not observe an LPC-like effect (i.e., old items are typically observed to be more positive between the time window ~500 - 800 ms post stimulus at parietal sites) during the encoding stage at the parietal electrodes. However, during the 600-1000 ms post-stimulus onset time window, more positive amplitudes were elicited by SNR stimuli when compared to SR stimuli at frontal electrodes, whereas no such effect was observed at parietal or occipital electrodes. During the recognition stage, a significant LPC effect at parietal electrodes was observed. A discrimination effect between Hit and other response types (Miss and CR) at left-parietal electrodes was also observed. However, this effect appeared to be more centralized (see Figure 2.5, Topographic map) as compared to the LPC effect observed in other studies, which was more posterior (Paller and Voss, 2013; Leynes et al., 2017). Furthermore, the LPC discriminated correctly identified old (hit) from all other response types (new and miss) and these differences were observed at almost all parietal electrodes (see Figure 2.5).

2.6 Conclusion

Our results are compatible with the view that the FN400 component does not reflect a process exclusive to the memory process related to familiarity, rather this effect may also reflect conceptual fluency and/or familiarity depending upon the context (Bruett & Leynes, 2015; Lucas & Paller, 2013; Lucas, Voss, & Paller, 2012; Paller et al., 2007). Unfortunately, using the current paradigm we were not able to disentangle these individual processes. However, we have shown that when participants are asked to discriminate old items from new items, the second presentation of a stimulus may initiate several cognitive processes such as perceptual fluency, conceptual fluency, and familiarity because all three of these concepts appear to co-vary with the second presentation (Lucas & Paller, 2013; Lucas, Voss & Paller, 2012; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007). Consistent with previous observations, the present results using pictures of common objects indicate that the FN400 effect may be driven by top-down processing via conceptual implicit memory, and thus contaminate the explicit memory indices during recognition testing (Bruett & Leynes, 2015; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007). Further, we support the view that the phenomenon of familiarity is more complicated than the dual-process theory suggests (Parks and Yonelinas, 2007; Smith & DeCoster, 2000).

3 Chapter: Familiarity and Implicit Memory

3.1 Introduction

There is a growing consensus that recognition memory is supported by familiarity and recollection. Familiarity is the memory retrieval process where one has a feeling of "knowing" about a past event in question, whereas recollection refers to remembering a past event with all contextual details (Friedman & Johnson, 2000; Rugg et al., 1998). At present, there is controversy about whether familiarity is an expression of explicit memory (Rugg et al., 1998) or implicit memory (Paller et al., 2007; Voss et al., 2007). When it comes to memory research, there is a distinction between explicit and other forms of memory in terms of behavioural, neural, cognitive and subjective features (Voss et al., 2008; Paller et al., 2008). Explicit memory refers to an expression of memory where the participant is fully aware of recalling a prior learning event. For instance, if a participant identifies stimuli based on repetition, this would be called an expression of explicit memory. In contrast, implicit memory is a form of memory where a participant might have no conscious awareness that his/her behavior is being guided by previous experience (Schacter, 1987).

A large body of research supports the dual-process signal detection (DPSD) theory, which proposes that recognition memory is based on familiarity and recollection and assumes that these two processes are two distinct expressions of explicit memory (Rugg et al., 2008; Yonelinas et al., 2002; Friedman et al., 2000; Rugg et al., 1998). Findings from ERP studies on recognition memory have revealed that familiarity and recollection are associated with two distinct ERP components. Generally, recollection is attributed to the late positive component or left parietal complex (LPC) that is elicited in the 500-800 ms time range, mostly at parietal sites in the brain, whereas familiarity is associated with the mid-frontal FN400 component elicited in the 300–500 ms time window at mid-frontal sites (Rugg & Curran, 2007; Curran & Cleary, 2003; Curran, 2000). These studies appear to confirm the propositions of the DPSD theory and suggest that the FN400 effect is produced by familiarity-driven recognition and the LPC effect is the reflection of a threshold-based recollection process (Yonelinas et al., 2002).

Although at present researchers appear to agree that the LPC reflects the recollection process, the belief that the FN400 reflects the processes involved in familiarity is disputed. The dispute, in part, arises from the fact that the FN400 resembles the well-known N400 component, which reflects semantic or conceptual priming (i.e. a form of implicit memory) and occurs in the same time window as the FN400 (e.g.300-500 ms) (Packard et al; 2017; Kutas & Federmeier, 2010; 2000; Voss et al., 2010). Findings from previous studies have shown that conceptual semantic processing of meaningful stimuli is indexed by the standard N400 potential (Kutas & Hillyard, 1980). Paller and colleagues showed that the FN400 effect is functionally identical to the centro-parietal N400 effect (Voss & Paller, 2012; Paller et al., 2007). Therefore, in contrast to the FN400-reflects-familiarity theory, there is another view that conceptual fluency, guided by implicit memory, provides the basis for familiarity judgments and not explicit memory. In a series of studies, Paller and colleagues showed that familiarity and conceptual priming are correlated and that their respective neural signatures are difficult to disentangle (Voss et al., 2010; Paller et al., 2007; Voss et al., 2007). More support for this idea comes from the findings that cortical mechanisms underlying familiarity and conceptual priming processing highly overlap and rely on the same neural system (Manns et al., 2003). In our previous study, we observed that the second presentation of a stimulus during the recognition test phase may have initiated several cognitive processes such as perceptual fluency, conceptual fluency, and familiarity, because all three of these processes appeared to co-vary with the second presentation of a stimulus. Hence, there is the possibility that during recognition testing, the FN400 component reflects some of the same cognitive processes that influence implicit memory as well as familiarity (Wilding & Ranganath,, 2011). It is plausible that the FN400 effect may be driven by top-down processing via conceptual implicit memory, and thus contaminates the explicit memory indices during recognition testing (Bruett & Leynes, 2015; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007).

Findings from numerous studies have suggested that under restricted circumstances, the FN400 signals reflect conceptual implicit memory rather than familiarity (Paller et al., 2012; Voss et al., 2010a). Paller and colleagues showed that the FN400 potentials correlate with familiarity judgments only when stimuli have meanings associated with them (e.g. words, pictures with names). Thus, viewing a stimulus rich in meanings may initiate the activation of neural processes that lead to conceptual implicit memory (Wilding & Ranganath, 2011; Yovel & Paller, 2004; Olichney et al., 2000). The FN400 effect was absent when stimuli with no meaning were presented (complex geometrical patterns). Instead, they observed another ERP (280-400 ms) that was different in polarity and scalp location from the FN400 effect. This ERP, which could be called the fluency ERP was observed at parietal sites and has been reported to be associated with perceptual fluency (Paller et al., 2012; Rugg et al., 2007; Rugg et al., 1998). Interestingly, perceptual fluency is also found to modulate recognition performance under various conditions (Schott et al. 2005; 2002; Whittlesea & Williams, 2001a, 2001b; Paller et al. 2003; Rugg et al. 1998; Jacoby & Dallas, 1981). For instance, fluency can affect our subjective experience of familiarity because our sense of familiarity is sensitive to the facilitation of sensory processing (Jacoby & Dallas, 1981). If one experiences a stimulus to be more fluent than expected, the stimulus might feel familiar. Whittlesea and Williams (1998) asked participants to read words from a pool of real words (e.g., frog, cancer) and nonwords that included some pseudohomophones (e.g., phrawg, kanser) and decide if they had seen the words earlier. Although, real words were more fluent than nonwords, some new pseudohomophones were erroneously "recognized" as items previously presented. Therefore, they concluded that, fluency can generate an illusion of familiarity when a stimulus is processed more fluently than expected in a given situation (Whittlesea & Williams, 1998). These results also indicate that multiple forms of fluency contribute to shape recognition judgment and they are linked to different neural indices (Lucas & Paller, 2013).

While perceptual and conceptual fluencies are distinguishable from each other on the bases of polarity and scalp locations, it is hard to disentangle the neural correlates of conceptual implicit memory from familiarity processes as these processes tend to occur simultaneously and apparently share the underlying mechanism (Boehm et al., 2005; Paller et al., 2003). One of the main reasons is that the cortical mechanisms underlying familiarity and conceptual priming processing appear to overlap and may rely on the same neural system (Manns et al., 2003). Hence, there is the possibility that during recognition testing the FN400 component reflects some of the same cognitive processes that influence implicit memory as well as familiarity (Wilding & Ranganath,, 2011). Therefore, in order to ensure that the FN400 or any other neural signature exclusively reflects the processes involved in the expression of familiarity, it is important to discriminate between the neural signals of familiarity and the neural signals of implicit memory driven by priming effects.

If the FN400 effect reflects conceptual priming, then in principle, during recognition there should be no FN400 effect for meaningless stimuli or a stimulus with little meaning. In line with this assumption, some studies have shown that no FN400 was obtained when meaningless stimuli were used (Mackenzie & Donaldson, 2007; Yovel & Paller, 2004); however, other studies have observed FN400 effects for meaningless stimuli (Curran & Hancock, 2007). Paller and colleagues argued that FN400 effects are possible when participants see meaningless stimuli because participants can find meaning even in the most abstract stimuli (Paller et al., 2007). Moreover, they showed in multiple studies that in the absence of familiarity, the FN400 component reflected conceptual implicit memory during recognition tests (Paller et al., 2012; Voss et al., 2012). In defence of the FN400-reflects-familiarity effect account, it was argued that the FN400 is sensitive to the perceptual features of the stimuli and the magnitude of the FN400 effect changes according to manipulations of perceptual features of the stimuli (Wilding & Ranganath,, 2011; Stenberg at al., 2009). Hence, it remains unclear why the FN400 potentials were observed in some studies (Curran & Hancock, 2007) and not in others (Mackenzie & Donaldson, 2007; Yovel & Paller, 2004).

Some studies have shown that participants often attribute familiarity to "perceptual fluent" stimuli when being tested for recognition (Olds & Westerman, 2012; Kurilla & Westerman, 2008; Nessler et al., 2005; Westerman et al., 2002; Whittlesea, 2002; Westerman, 2001; Whittlesea et al., 1990; Jacoby & Whitehouse, 1989). Nessler and colleagues conducted a series of experiments to examine the ERP indices of perceptual fluency, semantic memory (which they refer to as semantic familiarity) and repetition using famous and non-famous faces. They found that repetition and perceptual fluency influenced the fluency ERP (~300 -450 ms) at parietal electrodes, whereas semantic familiarity influenced the FN400 effect. Similar findings from other studies suggested that repetition enhances perceptual fluency during recognition and that fluency ERPs are more positive for repeated stimuli as compared to stimuli that were presented only once (Henson et al., 2008; Kurilla & Westerman, 2008; Nessler et al., 2005). In other words, participants are more likely to associate perceptual fluency of a stimulus with a prior encounter if they are unaware of the source of the fluency of that stimulus. Therefore, in the absence of FN400 effects (familiarity or conceptual priming), it is likely that recognition responses are influenced by perceptual fluency, which is reflected in the early parietal fluency effect component (~200- 400 ms) (Bruett & Leynes, 2015; Leynes & Zish, 2012).

Similar effects of perceptual fluency were observed in an implicit memory task that involved primed and unprimed complex geometric figures (Wang et al., 2015; Voss et al., 2010a), suggesting that in the absence of conceptual implicit memory, recognition judgments were influenced by perceptual fluency. Also, these studies provide an explanation for the case when stimuli are considered familiar and there is no presence of FN400 effect. However, in these studies the polarity of the perceptual fluency ERP was reversed. Repetition of primed stimuli apparently enhanced perceptual fluency resulting in decreased amplitudes for the fluency ERP effect, which suggested that less cortical resources were required to process the more fluent stimuli.

Based on the controversy associated with the FN400, we chose an experimental design that would elicit shallow encoding to replicate and extend our previous results (Chapter 2) with an important new design modification – the presentation of meaningless and nameless stimuli as opposed to the meaningful stimuli presented in the previous experiment. A "shallow encoding" of the stimulus entails only a quantitative basis for judgment (i.e. familiarity) whereas "deep encoding" provides a qualitative account of the judgment (i.e. recollection; Baucher et al., 2016; Wilding & Ranganath,, 2011; Marzi et al., 2010).

Participants viewed fractals during the encoding phase and then had to provide recognition judgments about some of the old fractals along with some new fractals. Thus, in the recognition phase, we had two sets of stimuli (old and new) and could therefore control for perceptual fluency (due to repetition). To improve our understanding of familiarity and recognition memory, this study examined the effects of stimuli with little or no meaning (fractals) on visual memory using ERPs recorded during the encoding task and a recognition test. Voss and Paller (2012) reported that the FN400 component correlated with familiarity when familiarity co-varied with conceptual implicit memory. No FN400 was observed when conceptual fluency was reduced or eliminated in the stimuli (Voss & Paller, 2012; 2007). Voss and Paller (2007) used squiggles with variable conceptual associations such that some squiggles were capable of evoking conceptual associations in semantic memory while others were not. During recognition test, only meaningful squiggles correlated with FN400 (Voss, et al., 2011; Voss & Paller, 2007). Those squiggles, which were semantically empty, could not evoke an FN400 effect (Voss & Paller, 2007). Thus, the FN400 does not reflect a process exclusive to the memory process related to familiarity; rather this effect reflects conceptual fluency (Bruett & Leynes, 2015; Lucas & Paller, 2013; Paller et al., 2007).

Hence, to control for conceptual fluency, we created geometrical abstract shapes called fractals using mathematical functions and MATLAB scripts. These fractals are hard to associate with any known objects. It is important to note that our design enabled a unique test of the hypothesis concerning the conceptual and perceptual fluency captured by the FN400. This design allows us to avoid conflating neural correlates of conceptual fluency. Given that, repetition triggers fluency, familiarity or conceptual priming, one would expect that during the first exposure (i.e. encoding) of a stimulus there should be no FN400 or fluency ERP effect for meaningless stimuli. If the FN400 reflects familiarity (due to previous experience with a stimulus), then during the encoding phase, our fractals should not elicit an FN400 because the stimuli were novel and unfamiliar to the participants. If the FN400 reflects conceptual fluency, then during the encoding phase, the fractals would still not elicit an FN400 because these stimuli have no meanings associated with them. On the other hand, if the FN400 does indeed reflect familiarity, then during the recognition test, our fractals should elicit an old/new effect (explicit memory effect).

3.2 Method

3.2.1 Participants

After consenting to procedures approved by the Wilfrid Laurier University Research Ethics Board, 18 healthy individuals (n=18, nine females, ages 18-28 years) participated. All participants were right-handed and had normal or corrected to normal vision. No participant reported ever experiencing a psychiatric illness. Participants signed informed consent forms before the study and were granted course credit for their participation.

3.2.2 Stimuli and Procedures

During the encoding task, participants were sequentially presented with 800 fractals that were created by using custom Matlab scripts. To ensure that no semantic concepts or meanings were associated with these stimuli, we used the escape-time technique to generate these fractals. By using a recurrence relation at each point in the complex plane, we generated a series of Mandelbrot, Julia set, and Lyapunov fractals. Participants were told in advance that they would be tested for their memory of the photographs and to watch each item carefully. Encoding session was divided into 8 blocks of 100 fractals each. There were short breaks after each block (approximately 8 minutes). Participants initiated each block by pressing a button on a response pad, however, they were not in control of the rest of the trials of the block. Each trial started with a 1,000 ms pre-encoding period, where participants had to focus on a blank screen with a central fixation dot. Each picture was presented for 250 ms, followed by a 1,000-ms encoding period, during which the computer screen remained blank. After a short break, participants performed the recognition session during which 500 fractals (300 old, 200 new) were randomly presented. During the recognition test, fractals were presented on the screen until a response was recorded. Participants were instructed to press ‘1’ on the response pad if they remembered seeing the picture or press ‘2’ if they did not previously see the picture.

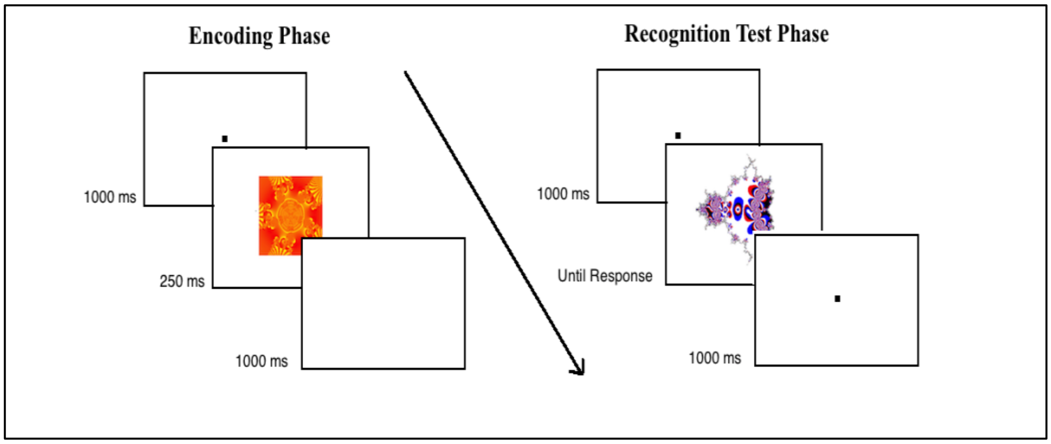


***Figure 3.1**:* Schematic diagram of the experimental trials during the encoding and recognition test phases.

3.2.3 EEG data and Acquisition

EEG data were recorded using a NeuroScan GSN 64 1.0 Ag/AgCl electrode Quik-cap (Compumedics, Charlotte, NC, USA) in a sound-attenuated, electrically shielded booth (Raymond EMC, Ottawa, ON, Canada) while participants performed the encoding and recognition tasks. Electrodes were positioned according to the International 10-20 EEG System with one ground electrode such that electrodes were fixed over the frontal lobes (FP1, FP2, F7, F3, FZ, F4, F8, FC3, FCZ, FC4), temporal lobes (FT7, FT8, T7, T8, TP7, Tp8), parietal lobes (CP3, CPZ, CP4, P7, PZ, P4, P8), occipital lobes (O1, O2), and at the central position of the scalp (C3, CZ, C4). Electrode CZ was visually centered above the central vertex found halfway between the glabella and the external occipital protuberance medially and the preauricular points laterally. Electro-gel was used to improve conduction between the skin and the electrode surface. Surface electromyographic electrodes were positioned at the outer canthi of both eyes and above and below the left eye. EEG signals were initially referenced to mastoid electrodes (M1, M2), which were placed on the mastoid process behind each ear. Impedances were kept below 5kΩ. The presentation of stimuli was controlled by programmable experiment generation software Stim2 (Compumedics, Charlotte, NC, USA) and signals were acquired across all 64 electrodes.

3.2.4 ERP preprocessing and analyses

Custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme and Makeig 2004, http://sccn.ucsd.edu/eeglab) were used to analyze the data. We inspected and corrected the continuous data for outliers, body movements, and muscle and cardiac artifacts by using Artifact Subspace Reconstruction (ASR) (Bigdely-Shamlo et al., 2015). For further artifact correction, independent component analysis (ICA) (Delorme &Makeig 2004) was applied separately to single subject datasets (Palmer et al., 2008). The ICA decomposition method has the ability to linearly un-mix EEG channel data into temporally independent component activities with a fixed spatial projection pattern (Onton & Makeig, 2011; Onton et al., 2006; Makeig et al., 2004a). Thus, ICA is capable of isolating cortical signals from the noisy non-brain source activities (Onton & Makeig, 2011) (see Chapter 2 for details). Statistical analyses were carried out using SPSS Statistics (SPSS, Inc., 2009, Chicago, IL, www.spss.com) on the mean voltage differences at the corresponding electrodes and time windows.

Signals were averaged, re-referenced and initially high-pass filtered (1 Hz) (Winkler et al., 2015). For ERP analysis, signals were passband filtered between 1 and 30 Hz. Trials above 5 μV voltage potential from baseline were rejected. On average, 15% of the trials per participant were rejected. For encoding ERPs, trials were grouped into subsequently remembered items (SR) and subsequently not remembered items (SNR), based on the participants' responses during the recognition task. After a short delay, participants were tested with these "old" fractals randomly intermixed with "new" fractals during the recognition test. Participants had to discriminate whether each fractal was old or new.

3.2.5 ERP data and analysis procedures:

ERP components were computed as the average voltage relative to a -200 to 0 ms pre-stimulus baseline voltage (Luck, 2014). Based on the performance of participants during the recognition test, studied fractals in the encoding task were categorized as subsequently-remembered (SR) and subsequently-not-remembered (SNR) items and the difference between the neural activities of the SR and SNR was called the subsequent memory effect (SME) (Voss et al., 2010; Paller & Wagner, 2002; Rugg & Allan, 2000). ERPs at the recognition test were averaged separately for recognized/remember old items (Hit), new items that were correctly identified as new items (correct rejection; CR), old items that participants failed to remember as old items (Miss), and new items that participants reported to be old items (False Alarm; FA). Findings from previous studies have linked perceptual fluency with an ERP in an early time window (~200–400 ms), where new items elicit more positive ERPs than old items revealing that old items use fewer neural resources as being fluent (e.g., Wang et al., 2015; Bruett & Leynes, 2015; Leynes & Zish, 2012).

To investigate the hypotheses, we used several levels of analysis. First we analyzed our ERP with a repeated-measures ANOVA with the factors of SME (Subsequently-Remembered/SR, Subsequently-not-remembered/SNR) X Electrode location (5 levels from anterior to posterior; frontal, fronto-central, central, centro-parietal, and parietal) X Laterality (3 levels, left, center, right) for the encoding phase and response types (Hit, Miss, CR, FA) X Electrode location (5 levels) X Laterality (3 levels) for the recognition task. In our second analysis, in order to analyze the effect of laterality and topography, an ANOVA model that contained a within-subjects factor of Condition (SR, SNR), electrode site as anterior to posterior (3 levels, frontal, central, and parietal), and left/center/right (LCR) electrode site (3 levels, left, center, and right) was conducted (Leynes et al., 2017). Next, a series of pair-wise, post hoc t-tests further examined ERP differences across response types. Fluency ERPs were quantified by computing the average activity at the central (C3, C1, CZ, C2, and C4) and parietal electrodes (P7, P3, PZ, P4, and P8; Bruett & Leynes, 2015). The FN400 analyses examined ERP measures during the 300–500 ms time interval at mid-frontal electrode sites (i.e., F3, F1, Fz, F2, F4, and FC3, FCz, FC4). The LPC analyses evaluated ERPs during the 500–700 ms time interval at central (C3, C1, CZ, C2, and C4) and parietal electrode sites (P7, P3, Pz, P4, P8; Curran, 2000; Curran & Hancock, 2007; Leynes & Zish, 2012; Paller et al., 2007; Rugg & Curran, 2007).

Group Comparison between Experiment 1 and Experiment 2: Finally, a comparison analysis of the group effect between the two experiments (Chapter 2: Pictures and Chapter 3: Fractals) was conducted. For comparison, amplitude measures were computed as the average activity during our intervals of interest i.e. Fluency (200-400 ms), FN400 (300-500 MS), and LPC (500-800 ms) intervals. Note that in Experiment 1, a 32-channel EEG cap and in Experiment 2 a 64-channel cap were used. Therefore, the ERP measures were averaged at electrodes that were common in both caps. Such that, ERP potentials were analyzed and averaged at frontal (F3, Fz, F4), frontal-central (FC3, FCz, FC4), central (C3, Cz, C4), central-parietal (CP3, CPz, CP4), and parietal clusters (P3, Pz, P4) as well as left-parietal (P7, P3) and right-parietal (P4, P8) for all intervals. An analysis of variance model that contained a between-subjects factor of Group (pictures, fractals) and within-subject factor memory (SR/SNR for encoding and Hit/Miss/CR for recognition) and electrode-sites was conducted.

Significant effects were corrected for non-sphericity using Greenhouse–Geisser corrections, and significant effects are reported with the corrected degrees of freedom when appropriate.

3.3 Results

3.3.1 Behavioural Results

The performance in the recognition task was analyzed. We investigated participant task accuracy and reaction time. Each participant's Hit, Miss, Correct-Rejection (CR) and False Alarm rates (FA) were extracted. Performance during the encoding phase was compared between the SR and SNR trials based on the performance in the recognition task that was extracted for each participant. Reaction times during the recognition task were analyzed using a one-way ANOVA with the within-subject factor Condition (Hit, Miss, CR, and FA). The perceptual sensitivity of the recognition task was estimated using signal detection theory (SDT) by computing A′ for each participant. A′ was used as our main index of performance (Stanislaw & Todorov, 1999) because A′ is capable of distinguishing response bias from sensitivity. A′ can take any values between 0.5 and 1, with 1 denoting perfect performance and 0.5 denoting failure to distinguish the old from the new stimuli.

Our results for memory performance showed that participants, in general, were capable of discriminating old from new pictures above chance, as indicated by an average A′ of 0.54 (SD: +/− .07; range 0.47 to 0.61). Reaction times differed among the four primary responses used for ERP analyses i.e., $F(3, 9290) = 3.34$, $p = .02$. Pairwise comparisons revealed that Hit responses were faster than Miss (all $p < 0.01$). However, the differences between Hit and other responses were not significant ($p > .05$). On average, participants performed the recognition task successfully. They successfully rejected 64.87% of the new objects and were able to identify 36.99% of the old stimuli objects. It is clear from Table 3.1 that there were large standard deviations for both accuracy and RTs, demonstrating the variability across participants and the type of stimuli.

Additionally, we compared the hit, FA rates and A’ means from Experiment 1 (pictures) and 2 (fractals) and found that all measures except FA rates were higher for fractals as compared to pictures (see Figure 3.2).

Table 3.1

Accuracy (percentage) and response time (ms) values, reported along with their standard deviations across participants in parentheses.

	Accuracy (%)	**Response Time (ms)**
Hits (old)	36.99 (58.79)	1320.95 (1344.12)
Misses (old)	63.01 (63.40)	1440.12 (1641.26)
Correct Rejection (new)	64.87 (21.66)	1370.19 (1665.26)
False alarms (new)	35.13 (21.66)	1390.54 (1309.05)

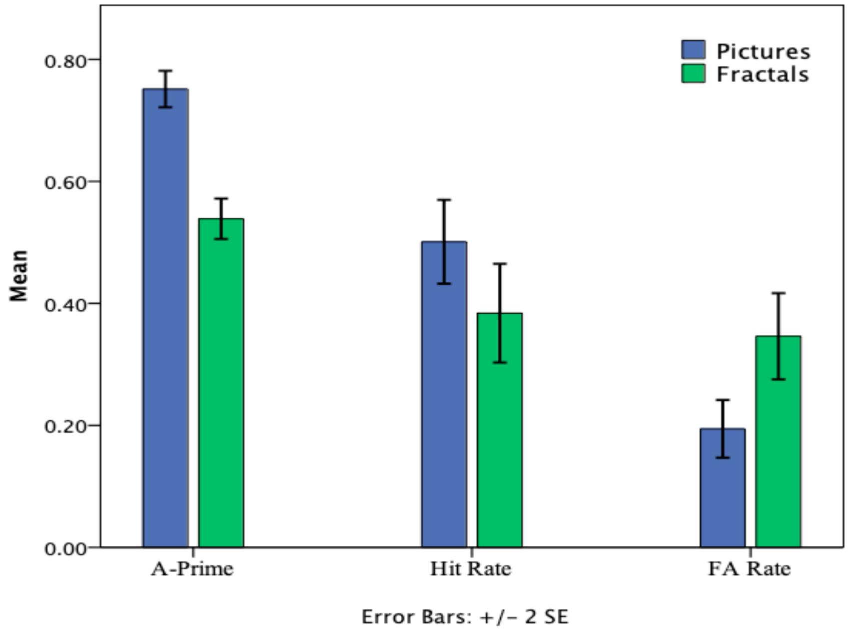


Figure 3.2. Mean A', Hit and False Alarm rates from Experiment 1 (pictures) and Experiment 2 (fractals).

3.2 ERP Results

3.3.2.1 Encoding Task

At the encoding phase, for the three time windows reflecting the fluency ERP (200 – 400 ms), FN400 (300 – 500 ms) and the LPC effect (500 – 800 ms), a three-way repeated-measures ANOVA with SME (Subsequently-Remembered/SR, Subsequently not remembered/SNR) X Electrode locations (from anterior to posterior) X Laterality was computed to quantify these effects. In agreement with previous studies (Fellner et al., 2013; Schnieder et al., 2016), our results revealed a significant SME (e.g., Fluency ERP (200 – 400 ms: $F(1, 17) = 5.753$, $p = 0.028$, $\eta 2 = 0.253$; FN400 effect (300-500 ms): $F(1, 17) = 16.88$, $p = 0.001$, $\eta 2$=0.0.498; LPC effect (500-800 ms): $F(1, 17) = 4.52$, $p = 0.048$, $\eta 2 = 0.21$) as shown in Table 3.2

In a separate analysis of group comparisons between pictures and factors revealed significant differences for the following intervals, which are listed as follows:

Fluency ERP (200–400 ms): A three-way repeated-measure ANOVA revealed a main effect of subsequent fluency ERP effect as well as a significant interaction of SME X electrode location, and condition X laterality (see Table 3.2; Encoding). Further analysis revealed that this effect was maximal at left-parietal sites where subsequently-not-remembered ERPs were significantly more positive than subsequently- remembered ERPs (P7: $t(17) = -3.03$, $p=0.008$), which is in accordance with previous studies (Yonelinas et al, 2014; Lucas & Paller, 2013; Voss et al., 2010; Rugg et al., 2008; Voss & Paller, 2006; Yonelinas et al., 2002; Friedman et al., 2000; Rugg et al., 1998).

FN400 (300 – 500 MS): We were able to replicate classic mid-frontal ERP components at the encoding stage for subsequently remembered items at frontal and mid-frontal sites. Details are given in Table 3.2. Our three-way ANOVA revealed a significant main effect and interactions of the subsequent memory effect for the FN400 latency (see Table 3.2, Encoding). There was a significant three-way interaction of SME (SR/SNR) X anterior/posterior location of electrodes X Laterality. Thus, we conducted further analyses. A paired-sample, two-tailed t-test for the subsequent hits and subsequent misses further revealed significantly higher negative amplitudes for SNR items than for SR items at frontal and mid-frontal regions of the brain, whereas the effect was maximal at FC4 [FC4: $t(17) = 5.25$, $p < 0.001$; F4: $t(17) = 4.01$, $p = 0.001$; Fz: $t(17) = 2.94$, $p = 0.008$; FCz: $t(17) = 3.16$, $p = 0.006$; CZ: $t(17) = 3.66$, $p = 0.002$]. These results show that this effect was slightly more robust at the right hemisphere of the brain (see Figure 3.3d(ii)).

Late positive component (500 – 800 ms): Our repeated-measures three-way ANOVA conducted for the 500-800 ms time window revealed a three-way interaction between Condition (SR/ SNR), laterality and electrode location [$F(8, 136) = 3.07$, $p = 0.003$, $\eta 2 = 0.21$] (see Table 3.2, Encoding, LPC). Paired samples t-tests indicated that the two SR ERPs were more positive at central [Right-central: C4: $t(17) = 2.64$, $p = 0.02$; Mid-central: CZ: $t(17) = 2.61$, $p = 0.02$] and negative at parietal sites [Right-parietal: P8: $t(17) = -2.11$, $p = 0.05$; P4: $t(17) = -2.28$, $p = 0.04$; Left-parietal] when compared to SNR ERPs. It is interesting to note that the polarity of the effect is altogether different at parietal electrodes as compared to central electrodes; subsequently remembered items stimuli were more positive at central electrodes than subsequently not remembered items, whereas the polarity of amplitudes for subsequently remembered stimuli at parietal electrodes was the opposite.

Group Effect: An ANOVA model that contained a between-subjects factor of group (pictures, fractals) and within-subject repeated–measure factors memory (SR/SNR) and clusters (central (C3, Cz, C4), central-parietal (CP3, CPz, CP4), and parietal (P3, Pz, P4) revealed that there was no effect of group for fluency ERP interval. Likewise, no significant effect of group was observed for the FN400 and LPC intervals (see Table 3.3).

Table 3.2

Significant fluency ERP, FN400, and LPC effects from the encoding and recognition phase.

		Encoding	Recognition
Fluency	**Memory**	F(1, 17) = 5.753, p = 0.028, η2=0.253	F(2.25,38.26) = 3.32, p = 0.04, η2=0.16
	LCR * Memory	F(1.764, 29.99) = 4.12, p=0.031, η2=0.20	-
	AP * Memory	F(1.33, 22.68) = 3.31, p=0.0371, η2=0.16	F(3.23, 54.97) = 3.15, p=0.03, η2=0.16
	LCR * AP * Memory	-	-
FN400	**Memory**	F(1, 17) = 16.88, p = 0.001, η2=0.0.498	F(3, 51) = 3.29, p = 0.03, η2=0.0.16
	LCR * Memory	F(2, 34) = 3.79, p=0.033, η2=0.18	-
	AP * Memory	F(1.43, 24.28) = 4.93, p=0.025, η2=0.23	F(3.48, 59.21) = 4.50, p=0.004, η2=0.21
	LCR * AP * Memory	F(3.81, 64.82) = 2.57, p=0.05, η2=0.13	-
LPC	**Memory**	F(1, 17) = 4.52, p = 0.048, η2=0.21	F(3, 51) = 6.73, p = 0.001, η2=0.0.28
	LCR * Memory	-	-
	AP * Memory	F(1.72, 29.20) = 3.62, p=0.045, η2=0.18	-
	LCR * AP * Memory	F(8, 136) = 3.07, p=0.003, η2=0.15	-

Note. Memory = SME for Encoding, Memory for Recognition ; AP = Anterior/posterior electrode position;
LCR = Left/Center/Right electrode site position

3.3.2.2 Recognition Task

Fluency ERP (200–400 ms): A repeated-measure ANOVA for response-types revealed a main effect of the latency of fluency ERP and an interaction between electrode location and response type (see Table 3.2, Recognition, Fluency). However, further analysis revealed that the difference between amplitudes were mainly between Hit and Miss ERPs. ERP amplitudes for correct rejection 'CR' (for identifying stimuli as new) was observed only at left-parietal electrode P8 (P8: $t(17) = -2.32$, $p = 0.04$) (see Figure 3.4a).

FN400 Effect (300–500 ms): Our three-way repeated-measures ANOVA revealed a significant difference between the amplitudes for all four response-types during the 300-500 ms interval. However, further analysis revealed that the difference of amplitudes was mainly between Hit and Miss ERP amplitudes. A marginal difference between the amplitudes for correctly remembered old items (Hits) and correctly identifying new items (CRs) was observed (see Figure 3.4b) at mid-frontal electrodes [Fz: $t(17) = 2.13$, $p = 0.05$; FCz: $t(17) = 2.04$, $p = 0.06$].

Late positive component (500–800 ms): During the recognition test, a main effect of response-type emerged [$F(3, 51) = 6.73$, $p = .001$, $\eta 2 = 0.28$], indicating more positive ERPs for Hits when compared to CRs. No significant interaction was observed (see Table 3.2, Recognition, LPC). However, a more pronounced difference between ‘Hit’ and all other response types was observed at central and central-parietal electrodes [CPz: $t(17) = 4.33$, $p < 0.001$; Cz: $t(17) = 3.66$, $p = 0.002$; Pz: $t(17) = 2.93$, $p = 0.009$; C2: $t(17) = 3.56$, $p = 0.002$; C1: $t(17) = 3.4$, $p = 0.003$] (see Figure 3.4c).

Table 3.3

Significant effects in Experiment 1 (Pictures) and Experiment 2 (Fractals).

		Encoding	Recognition (Hit/Miss/CR)
Fluency	**Memory**	F(1,41) = 7.10, p=0.01, η2=0.15	F(1.72, 70.64) = 2.61, p = 0.089, η2=0.06
	Memory * Groups	-	-
	Memory * Clusters	F(1.72, 70.39) = 6.72, p=0.002, η2=0.14	F(2.01, 82.58) = 4.71, p=0.011, η2=0.10
	Memory * Clusters *Groups	-	-
FN400	**Memory**	F(1,41) = 20.70, p < 0.001, η2=0.34	-
	Memory * Groups	-	F(1.77, 72.71) = 10.33, p < 0.001, η2=0.20
	Memory * Clusters	-	F(1.47, 60.39) = 8.74, p=0.001, η2=0.18
	Memory * Clusters *Groups	-	F(1.47, 60.39) = 11.38, p<0.001, η2=0.22
LPC	**Memory**	-	F(1.68, 68.72) = 6.17, p = 0.005, η2=0.13
	Memory * Groups	-	-
	Memory * Clusters	F(1.63, 66.96) = 3.87, p=0.03, η2=0.09	F(4.04, 165.64) =2.37, p = 0.05, η2=0.06
	Memory * Clusters *Groups	-	-

Note. Memory = SME for Encoding, Memory for Recognition ;Groups = Pictures and Fractals; Clusters = Groups of electrode

Group Effect During Recognition: A mixed 3x3x2 ANOVA analysis with one between-subjects factor group (pictures/ fractals) and two within-subject repeated–measure factors memory (Hit/ Miss/ CR) and clusters frontal (F3, Fz, F4), fronto-central (FC3, FCz, FC4), and central (C3, Cz, C4) was conducted to examine the group effects of the two different kinds of stimuli (pictures with meanings and fractals with no meanings). Our analysis revealed that there is no significant between-group difference between the FN400 potentials for picture and fractal groups [$F(1, 41) = 1.55$, $p = 0.22$]. However, we observed that despite there being no main effect of groups, the picture-group elicited higher amplitudes than the fractal-group. Interestingly, no significant group effects were observed for the fluency ERP and LPC intervals (see Table 3.3). Further analysis revealed that the main difference in the potentials was at a fronto-central cluster (FC3, FCz, FC4).

Topographical Differences During the Encoding and Recognition Phases: In order to investigate the effect of condition on hemisphere and region during the encoding phase, an exploratory 3x5x3 ANOVA model that included laterality (left, mid, right), region (frontal, front-central, center, centro-parietal, parietal), and response-type (SR/ SNR for the encoding phase and Hit/Miss/CR for the recognition test) as factors was conducted for our three time windows of interest; i.e. Fluency ERP (200-400 ms), FN400 (300-500 ms), and LPC (500-800 ms). Topographic visualization was performed with the EEGLAB Matlab toolbox (Delorme & Makeig, 2004). A careful observation of topographic maps regarding fluency ERP, FN400, and LPC effects revealed that fluency ERPand FN400 effects were not only similar to each other, but also similar across the studies i.e. these effects had similar patterns during the encoding as well as the recognition phase as can be seen in Figures 3.2d and 3.3d.

The exploratory analysis revealed significant interactions for all durations during the encoding and test phases (see Table 3.2, for details). Overall, laterality was significantly influential in this analysis. The topographic patterns of the FN400 effects between SR and SNR were not different from those of Hit and Miss.

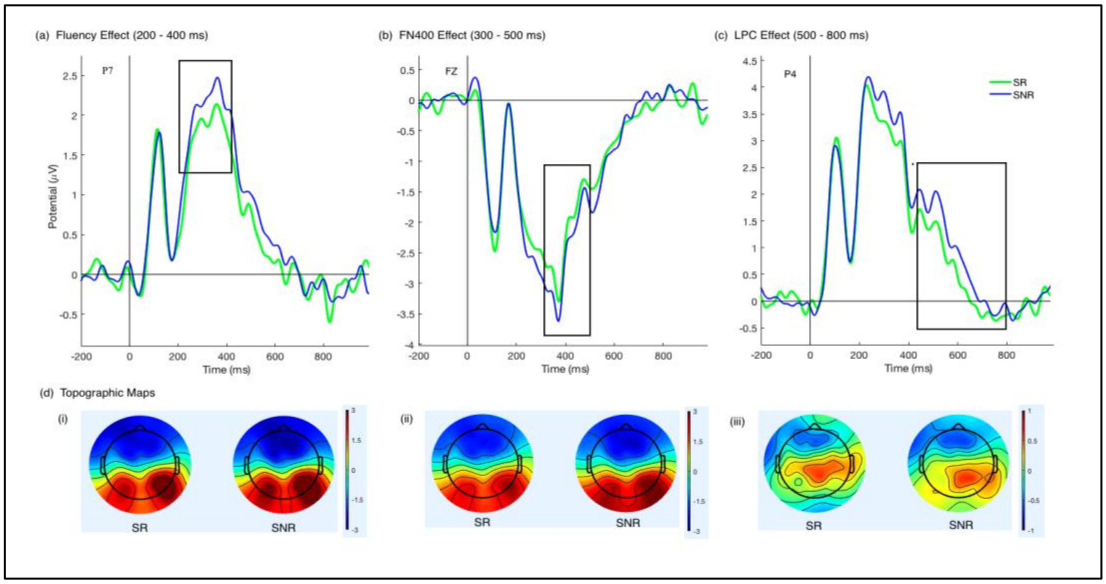


Figure 3.3. Grand-average ERPs at selected electrode sites elicited by novel fractals during the encoding phase. Topographic maps show the activity elicited by subsequent remembered (SR) and subsequently not remembered (SNR) stimuli during fluency, FN400, and LPC time intervals.

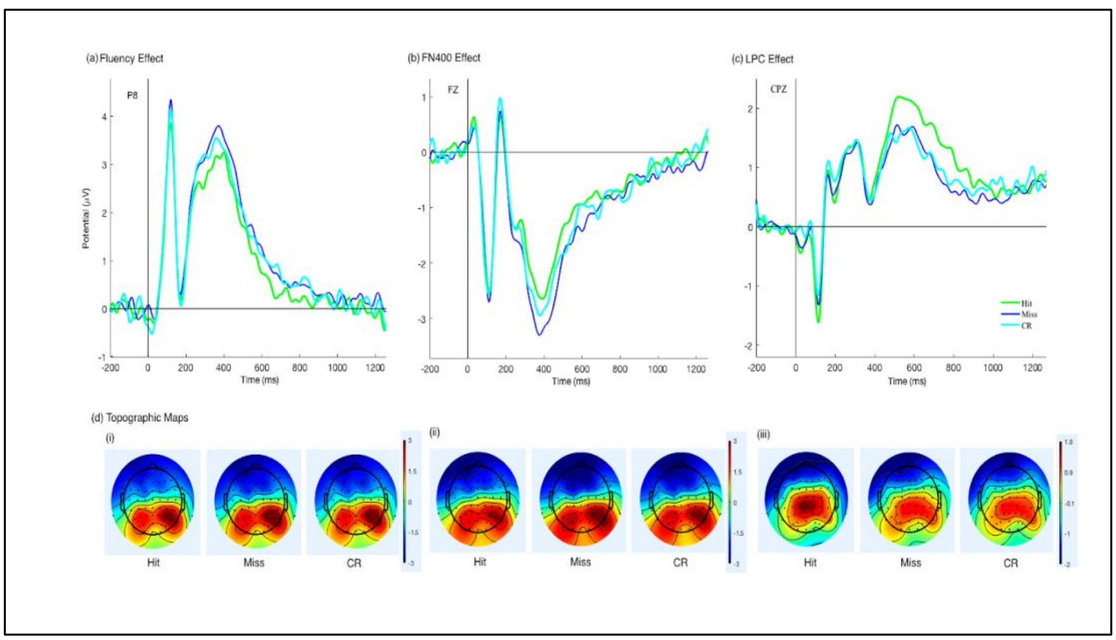


Figure 3.4. Grand-average ERPs at selected electrode sites elicited by novel fractals during the recognition test. Topographic maps show the activity elicited by Hit, Miss, and CR stimuli during fluency ERP, FN400, and LPC time intervals.

3.4 Discussion

The purpose of the present study was to replicate the results presented in Chapter 2 and determine whether the FN400 component reflects conceptual implicit memory (Voss et al., 2012; Voss & Paller, 2010; Paller et al., 2007) or familiarity (Yonelinas et al., 2007; Parks & Yonelinas, 2007; Rugg & Curran, 2007) or a combination of both (Mecklinger et al., 2012). Assuming that repetition of a stimulus triggers fluency, familiarity or conceptual priming, we expected that during the first exposure (i.e. encoding) of a stimulus there should be no FN400 or fluency ERP for meaningless stimuli. However, our results indicate that both forms of fluency (perceptual and conceptual) were reflected by the FN400 component and that the neural correlates of conceptual implicit memory during the encoding phase were not different from the neural correlates of conceptual implicit memory exhibited during the recognition test phase.

3.4.1 Encoding ERPs

During the encoding task, a comparison of SR and SNR stimuli revealed significant subsequent memory effects (see Figure 3.3). A brief presentation of the novel unfamiliar meaningless stimuli (250 ms) was not expected to activate any implicit memory associations during the encoding phase (Bruett & Leynes, 2015; Paller et al., 2012; Schupp et al., 2004). However, previous studies have shown that early subsequent memory (SM) ERPs, ERP components that are typically linked with recognition, were observed during encoding and were predictive of some of the subsequent memory performance (Chen et al., 2014; Griffin et al., 2013). To our surprise, we found a robust FN400 during the encoding phase, such that SR stimuli triggered more positive amplitudes than SNR stimuli. This effect was maximal at fronto-central electrodes. Moreover, a fluency ERP was also observed at left-parietal sites where SNR stimuli were more positive than SR stimuli. We did not observe a late positive component (LPC) at parietal sites during the encoding phase, which can be reconciled with the fact that participants had never seen these fractals before, hence there could be no recollection. Interestingly, at central electrodes, particularly at right-central sites, the SR stimuli elicited significantly more positive ERPs than SNR stimuli. We discuss these findings in detail in the following paragraphs.

The result that SR stimuli elicited a more positive FN400 than SNR during the encoding/study phase is difficult to reconcile with either the view that "FN400 reflects familiarity" or the view that the "FN400 captures conceptual implicit memory", particularly when there was no familiarity and no meanings that would trigger conceptual associations. According to the classic view of familiarity, it is a form of 'explicit memory'; a feeling that an event in question has been experienced before. If that is the case, then it is not possible that the FN400 amplitudes elicited during the encoding phase could reflect familiarity because, first, our stimuli were novel so there was no way that participants had seen them before, and second, these stimuli could not be unitized or labelled. Similarly, if the FN400 component is solely linked to conceptual implicit memory (Lucas & Paller, 2013; Voss et al., 2010; Voss & Paller, 2006), then again we would not expect an FN400 effect when the stimuli are meaningless fractals that cannot be unitized or labeled, and should therefore trigger no implicit processing (Parks and Yonelinas, 2007; Wixted, 2007). However, we did observe a strong FN400 effect at mid-frontal and frontal electrodes and in the following section, we discuss a few problems strictly attributing this effect to conceptual implicit memory.

Based on the view that the FN400 effect captures conceptual implicit memory processing, it is possible that the perceptual fluency of the stimuli triggered the activation of implicit memory processing, which eventually produced the observed FN400 effect. It has been shown that familiarity is sensitive to both conceptual and perceptual fluency of stimuli (Bruett & Leynes, 2015; Lucas and Paller, 2013). However, the possibilities that participants would have conceptual implicit associations to these fractals are remote, although these possibilities still exist. The only fluency that is associated with our stimuli was expected to come from the stimuli's perceptual fluency (i.e., colors, shape).

To understand the presence of the FN400 during our encoding phase, we sorted the stimuli based on their frequency of subsequent remembrance by the participants. Next, we examined those stimuli that were subsequently remembered by almost all participants and those which were missed by all participants. Interestingly, SR-by-most fractals anecdotally appear to be perceptually more fluent than SNR-by-most fractals (see Figure 3.5). On the other hand, we maintain our assumption that these fractals cannot be obviously unitized into a label. It is important to note, however, that we used a shallow encoding task; i.e. participants viewed each fractal for a fraction of a second (250 ms) and thus created a weak memory trace, such that recognition was driven by conceptual and perceptual fluency and/or familiarity rather than recollection (Leynes and Zish, 2012; Whittlesea and Price, 2001). It is possible that the remembered-by-most fractals were less complex and that the brief look (250 ms) might have led participants to think that these less complex fractals resembled a familiar shape. Upon visual inspection, these fractals appear to contain fewer colors than those that were missed. Thus, we speculate that the remember-by-most fractals possessed greater perceptual fluency, which triggered an associative concept that was reflected by the FN400.

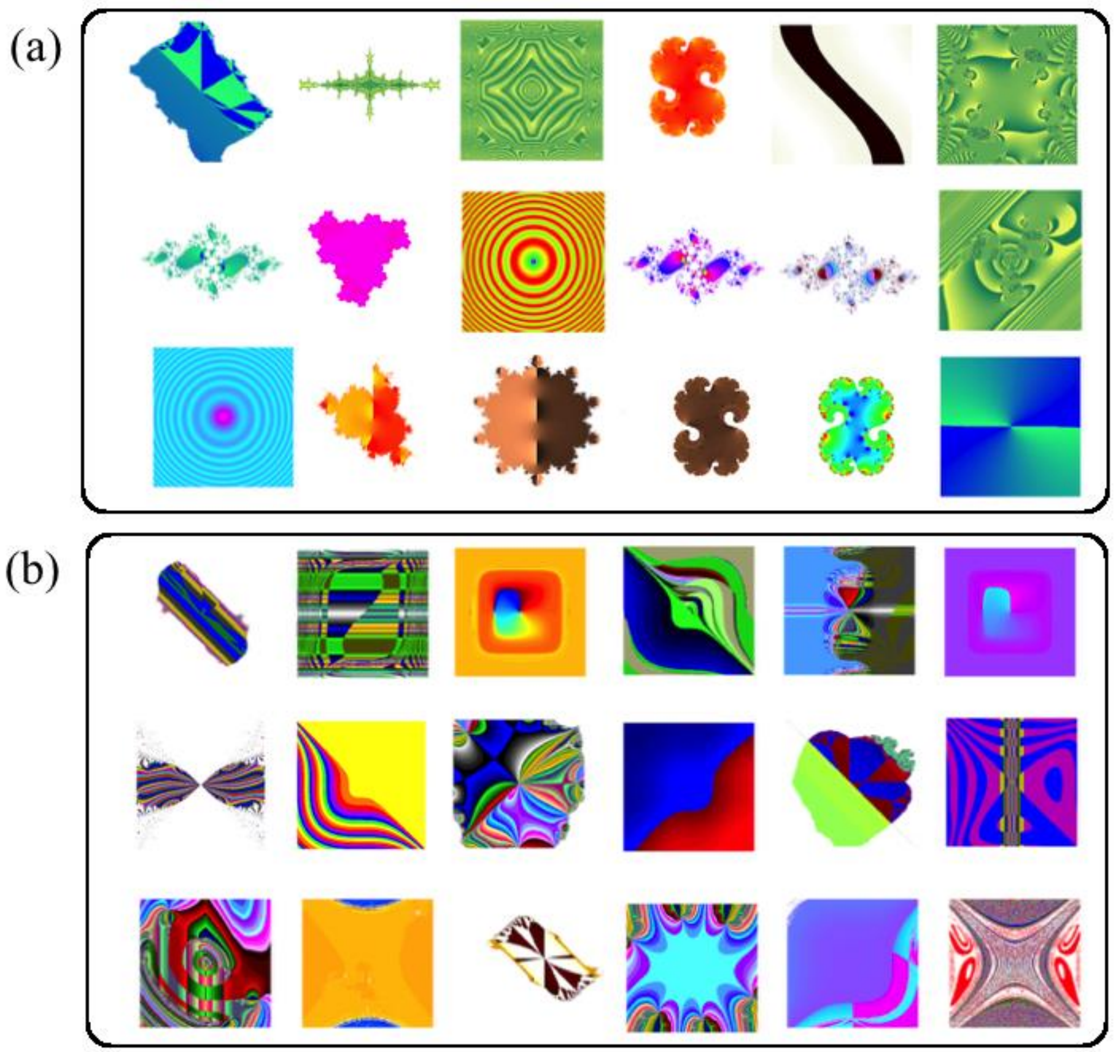


Figure 3.5. Fractals in category (a) were remembered by most of the participants whereas fractals in category (b) were missed by most of the participants.

The presence of the fluency ERP, both during the encoding phase and during recognition, suggests that recognition judgments were supported by perceptual fluency (Whittlesea and Leboe, 2003). The fluency ERP is a positive deflection that appears at parietal sites a little earlier than the FN400 component (peaking around 300 ms) and it is linked to perceptual fluency (Kurilla & Gonsalves, 2012; Leynes & Zish, 2012; Nessler et al., 2005). It is temporally and spatially distinct from the FN400 effect (Kurilla & Gonsalves, 2012; Rugg et al., 1998). In sum, findings from these studies suggest that perceptual and conceptual fluency, which are differed by polarity, time course and scalp location (hence driven by different neural mechanisms) contribute to the behavioural indices of recognition (Wang et al., 2016; Lucas & Paller, 2013; Voss et al., 2012; Leynes & Zish, 2012).

On the other hand, the presence of an FN400 (SR more positive than SNR) during the encoding phase, but the absence of the classic FN400 (old more positive than new) during recognition is hard to explain on the basis of either of the models. We believe that these effects may be explained by the *Discrepancy Attribution Hypothesis* (Whittlesea & Williams, 2001a; 2001b). Based on the discrepancy-attribution hypothesis, when encountering a stimulus, subjects tend to create a context based on their previous experiences with the stimulus, their subjective biases and the type of task they are engaged in. That context is used by participants to establish an expectation regarding the stimulus (e.g., “norm on the fly”, Kahneman & Miller, 1986). This expectation is compared to their next experience with another stimulus. The outcome of this evaluation can lead to different behavioural responses. One possible outcome that can result from this evaluation process is the conclusion that their experience processing the stimulus matches their expectations. In this case participants perceive their processing outcome as "coherent". Another possible outcome of the evaluation is that their experience processing the stimulus does not match their expected experience so that they perceive their processing experience as "incongruent" or surprising. Whittlesea and Williams (2001a; 2001b) proposed that the surprise caused by a violation of expectation can lead to the illusion of familiarity as participants always look for the source of the surprise. If the stimulus was expected to be easy to process (more fluent) but was surprisingly difficult to process (less fluent), then the violation of expectation would not be attributed to familiarity (Whittlesea & Williams, 2001a; 2001b). If the stimulus was expected to be difficult to process (less fluent) but was surprisingly easy to process (less fluent), but the source of surprise is obvious, then the violation of expectation again would not be attributed to familiarity (Whittlesea & Williams, 2001a; 2001b). However, when a participant encounters a stimulus that is un-expectantly easy to process, but there is uncertainty regarding the source of this fluency participants will attribute this ease of processing to an earlier experience with the stimulus (repetition), even if they have not seen that stimulus before.

Therefore, during encoding, some fractals may have been processed more fluently relative to other fractals. The ease of processing of these stimuli may have violated expectations of fluency based on the participant's experience processing the large number of other fractals. The discrepancy between one's expectations and the processing complexity of the stimulus may have given rise to an illusion of "knowing" the stimulus from the past based on the relative ease of processing the stimulus (Bruett & Leynes, 2015; Leynes & Zish et al., 2012; Whittlesea & Williams, 2001a, 2001b) and this evaluation would be reflected in the FN400 ERP. If the source is perceived to be coming from perceptual fluency, however, it may be reflected in the fluency ERP.

It is also possible that the subjective biases of participants contributed to the experience of familiarity, according to the norm theory (Kahneman & Miller, 1986). Kahneman and Miller propose that upon exposure to a stimulus, a person adopts a “norm” or pattern that is driven by some of its features and that this norm is applied to the rest of its features. This process of setting up a norm is purely subjective and may happen instantaneously when one encounters a stimulus (Whittlesea & Leboe, 2003; Kahneman & Miller, 1986). In terms of our experiment, the norm during the encoding phase may have derived from the sum of the subjective expectations stimulated by geometrical shapes hidden in these stimuli (fractals). Unnamable fractals may have caused the participants to focus more on individual features within each fractal instead of the whole picture and a familiar shape within each fractal may have triggered richer associations in terms of implicit memory processing. Also, those fractals that were different in shape from the majority of other fractals(e.g., some fractals from Julia set) may have caused a violation of the norm and may have triggered an associated neural process (see Figure. 3.4). As mentioned previously, it has been shown that participants have managed to find meanings (subjectively) when viewing subsequently remembered meaningless stimuli or stimuli with little meanings (Voss & Paller, 2007).

As expected, we did not observe an LPC-like effect during the encoding phase at parietal electrodes. However, during a similar time window (500-700 ms) post-stimulus, SR stimuli elicited more positive amplitudes when compared to SNR stimuli at central and centro-parietal electrodes, whereas no such effect was observed at parietal or occipital electrodes. This effect was maximal at central electrodes, particularly at Cz and C4. Interestingly, this effect was also observed in our previous experiment (see Chapter 2). In line with the previous studies, a positive ERP for SR stimuli peaking around ~500 ms post stimulus reflects successful encoding process (Paller et al., 2017).

3.4.2 Recognition ERPs

During the recognition test, participants viewed a random mix of old and new fractals and discriminated between the old (repetition) and new stimuli with the assumption that pre-experimental familiarity and semantic content were constant. We believe that our behavioural and ERP results suggest that recognition judgments were not based on recollection for three reasons (Leynes et al., 2017; Leynes & Zish, 2012; Whittlesea & Price, 2001). First, we did not observe an old/new FN400 effect, however, we did find an effect where Hit and CR were more positive than Miss, but there was no significant difference between Hit and CR. Second, a fluency ERP (200-400 ms post-stimulus at left-parietal electrodes) discriminated Hit (old) stimuli from the other response categories. And third, an LPC-like effect was observed at central and centro-parietal electrodes where Hit stimuli elicited more positive amplitudes than the other response categories (Paller & Wagner, 2002; Friedman, 1998). We discuss these findings in detail below.

No FN400 effect was detected during the recognition test, although a fluency ERP was observed at the right parietal site. A similar effect is reported in earlier studies (Paller et al., 2012; Rugg et al., 2007; Rugg et al., 1998). In the absence of meaningful stimuli (conceptual fluency), it was expected that we would not see an FN400 effect. However, in accordance with the FN400-reflects-familiarity theory, we expected to see a familiarity effect, which we did not. Instead, we observed a fluency ERP that corresponded with the behavioural indices of recognition. These findings reveal that recognition judgment relied on perceptual fluency rather than familiarity (Leynes & Zish, 2012; Paller et al., 2012; Rugg et al., 2007).

As described earlier, fluency and familiarity are two different perceptions that result from interpretive discrepancies (Whittlesea and Williams, 2001a, 2001b). For instance, the presentation of novel stimuli as well as familiar (old) stimuli may create a scenario where raw perceptual fluency and repetition fluency operate in parallel during recognition. As a result, these inconsistencies may have increased discrepancies between expectations and actual experiences, which eventually would lead to perceptions of familiarity (Leynes & Zish, 2015; Whittlesea and Leboe, 2003; Whittlesea and Williams, 2001a, 2001b). Therefore, we expected that the repetition (i.e. old more fluent than new) would serve as a basis for recognition by creating a context where repetition fluency would overcome semantic-emptiness to yield a familiarity signal (Westerman et al., 2002; Whittlesea & Williams, 2001a, 2001b).

That would mean that the FN400 signal would reflect a pattern where Hit (Old) > Miss (Old) > New (CR). Instead, we observed a memory signal where Hit (Old) > New (CR) > Miss (Old). Rugg and colleagues (1998) used a shallow task to examine familiarity during recognition and found a different pattern (i.e. Hit (Old) > Miss (Old) > New (CR). They argued that the neural activity linked to Miss (old) ERP reflected implicit memory, which was active even when the word was not consciously recognized, suggesting that it represents a neural correlate of implicit memory. Consequently, in the present study, the absence of meanings associated with stimuli eliminated the presence of conceptual fluency resulting in reliance on perceptual fluency for recognition memory (see Table 3.2) (i.e. Hit (fluency + old) < CR (fluency) < Miss (old)) (also see Bruett & Leynes, 2015; Leynes & Zish, 2012; Voss & Paller, 2010). Previous studies have shown that a stimulus that is experienced in the past is processed more fluently, thus uses fewer neuronal resources to process (Whittlesea & Williams, 2001a; Jacoby & Dallas, 1981). Thus, we observed that "Hit" stimuli produced the least positive amplitudes than all others. The same pattern was observed during the encoding session.

Rugg et al. (1998) reported that old stimuli elicited more positive potentials irrespective of the accuracy of recognition judgments. However, the pattern of our ERP results for recognition (Hit << CR, Miss) show that the fluency ERP effect contributed to recognition. The pattern of FN400 results (Hit > CR> Miss) shows that the FN400 is elicited by the illusion of familiarity and not repetition-driven familiarity. Had familiarity (repetition-driven) been responsible for the FN400, the pattern would have been (Hit > Miss > CR). It seems that a context based on the perceptual fluency of stimuli was developed and within that context, the violation of expectations surprised the participants, which led them to look for the cause of their surprise. The absence of a source for the surprise eventually led to an illusion of familiarity which was reflected in the FN400 pattern such that Hit stimuli (fluent + old) were correctly identified as old stimuli, correctly-rejected stimuli (fluent + new) were identified as new stimuli, but Miss stimuli (not-fluent) although old, were categorized as new as the cause of non-fluency could not be attributed to the oldness of the stimuli. This argument is based on the assumption that new items could be perceived fluent based on perceptual features (Snodgrass et al., 1996). Furthermore, it appears that the FN400 signal potentially reflected a perceptual fluency ERP effect; those stimuli which were perceived more fluently during the encoding task (SR items) were more positive than the new but fluent (CR) stimuli, whereas “Miss” items (i.e. SNR during the encoding phase) were the least positive of all (see Figure 3.4). Also, our data reveals that the difference between Hit and Miss at the mid-frontal electrode (Fz) during the recognition test was almost double of what it was during encoding (Encoding: M=0.3; Recognition: M=0.64) revealing that this effect gained from repetition (Bruett & Leynes, 2015; Leynes & Zish, 2012). Therefore, the pattern of the FN400 ERPs (Hit > CR > Miss) suggests that the basis of discrimination was perceptual fluency repetition leading to the discrepancies between expectations and actual experiences (Whittlesea & Williams, 2001a; Jacoby & Dallas, 1981).

These observations also support the idea that FN400 is “multiply determined” and suggest that different forms of implicit memory may contribute to either relative or absolute familiarity in some conditions (Mecklinger et al., 2014; Paller et al., 2012; 2007). It is argued that, depending on the context and stimuli, familiarity and conceptual implicit memory may co-occur in some circumstances, or that processes other than conceptual implicit associations can cause familiarity, or that conceptual implicit processing may happen with no resulting familiarity (Paller et al., 2012; 2007; Rugg et al., 2007). Therefore, we suspect that the FN400 component here reflected an illusion of familiarity that emerged from processing the violations of expectations that were attributed to either “oldness” of the stimuli (in some cases) or fluency in other cases (e.g., ‘‘norms on the fly”, Whittlesea & Leboe, 2003). As argued by Leynes and colleagues (2017), the processing of discrepancy must be noticed, and expectations must be violated to generate an experience of familiarity. Hence, the stimuli that were relatively unique popped out during the “norm on the fly" moment and generated a "familiarity perception strong enough to be revealed in the FN400 component (see Figure 3.5).

The presence of fluency ERP as well as an LPC effect at parietal and centro-parietal electrodes supports the idea that recognition was supported by perceptual fluency; Hits (correctly remembered stimuli) elicited the highest positive amplitudes at central electrodes (C1, Cz, C2) and centro-parietal electrodes. Importantly, this effect was a replication of the effect we observed in our previous experiment (see Chapter 2). Results from both experiments showed strong discrimination between "Hit" and other response categories (Miss and CR) at central electrodes. Multiple studies have shown that correct source judgments elicit more positive amplitudes at parietal electrodes during a time window similar to that of the LPC effect (i.e., 500-800 ms) (Leynes & Phillips, 2008; Rugg & Curran, 2007; Mecklinger, 2006; Rugg & Wilding, 2000; Friedman & Johnson, 2000; Wilding, 1999).

The Grand Comparison Between Experiment 1 and Experiment 2: The grand comparison between Experiment 1 (pictures) and Experiment 2 (fractals) supports the idea that different forms of implicit memory play a crucial role in learning and encoding. The only difference between the two experiments was the level of semantic associations that the stimuli carried, and this difference in stimulus context produced a significant difference in the FN400 potentials (see Table 3.3). This pattern of results suggests that the FN400 is linked to implicit memory. Furthermore, in the absence of conceptual fluency, perceptual fluency may help create a perception of familiarity that may appear in the FN400 effect.

3.5 Conclusion

The findings of the current experiment suggest that explicit memory is not the only source of familiarity. Different forms of implicit memory (perceptual and conceptual fluency) may also contribute to make a stimulus feel familiar. These findings also indicate that familiarity and its association with the FN400 are complex. We believe that the Discrepancy Attribution Hypothesis provides an alternative explanation for the complex nature of familiarity (Whittlesea and Williams, 2001a, 2001b). Our results are compatible with previous findings that the FN400 component is multiply determined and reflects a number of processes, which could include familiarity and/or conceptual implicit memory processing, depending upon the context and type of stimulus (Bruett & Leynes, 2015; Lucas & Paller, 2013; Mecklinger et al., 2012); Voss et al., 2012; Paller et al., 2007; 2003). Also, perceptual fluency is capable of supporting the process of recognition when the other sources of familiarity are not available (Leynes et al., 2017). Collectively, and in agreement with previous findings, we suggest that the neural correlates of perceptual (fluency ERP) and conceptual (the FN400 component) implicit memory can influence decisions made by explicit memory.

Limitations: It is important to note that the subsequent memory effect (500-1000 ms) observed in the present study differs in polarity from those reported in other studies (Paller & Wagner, 2002; Friedman, 1998; Paller et al., 2003). These studies have reported more positive amplitudes to later remembered items as opposed to later not-remembered items during this time window. Further, these stimuli generated a negative component as opposed to the LPC signal during the encoding phase, however, a positive LPC signal was observed during the recognition test. We are unsure why this polarity difference existed; however, different reasons may account for the discrepancy. These polarity differences within the study suggest that several factors may have shaped the LPC or the SME effect. One possibility is that different underlying mechanisms may be involved in these processes. For instance, the nature of the task or the types of stimuli that may elicit implicit or explicit processing may have led to certain interpretive discrepancies (Whittlesea and Leboe, 2003; Köhle et al., 2000). A better understanding could be achieved if we could disentangle these complex processes, which appear to co-vary in the same time window. Our experimental design was not capable of distinguishing different levels of cognitive processing. In future, we would consider a design where we could manipulate different levels of perceptual and conceptual fluency during encoding.

4 Chapter: The familiarity heuristic and the FN400 effect

4.1 Introduction

The FN400 ERP component (a negative deflection at frontal electrode around 400 ms post-stimulus) results from a number of processes, which could include familiarity and/or implicit memory processing depending upon the context (Paller et al., 2017; Bruett & Leynes, 2015; Lucas & Paller, 2013; Voss et al., 2012; Paller et al., 2007; Tsivilis et al., 2001). In our previous experiments, we received mixed evidence that conceptual fluency as well as perceptual fluency contribute to the FN400 ERP component (see Chapters 2 and 3). Given that implicit memory has multiple aspects including perceptual and conceptual fluency, it remains to be known how and which aspects of implicit memory affect recognition judgments.

Explicit memory typically refers to conscious voluntary recollection of prior experiences, whereas implicit memory refers to another type of memory that involves an unconscious, unintentional and involuntary recollection (Jacoby, 1984). The question whether recognition memory strictly depends on explicit memory or whether it is influenced by the processes related to implicit memory has divided the recognition literature into two camps; those who support either the *single*- or *dual-process* models of recognition. While researchers who support the *single-process* account and researchers who support the *dual-process* account agree that recollection is a conscious process that captures the contextual details of an event, including source information, there is a great deal of controversy regarding familiarity, which refers to a sense of oldness with no contextual details (Diana et al., 2008; Parks & Yonelinas, 2007; Wixted, 2007). Supporters of the '*dual-process signal detection'* (DPSD) model posit that familiarity and recollection are two distinct expressions of explicit memory that have different underlying neural mechanisms (Rugg et al., 2008; Yonelinas et al., 2002; Friedman et al., 2000; Hockley & Consoli, 1999; Rugg et al., 1998) and have distinct ERP signatures such that familiarity is reflected by the FN400 component whereas recollection is reflected by the late parietal component (a positive deflection elicited between 500 - 800 ms time window at parietal sites (LPC)) ((Rugg et al., 2008; Rugg & Curran, 2007; Yonelinas et al., 2002; Friedman et al., 2000; Rugg et al., 1998). On the other hand, supporters of the '*single process'* model suggest that recognition is determined by the strength of a single, continuously varying process that results from the strength of a neural signal in response to a stimulus process, of which, familiarity and recollection lie at the two hierarchical levels (Squire et al., 2007; Wixted, 2007; Yonelinas, 2002).

They also assume that implicit memory may support recognition and believe that the FN400 component reflects conceptual implicit memory in cases where strong concepts are associated with the stimulus (Paller et al., 2012; Nessler et al., 2006; Schott et al., 2005; Tulving & Schacter, 1990). While researchers from both sides appear to agree that the LPC component reflects the recollection process, the status of the FN400 component remains disputed.

The FN400 resembles the well-known N400 component, which reflects semantic or conceptual priming and occurs in the same time window as the FN400 (e.g. 300-500 ms) (Kutas & Federmeier, 2011; Voss et al., 2010). Priming is an expression of implicit memory, which unconsciously facilitates the response to that stimulus based on a previous experience with the same or a related stimulus (Schacter & Buckner, 1998; Tulving & Schacter, 1992; Schacter, 1987). Priming induces fluency, that is ease of processing, and therefore alters the behavioural measures of a response to a stimulus (Voss et al., 2012; Voss et al., 2010; Schacter, & Tulving, 1994; Schacter & Buckner, 1998; Roediger et al., 1987; Schacter, 1987). This could be done in multiple ways based on the stimulus type and the relationship between the priming stimulus and the test stimulus (Schacter & Buckner, 1998; Whittlesea, 1993). For instance, the repetition of perceptually similar stimuli induces an ease of sensory processing referred to as perceptual fluency that does not involve the meanings of the stimuli (Voss et al., 2012; Paller et al., 2007). In contrast, a word prime right before a stimulus will enhance conceptual fluency driven by the meaning of the stimulus - information that is beyond the physical characteristics of the stimuli (Paller et al., 2007). In most cases, both perceptual and conceptual fluency are attached to a stimulus because it is difficult to disassociate one from the other (Guo et al., 2015; Voss et al., 2010).

Studies have linked conceptual and perceptual fluency to different neural mechanisms (Wang et al., 2015; Voss et al., 2010; Woollams et al., 2008). Thus, if these fluencies contribute to familiarity, it is likely that familiarity originates from multiple neural sources (Nessler et al., 2005; Henson, 2003). Moreover, the FN400 effect is related to the famous N400 effect, which is linked to conceptual priming (Voss & Paller, 2012; Paller et al., 2007; Kutas & Nessler et al., 2005; Kutas & Hillyard, 1980), suggesting that conceptual fluency may be capable of providing the basis for the FN400 effect. Furthermore, findings from recent studies suggest that it is conceptual fluency that contributes to FN400 (Paller et al., 2012; Voss et al., 2012; Voss & Paller, 2010a). In fact, it has been claimed that in a paradigm where conceptual memory co-varies with the familiarity indices, the FN400 component captures conceptual implicit memory instead of familiarity (Paller et al., 2012; Voss et al., 2012).

Voss and Paller (2012) reviewed a series of experiments to disentangle the neural correlates of conceptual implicit memory and familiarity using different stimuli that involved meaningfulness and priming. One of their experiments contrasted ERPs linked to different kinds of squiggles such that some squiggles could evoke conceptual associations whereas others had no meanings associated with them (Voss et al., 2011; 2010; Voss & Paller, 2007). In their recognition test, the FN400 component was found to correlate with familiarity of meaningful squiggles only, indicating that FN400 captured conceptual implicit memory *and* familiarity. No FN400 was observed for meaningless squiggles (Voss & Paller, 2007). In their other experiments, they used the same squiggles with related and unrelated primes to enhance the effects of conceptual implicit memory and familiarity. They found that the size of the FN400 effect was directly related to the degree of conceptual priming of meaningful squiggles (Voss, et al., 2010). In other words, the FN400 amplitudes seem to capture familiarity because familiarity accompanies conceptual fluency in most cases (Voss, et al., 2012; Lucas et al., 2012; Woollams et al., 2008). Put another way, conceptual fluency seems to contaminate the neural measures of familiarity when familiarity and conceptual implicit processing co-occur, creating an FN400 effect. However, Mecklinger and colleagues (2012) did not agree with this claim, and showed in their study that the FN400 amplitudes do not always correlate with the behavioural measures of conceptual priming even though it co-varies with perceptual manipulations (Mecklinger et al., 2012; Stenberg et al., 2009). They argued that conceptual implicit memory may contribute to FN400 in some circumstances, but it is unlikely that the FN400 exclusively reflects conceptual implicit memory (Mecklinger et al., 2012). Other studies have reported that perceptual fluency may also contribute to relative familiarity and therefore may influence the FN400 (Lucas et al., 2012; Leynes and Zish, 2012; Woollams et al., 2008; Nessler et al., 2005; Whittlesea, 2002; Rajaram, 1993; Jacoby & Whitehouse, 1989). However, perceptual fluency is attributed to familiarity in cases when participants are uncertain about the source of fluency (Whittlesea & Williams, 2001a, 2001b).

Conversely, the perceptual fluency effect is linked to a positive ERP component around 300 ms post stimulus at the parietal region of the brain (Schott et al., 2002; Tulving & Schacter, 1990). Similarly, we found in our previous experiments that ERP indices of recognition judgments were affected by the perceptual fluency, such that subsequently-remembered stimuli elicited fewer positive amplitudes than subsequently-not-remembered stimuli at parietal electrodes during the 200–400 ms interval (Chapter 2 and 3). We called this effect a fluency ERP as it has been linked to the perceptual fluency of stimuli (Bruett & Leynes, 2015; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007). Schott and colleagues (2002) observed that processes associated with perceptual fluency occurred earlier than those processes that were associated with explicit memory. Given that perceptual fluency is another form of implicit memory, Jacoby and Dallas (1981) noted that the "oldness" of an item makes it more fluent when processed (Jacoby & Dallas, 1981). Studies have shown that perceptually fluent but novel items may get mistaken as old items if the participants are uncertain about the source of fluency (Westerman, 2008; Whittlesea & Williams, 2001a, 2001b). In other words, participants are more likely to attribute "perceptual fluency" to familiarity as a result of a past experience (Olds and Westerman, 2012; Kurilla & Westerman, 2008; Nessler et al., 2005; Westerman et al., 2002; Whittlesea, 2002; Westerman, 2001; Whittlesea et al., 1990; Jacoby & Whitehouse, 1989). For example, Whittlesea and Williams (1998) instructed participants to memorize words from a pool of real words (e.g., frog, cancer) and pseudohomophones (e.g., phrawg, kanser) in random order. During recognition, they were asked to read some of the old words mixed randomly with some new words and nonwords and were instructed to decide if they had seen the words previously. Although, the real words were more fluent than the nonwords, some new pseudohomophones were erroneously "recognized" as items from the past (study). Therefore, Whittlesea and Williams (1998) suggested that familiarity resulted not only from the absolute fluency of the real words but also emerged erroneously from the nonwords that were processed relatively more fluently than expected.

According to the *discrepancy-attribution hypothesis*, unexpected fluency of performance is erroneously attributed to familiarity (Whittlesea & Williams, 2001a; 2001b). If the processing of a stimulus is easier than expected, and the source of the fluency enhancement is unknown, this unexpected ease is surprising. The 'surprise' caused by unexpected fluency, is unconsciously attributed to an experience in the past and to a subjective feeling of familiarity in the present (Whittlesea & Leboe, 2003; Jacoby & Whitehouse, 1989). Whittlesea and Leboe (2003) argued that the feeling of familiarity is an acknowledgment of the perception that the processing of an event is unknowingly strange. Who is this person in the mall? Why does she look so familiar? Perhaps, she is someone from my workplace! Therefore the *discrepancy* between one's expectations and one's experience of processing the event ('that person is familiar to me') engages an attribution process based on the magnitude of the violation, which eventually leads to an evaluation of the fluidity of the processing. For example, it was reported that when clear and blurred images of common objects were randomly presented, an FN400 effect was observed. Apparently, random variations in perceptual fluency helped participants develop a context, based on which the processing of some stimuli (clear images) were unexpectedly more fluent than others based on the “norm” generated by the participants (e.g., “norm on the fly," Kahneman & Miller, 1986). This violation of expectation was unconsciously attributed to familiarity, hence this discrepancy was reflected in the FN400 component (Leynes & Zish, 2012). Whittlesea et al. (2001a; 2001b) called this attributed familiarity ‘relative familiarity’ (Whittlesea & Leboe, 2003; Whittlesea, 2002; Whittlesea & Williams, 2001a, 2001b). On the other hand, variations in perceptual features of face types (Nessler et al., 2005) or variations in repetition (Woollams et al., 2008) correlated with a fluency ERP that was temporally and spatially distinct from the FN400 effect and the enhanced fluency was attributed to familiarity.

To sum it up, this debate suggests that the role of the fluency ERP is key to understanding the heuristic of familiarity (Leboe et al., 2000). Knowing that the FN400 component indexes an unknown combination of familiarity and implicit memory including processes of perceptual and conceptual fluency (Voss & Paller, 2017; Leynes & Bruett, 2017), the relative contribution of these fluencies to creating the experience of familiarity and their impact on the FN400 component is unclear (Leynes & Zish, 2012; Whittlesea & Leboe, 2003; Whittlesea, 2002; Whittlesea & Williams, 2001a, 2001b). A predominant method for manipulating familiarity is by exposing participants to stimuli a varying number of times (Stenberg et al., 2009; Jacoby, 1984; Mandler, 1980). However, the repetition of a stimulus appears to initiate several cognitive processes, including perceptual fluency, conceptual fluency, and/or familiarity, as all three of these phenomena co-vary with repetition (Bruett & Leynes, 2015; Leynes & Zish, 2012) making that their respective neural signatures difficult to disentangle (Voss et al., 2010; Paller et al., 2007; Voss et al., 2007). Therefore, a new design is required to disentangle these processes for examination.

4.2 Hypothesis

Traditionally, much of previous literature on encoding has focused on classic subsequent memory effects (SME) and involve a single presentation of a stimulus that distinguishes subsequently remembered items from subsequently forgotten items. To our knowledge, few studies have examined effects beyond the SME. Griffin and colleagues (2013) attempted to examine the differences between implicit and explicit memory effects on the FN400 component during encoding when participants were engaged in implicit recognition during an incidental encoding task (Griffin et al., 2013; Reder et al., 2009). They showed that FN400 effects can reliably appear at encoding. Griffin and colleagues demonstrated that the FN400 ERP traditionally thought to reflect explicit memory processes was present when participants were engaged in implicit recognition during an incidental encoding task (Griffin et al., 2013; Reder et al., 2009).

ERP components traditionally associated with explicit memory tests at the encoding stage were measured (Griffin et al., 2013). We expected that back-sorting based on response-based performance from the recognition test would reveal the effects of priming, fluency and repetition without the contamination of associated motor responses (Griffin et al., 2013; Reder et al., 2009). This paradigm allowed us to examine the relationship between FN400 amplitudes and priming and repetition, in light of the previous research that has demonstrated that the FN400 component is associated with both conceptual implicit memory (Voss & Paller, 2017; Voss et al., 2010; Voss and Paller, 2009; Paller et al., 2007) and repetition (Rugg et al., 2008; Rugg & Curran, 2007; Yonelinas et al., 2002; Friedman et al., 2000; Rugg et al., 1998).

In an attempt to disentangle the “mix of familiarity and other co-occurring memory phenomena” (Paller et al., 2007), we employed a subsequent-memory design where we manipulated perceptual fluency, conceptual fluency, and repetition-driven familiarity. A shallow task was chosen to ensure that our ERPs captured the familiarity effect and not recollection. The duration of presentation of the images was brief to generate only weak memory traces such that retrieval would be based on familiarity and not recollection (Rugg et al., 1998). The experimental protocol involved presenting primed and unprimed images of common objects one at a time. Similarly, some images were presented more than once to examine the effects of repetition and to increase familiarity based on repetition. In order to uncover the effects of perceptual fluency on recognition performance, the image clarity was manipulated by applying two levels of blur to some of these images. Additionally, guided by the discrepancy attribution hypothesis (Whittlesea & Williams, 2001a, 2001b) we also examined the link between fluency and familiarity (the FN400 component). The multi-factor design allowed us to test multiple sources of fluency and how discrepancies may arise from different combinations of these fluencies. In sum, we attempted to disentangle the effects of many of the factors that affect memory encoding or recognition performance such as familiarity, implicit memory or fluency of the images, but remain in dispute (see Figure 4.1). Event-related potentials (ERPs) were recorded while participants viewed primed and unprimed, blurred and clear images of common objects that were presented once, twice or three times during the encoding phase. Based on these manipulations stated above, we expected that:

1. Given that familiarity may result from assessing inconsistencies between experienced and expected fluencies (Whittlesea & Leboe, 2003), we expected that the primed stimuli would become more fluent than unprimed stimuli which would lead to larger FN400 effects in the primed condition.
2. The fluency differences between blurred and clear images would result in a fluency ERP effect.
3. If the FN400 component reflects processes involved in conceptual implicit memory, then primed stimuli should trigger a robust FN400 effect, as conceptual priming would provide a strong basis for implicit memory.
4. Or, if the FN400 is driven by repetition-based familiarity, then repeated stimuli should elicit a stronger FN400 effect.

Additionally, the manipulation of image clarity allowed us to examine the effects of perceptual fluency on the subsequent fluency ERP effect and the FN400.

4.3 Methods

4.3.1 Participants

Twenty-one students (11 females, ages 18-22 years) at Wilfrid Laurier University were recruited through the online Participant Research Experience Program (PREP) system and consented to the procedures approved by the Wilfrid Laurier University Research Ethics Board. These students participated for course credit and were healthy, right-handed individuals with normal or corrected to normal vision. No participant reported ever experiencing a psychiatric illness.

4.3.2 Stimuli and Procedures:

The stimulus pool consisted of three blocks that each included 108 black and white pictures of common objects. These blocks varied in terms of filter conditions (F0, F1, and F2) such that block one consisted of unaltered images (F0), block two consisted of lightly blurred but recognizable images (F1) and block three consisted of highly blurred images (F2). To blur the images, we added Gaussian noise (a MATLAB function) of variance 0.01 (F1, slightly blurred) and 0.07 (F2, highly blurred). Furthermore, within each block, 36 images were presented once (R1), 36 were presented twice (R2), and 36 were presented three times (R3). Half of the stimuli in each block were primed using words presented in black Arial font of font-size 44. The words were conceptually related to the corresponding image and presented for 50 ms immediately prior to the display of the stimulus (for more details see Appendix A1). The primes were presented before the last presentation of the image during the encoding phase. In other words, for an image that was repeated three times, the prime was presented right before the third presentation. The repeated images in the study phase were randomized within the block; however, each participant was presented with the same order of images. Participants were informed in advance that they would be tested for their memory of the photographs and to watch each item carefully so that they could subsequently perform the recognition memory test.

There were short breaks after each block. Participants initiated each block by pressing a button on a response pad. The rest of the trials of the block were automatically run with no control from participants. Each trial started with a 1,000 ms pre-encoding period, where participants had to focus on a blank screen with a central fixation dot. Each image was presented for 250 ms, followed by a 1,000-ms encoding period, during which the computer screen remained blank.

After a short break, participants performed the recognition session during which 524 pictures (324 old, 200 new) were randomly presented to them. During the recognition test, pictures were presented on the screen until a response was recorded. Participants were instructed to press ‘3’ on the response pad if they remembered seeing the picture or press ‘4’ if they did not previously see the picture.

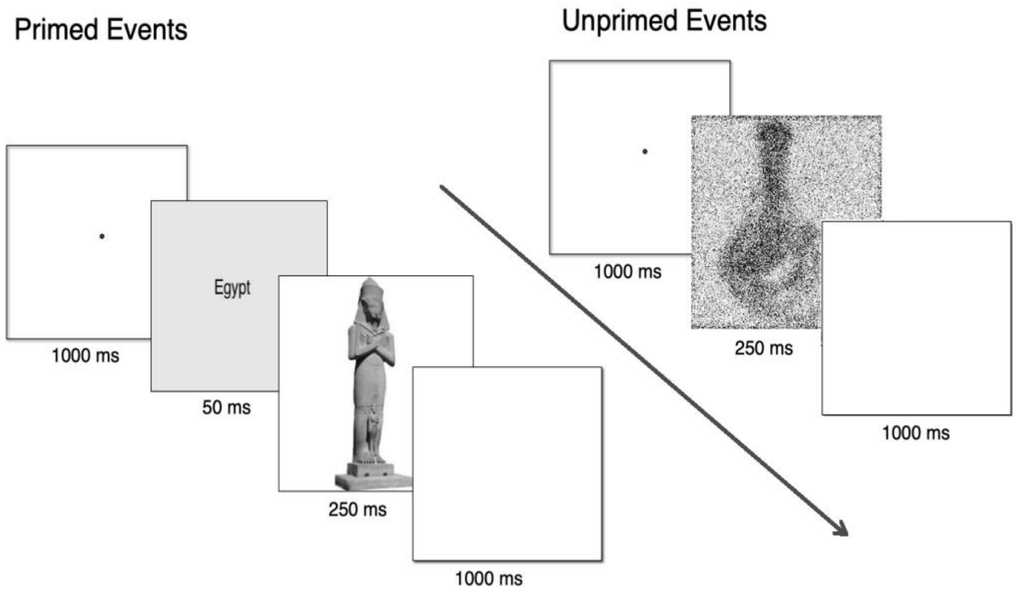


Figure 4.1. Schematic diagram of the encoding phase of the experiment.

4.3.3 EEG data and Acquisition

EEG data were recorded using a NeuroScan GSN 64 1.0 Ag/AgCl electrode Quik-cap (Compumedics, Charlotte, NC, USA) in a sound-attenuated, electrically shielded booth (Raymond EMC, Ottawa, ON, Canada) while participants performed the encoding and recognition tasks. Electrodes were positioned according to the International 10-20 EEG System with one ground electrode such that electrodes were fixed over the frontal lobes (FP1, FP2, F7, F3, FZ, F4, F8, FC3, FCZ, FC4), temporal lobes (FT7, FT8, T7, T8, TP7, TP8), parietal lobes (CP3, CPZ, CP4, P7, PZ, P4, P8), occipital lobes (O1, O2), and at the central position of the scalp (C3, CZ, C4). Electrode CZ was visually centered above the central vertex found halfway between the glabella and the external occipital protuberance medially and the preauricular points laterally. Electro-gel was used to improve conduction between the skin and the electrode surface. Surface electromyographic electrodes were positioned at the outer canthi of both eyes and above and below the left eye. EEG signals were initially referenced to the mastoid electrodes (M1, M2), which were placed on the mastoid process behind each ear. Impedances were kept below 5kΩ. The presentation of stimuli was controlled by programmable experiment generation software Stim2 (Compumedics, Charlotte, NC, USA) and signals were acquired across all 64 electrodes.

4.3.4 Data Processing

Behavioural data: The performance in the recognition task was analyzed first. We investigated participant task accuracy and reaction time. Each participant's Hit, Miss, Correct-Rejection (CR) and False Alarm rates (FA) were computed for each condition. The perceptual sensitivity of the recognition task was estimated using signal detection theory (SDT) by computing A' for each participant. The signal detection measure A', which is a measure of sensitivity, was calculated by computing Hit rates and FA rates. Performance during the encoding phase was compared between the subsequent hits (SH) and subsequent misses (SM) trials based on the performance in the recognition task. Reaction times during the recognition task were analyzed using a one-way ANOVA for each condition whereas the hit performance for each condition was analyzed using a repeated-measures ANOVA model with Item type (Primed, Unprimed), Filter (F0, F1, F3) and Repetition (R1, R2, R3) as factors.

EEG Data: Custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme and Makeig 2004, http://sccn.ucsd.edu/eeglab) were used to analyze the data. We inspected and corrected the continuous data for outliers, body movements, and muscle and cardiac artifacts by using Artifact Subspace Reconstruction (ASR) (Bigdely-Shamlo et al., 2015). For further artifact correction, independent component analysis (Delorme and Makeig 2004) was used (see Chapter 2 for detailed information). Statistical analyses were carried out using SPSS Statistics (SPSS, Inc., 2009, Chicago, IL, www.spss.com) on the mean voltage differences at the corresponding electrodes and time windows.

Signals were averaged, re-referenced and initially high pass filtered (1 Hz) (Winkler et al., 2015). For ERP analysis, signals were passband filtered between 1 and 30 Hz. Trials above 50 μV voltage potential from baseline were rejected. On average, 10% of the trials per participant were rejected. ERP components were computed as the average activity relative to a -200 to 0 ms pre-stimulus baseline activity (Luck, 2014). ERPs recorded during the encoding phase were grouped into subsequently hit items (SH) and subsequently missed items (SM), based on the participants' responses during the recognition task for each condition (Voss et al., 2010; Paller & Wagner, 2002; Rugg & Allan, 2000). Findings from previous studies have linked perceptual fluency with an ERP ~200 to 400 ms post stimulus onset, where old items elicit more negative ERPs than new items (e.g., Wang et al., 2015; Bruett & Leynes, 2015; Leynes & Zish, 2012).

To investigate the hypotheses, we used several levels of analysis. First we analyzed our ERPs with repeated-measures ANOVA with the factors of SME (Subsequently-Hit/SH, Subsequently Miss/SM) X Prime (Primed, Unprimed) X Repetitions (R1, R2, R3)

X Filter (F0, F1, F3) for the encoding phase based on the performance from recognition. We conducted this analysis on frontal and mid-frontal electrodes for the FN400 effect, whereas for the fluency ERP we did this analysis on posterior and occipital electrodes. Next, a series of pair-wise, post hoc t-tests further examined ERP differences across response types. Fluency ERPs were quantified by computing the activity during the 200 – 400 ms interval at all posterior electrodes as well as the central electrodes (C3, C1, CZ, C2, and C4). The FN400 analyses examined ERP measures during the 300–500 ms time interval at anterior electrodes sites as well as central electrodes. Significant effects were corrected for non-sphericity using Greenhouse–Geisser corrections, and significant effects are reported with the corrected degrees of freedom when appropriate.

4.4 Results

4.4.1 Behavioural Results

Our results for memory performance showed that participants, in general, were capable of discriminating old from new pictures above chance, as indicated by an average A' of 0.77 (SD: +/− .08; range 0.73 to 0.80). The further the A' value is away from 0.5; the better is the performance of the participants. Thus, a A' value of 0.77 would mean that participants were able to discriminate well above chance.

Table 4.1 displays means and standard deviations for hits and misses and the corresponding response times for each condition. A three-way interaction of priming, filter and repetition was observed, F (4, 1508) = 6.35, $p < 0.001$. Further analysis revealed that repetition as well as priming enhanced the recognition performance when images were blurred (F (4, 1508) = 29.11, $p < 0.001$; F (4, 1508) = 7.29, $p = 0.001$); however, repetition had no effect on priming ($F < 1$). Additionally, each factor (prime, filter and repetition) significantly differed from each other revealing that repetition had the strongest effect of all (Prime: $F(1, 377) = 11.76$, $p = 0.001$, $\eta_2 = .03$; Filter: $F(2,754) = 116.55$, $p < 0.001$, $\eta_2 = .24$; Repetition: $F(2,754) = 127.27$, $p < 0.001$, $\eta_2 = .25$).

Table 4.1

Proportion of Hits and response time (ms) values, reported along with their standard deviations across participants in parentheses for each condition.

		Primed			Unprimed		
		Hit	Miss	N (Hits)	Hit	Miss	N (Hits)
Clear Images	R1	1041.27 (767.81)	1048.02 (906.58)	0.52 (.5)	1217.42 (1122.36)	1244.52 (1208.80)	0.44 (.5)
	R2	917.10 (536.57)	1113.58 (970.84)	0.67 (.48)	1121.03 (1314.88)	1222.96 (1319.72)	0.7 (.46)
	R3	935.67 (725.83)	1297.34 (1222.43)	0.76 (.43)	977.69 (935.55)	1148.32 (968.53)	0.79 (.41)
Lightly Blurred Images	R1	1101.22 (892.37)	1170.20 (957.02)	0.48 (.5)	1166.53 (1010.88)	1224.99 (1224.39)	0.35 (.48)
	R2	1089.06 (911.05)	1344.83 (1579.20)	0.58 (.49	1020.47 (784.64)	1299.48 (1150.83)	0.53 (.5)
	R3	848.33 (590.62)	1668.79 (2407.24)	0.78 (.42)	1026.87 (1179.55)	1041.59 (1246.25)	0.68 (.47)
Highly Blurred Images	R1	1347.39 (1277.69)	1174.44 (1074.84)	0.36 (.48)	1394.45 (1256.37)	1193.15 (1089.17)	0.46 (.5)
	R2	1304.55 (1267.84)	1123.25 (918.01)	0.45 (.5)	1126.46 (853.49)	1104.43 (1075.53)	0.4 (.5)
	R3	1152.28 (803.63)	1272.60 (1349.98)	0.47 (.5)	1144.7 (897.75)	1076.51 (995.48)	0.4 (.5)

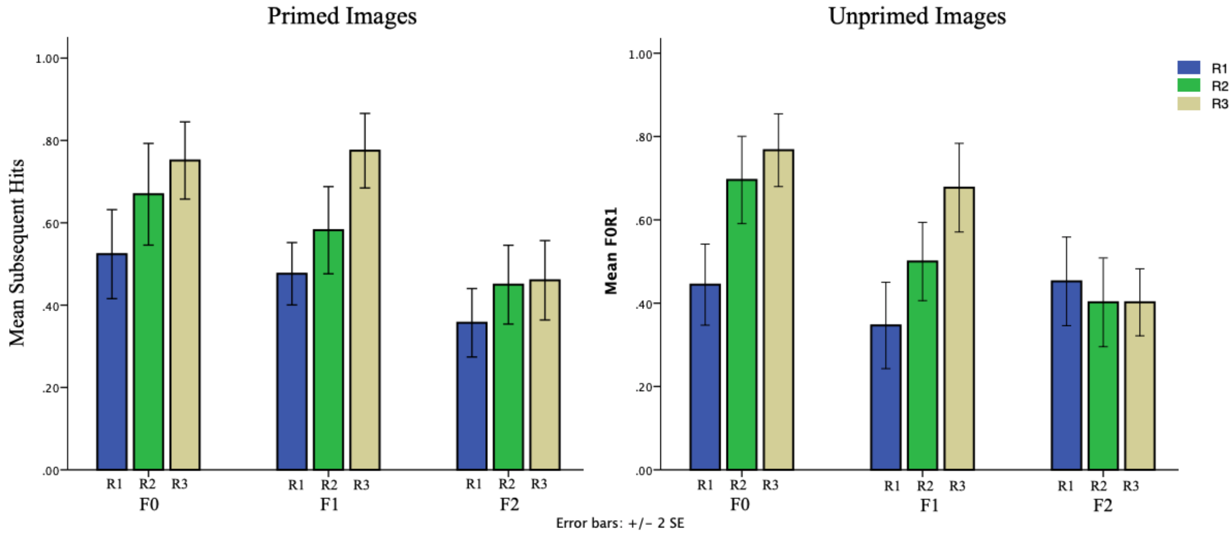


Figure 4.2. Subsequent Hit accuracy percentage for primed and unprimed images. Blue, green and yellow bars represent one, two and three exposures of the images, whereas F0, F1, and F2 illustrates unfiltered, slightly filtered and highly filtered images, respectively.

4.4.2 ERP Results

At the encoding phase, for the two time windows reflecting the Fluency ERP (200 – 400 ms) and the FN400 (300 – 500 ms), a three-way repeated- measures ANOVA with SME (Subsequent Hit /SH, Subsequent Miss/SM) X Prime effect (Primed, Unprimed) X Filter (F0, F1, F2) X Repetition (R1, R2, R3) was computed. The probe for the FN400 effect was focused on frontal and fronto central electrodes whereas the fluency ERP was more focused on centro-parietal and posterior electrodes. A general overview of the grand-average ERP data of both ERP components is presented in Figure 4.3. A group comparison analysis for each condition revealed significant differences for the following intervals, which are listed as follows:

Fluency ERP (200–400 ms): A four-way repeated-measures ANOVA revealed several significant interactions and main effects of all factors on the ERP within the fluency ERP window during encoding at certain electrode sites (see Figure 4.3).

A three-way interaction with SME X Repetition X Filter was observed at right as well as the left parieto-occipital electrodes revealing that the fluency ERP was affected by the clarity of the images when those images were presented repeatedly (PO3: $F(4,80) = 3.79$, $p = 0.007$, $\eta_2 = .16$; PO5: $F(4,80) = 3.5$, $p = 0.01$, $\eta_2 = .15$; PO7: $F(4,80) = 2.66$, $p = 0.04$, $\eta_2 = .12$; P7: $F(4,80) = 3.87$, $p = 0.006$, $\eta_2 = .16$) (see Figure 4.4, which shows the PO3 electrode where this effect was maximal). Furthermore, the interaction between clarity and priming was maximal at mid-occipital and mid-parietal sites (Prime X Filter: $F(2,40) = 3.4$, $p = 0.04$, $\eta_2 = .15$). Additionally, an interaction of Prime and fluency ERP was observed at central parietal and left parietal sites only (Prime X Fluency SME: $F(1,20) = 4.94$, $p = 0.04$, $\eta_2 = .2$).

It is apparent from Figure 4.3 that the fluency subsequent memory effect (SME) was concentrated at central and centro-parietal sites of the brain (CZ: $F(1, 20) = 3.88$, $p = 0.02$, $\eta_2 = .24$; CP1: $F(1,20) = 7.02$, $p < 0.02$, $\eta_2 = .26$; CPZ: $F(1,20) = 6.49$, $p < 0.02$, $\eta_2 = .25$; CP2: $F(1,20) = 5.91$, $p = 0.03$, $\eta_2 = .23$). The topographic effect map (Figure 4.3, and also Figure. 4.6) indicates that the effect of image clarity (Filter) on the fluency ERP component was bilateral. However, the priming effect was more concentrated on the left site, particularly at parieto-occipital sites (P07: $F(1, 20) = 5.41$, $p = 0.03$, $\eta_2 = .21$; P05: $F(1, 20) = 5.85$, $p < 0.03$, $\eta_2 = .23$; O1: $F(1, 20) = 9.6$, $p = 0.006$, $\eta_2 = .32$)(see Figure 8). Moreover, a repetition effect was observed mostly at the right-parietal site (P8: $F(1, 20) = 7.76$, $p = 0.001$, $\eta_2 = .28$; P6: $F(1, 20) = 8.38$, $p = 0.004$, $\eta_2 = .30$) (see Figure 4.9).

In sum, the filter effect was bilateral at posterior regions; however, the interaction between filter and priming was more prominent at central occipital and left parietal regions, whereas the filter effect interacted with repetition at the right parietal sites (see Figure 4.3).

FN400 (300 – 500 ms): A four-way repeated-measure ANOVA revealed a significant three-way interaction between the FN400 SME, Prime and Repetition at right fronto-central sites (FC6: $F(2,40) = 7.4$, $p = 0.002$, $\eta_2 = .27$). Further analysis revealed that not only priming affected the FN400 SME potentials but also repetition was observed to have a main effect at these sites (FN400 SME X Prime: $F(1,20) = 6.9$, $p = 0.02$, $\eta_2 = .26$; Repetition: $F(1,20) = 5.69$, $p = 0.007$, $\eta_2 = .22$) (see Figure 4.3).

Also, a three-way interaction of the FN400 SME X Repetition X Prime was observed at right fronto-polar sites (FN400 SME X Repetition X Filter: $F(4,80) = 2.71$, $p = 0.04$, $\eta_2 = .12$). Further analysis revealed that the FN400 potentials were affected by priming only during the first exposure. Primed stimuli were more negative than unprimed stimuli for all filter conditions. During the second exposure, unprimed stimuli were more positive (FN400 SME X Prime: $F(1,20) = 6.22$, $p = 0.02$, $\eta_2 = .24$) (see Figure 4.3).

Likewise, the FN400 effect seemed to be driven by Filter manipulations at the left frontal and fronto-central sites of the brain (FN400 SME X Filter: $F(2,40) = 3.6$, $p = 0.04$, $\eta_2 = .15$; Filter: $F(2,40) = 4.75$, $p = 0.01$, $\eta_2 = .19$) (see Figure 13). Moreover, the FN400 amplitudes appeared to be driven by repetition at the FC1 and C4 electrodes only; however, the effect was maximal at the FC1 electrode (FN400 SME X Repetition (FC1): $F(2,40) = 4.95$, $p = 0.01$, $\eta_2 = .20$; FN400 SME X Repetition (C4): $F(2,40) = 3.28$, $p = 0.05$, $\eta_2 = .14$).

Collectively, it was observed that the priming effect on the FN400 component was confined mostly towards anterior and right anterior sites of the scalp (see Figure 4.3).

However, the filter effect had an impact on FN400 SME potentials at the left fronto-central regions. An in-depth analysis of this interaction at the FC5 electrode revealed that this effect was observed in the absence of any filter effect (see Figure 4.3).

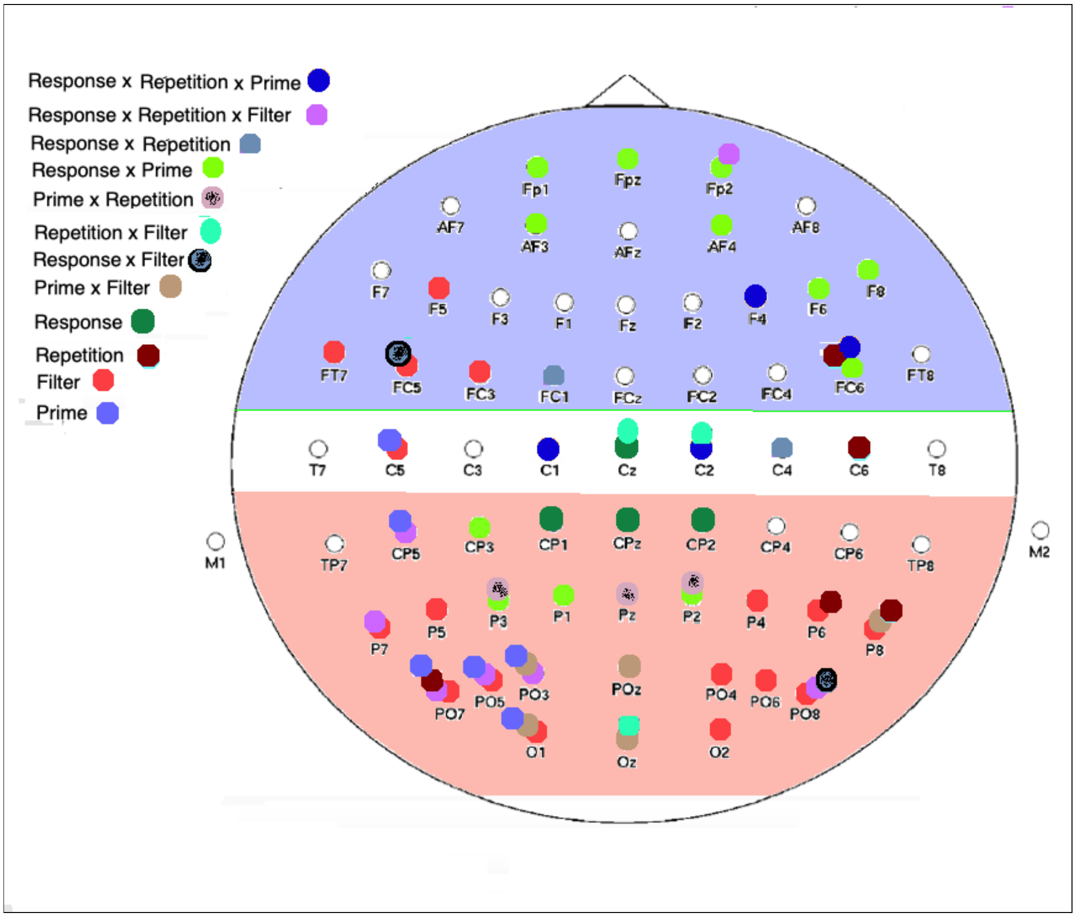


Figure 4.3. The significant results of the four-way repeated-measures ANOVA with SME (Subsequent Hit /SH, Subsequent Miss/SM) X Prime effect (Primed, Unprimed) X Filter (F0, F1, F2) X Repetition (R1, R2, R3) for the two time windows reflecting the Fluency ERP (200 – 400 ms) and FN400 (300 – 500 ms) are depicted in a topographic map revealing the effect and the location of the effect. Each colored circle represents a significant main effect and interaction. No significant effect was observed at the electrode sites with white circles.

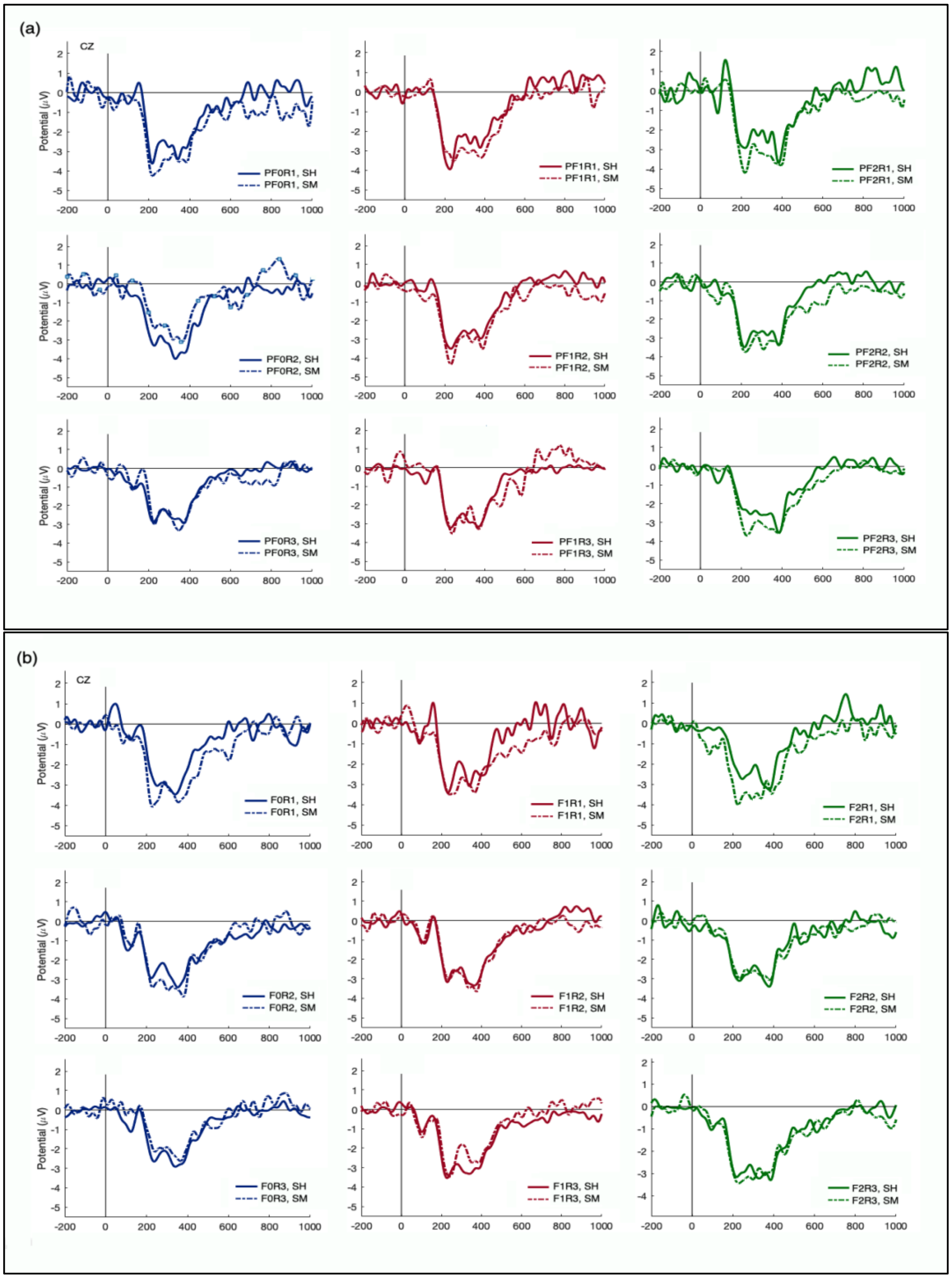


Figure 4.4. Grand-average ERPs at the mid-central (CZ) electrode. (a) (top panel) shows ERPs elicited by primed SR and SM stimuli, averaged across all participants, whereas (b) shows ERPs elicited by unprimed stimuli.

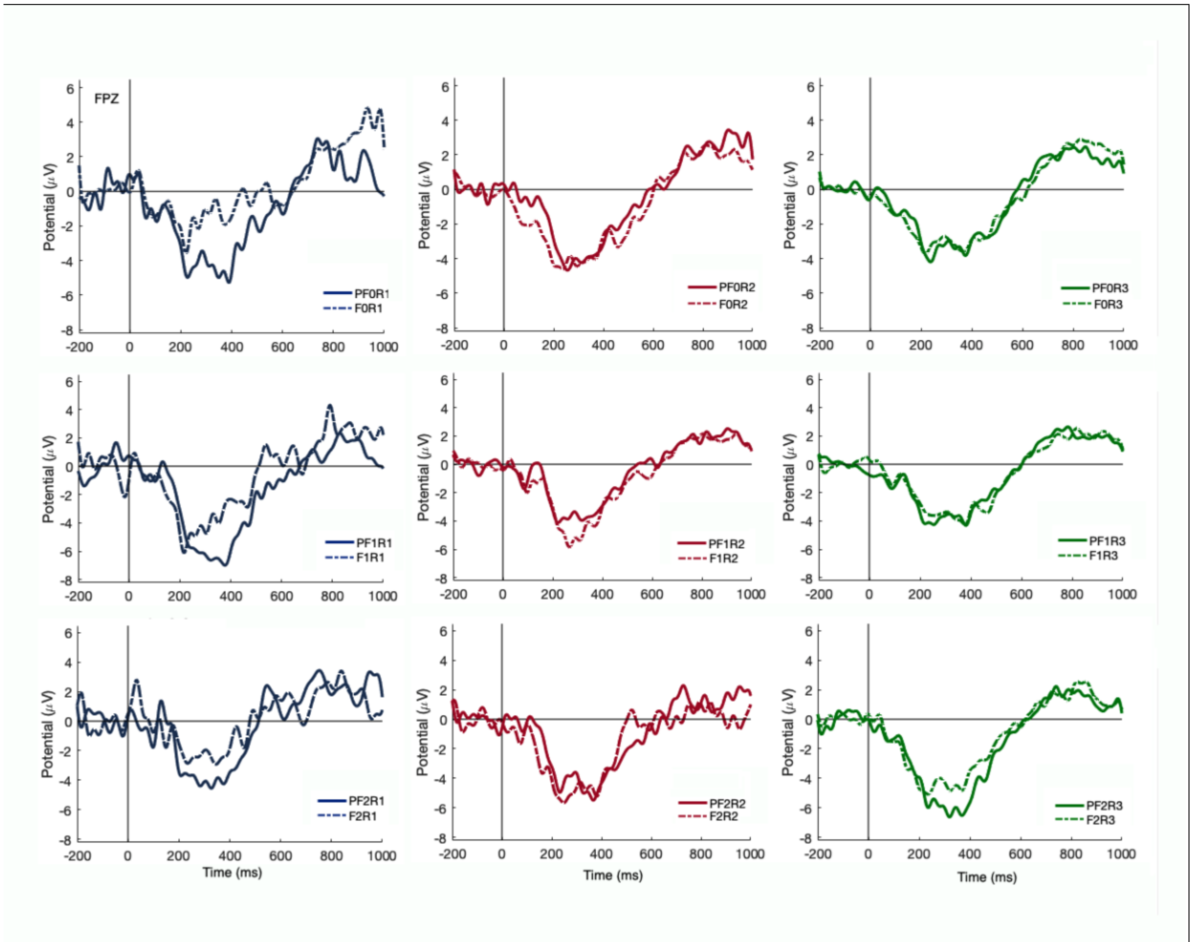


Figure 4.5. Grand-average ERPs elicited by primed and unprimed stimuli at FPZ electrode. R1, R2, and R3 corresponds to repetition 1, 2 and 3 respectively. Whereas F0, F1, and F2 represent clear, slightly blurred and highly blurred images respectively.

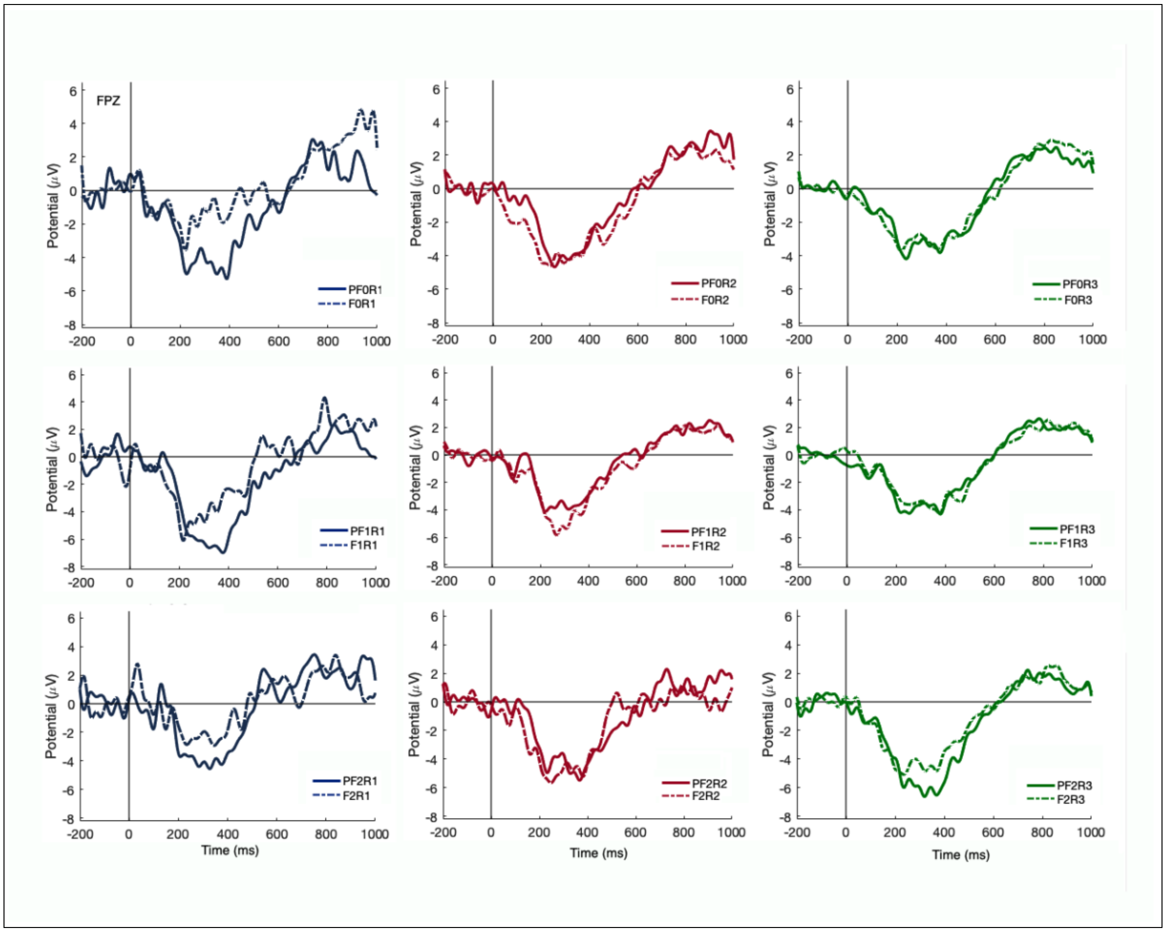


Figure 4.6. Grand-average ERPs elicited by primed and unprimed stimuli at FP2 electrode. Both Figure 5.5 and 5.6 reveal that primed ERPs elicited by first exposure (R1) were more negative than the unprimed stimuli. Similar effect could be seen by highly blurred R3 condition.

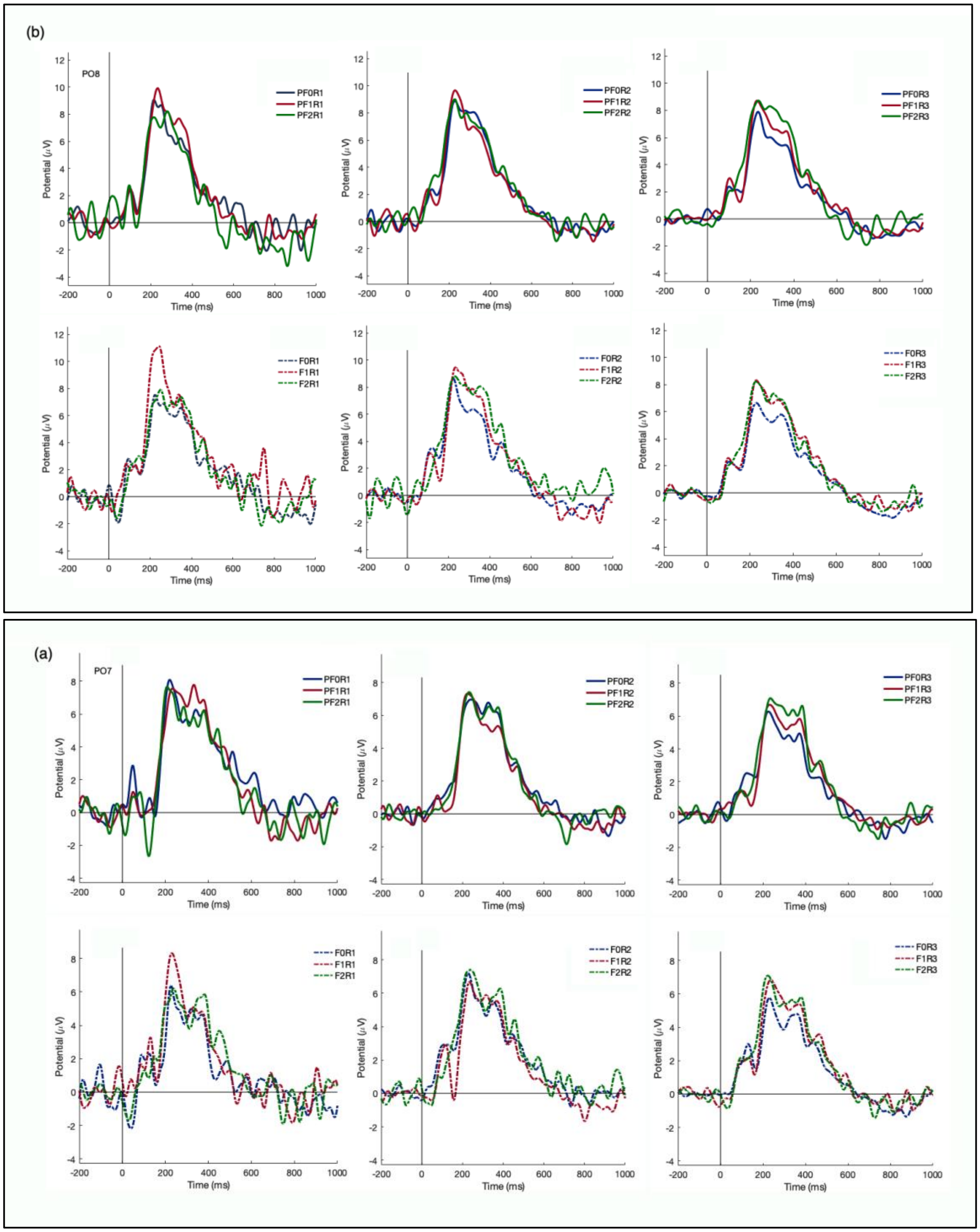


Figure 4.7. The grand average ERP at (a) PO7 and (b) PO8 electrodes reveal that filter condition (perceptual fluency) affected the fluency ERP bilaterally .

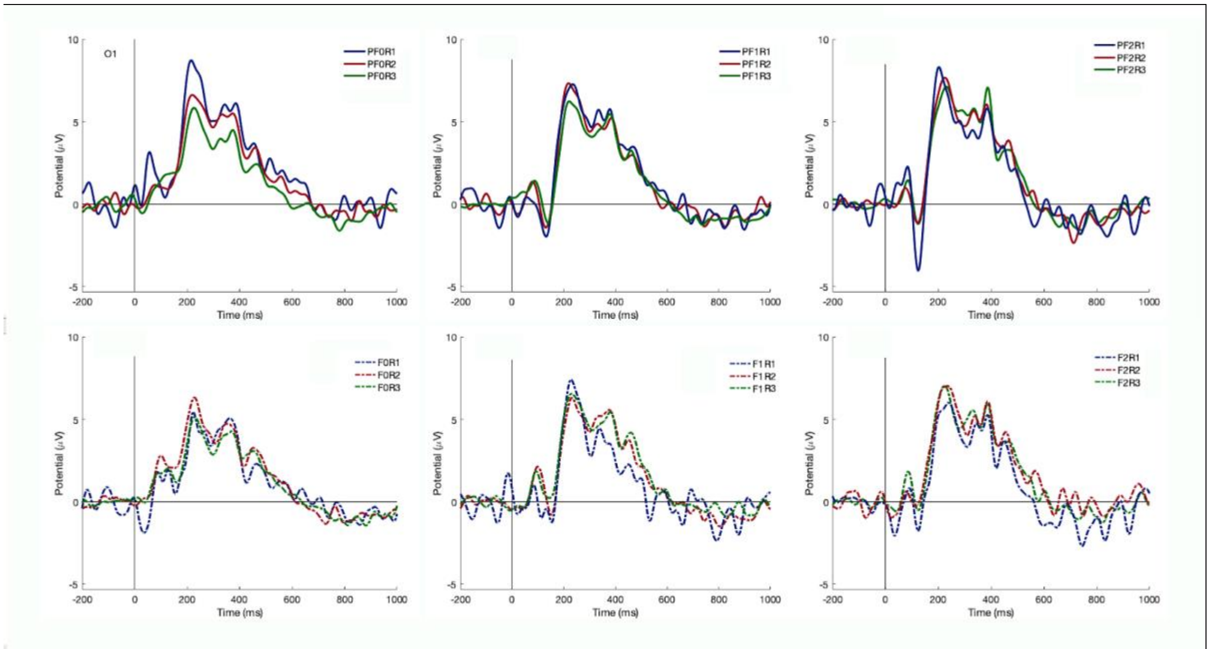


Figure 4.8. Grand-average ERPs elicited by primed and unprimed stimuli at O1 electrode. For primed condition, R3 stimuli were the least negative around 200 ms post-stimulus, particularly for clear images.

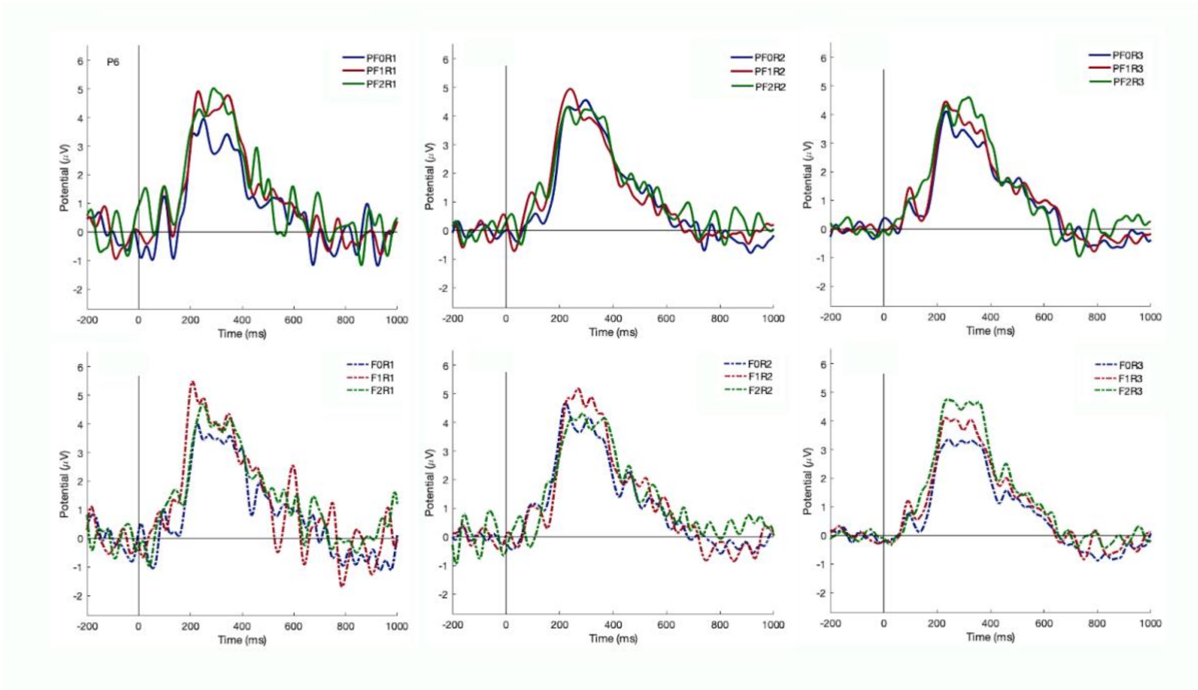


Figure 4.9. Grand-average ERPs elicited by primed and unprimed stimuli at P6 electrode based on perceptual fluency (filter condition). Figure reveals that for both primed and unprimed conditions, ERPs elicited by clear images during third exposure (R3) were the least positive.

4.5 Discussion

The main purpose of the present study was to examine the concept of familiarity by looking at the encoding strategies that influence the process of incidental recognition. Perceptual fluency, conceptual implicit priming and repetition were manipulated to examine their effects on the FN400 and fluency components. ur goal was to discriminate between two processes that have been proposed to elicit the FN400 effect. We hypothesized that if the FN400 captures conceptual implicit memory, then primed stimuli should elicit stronger FN400 effects regardless of the repetition condition. However, if the FN400 reflects familiarity as an exhibit of explicit memory then repeated stimuli should elicit strong FN400 effects regardless of the primed and unprimed condition. Additionally, the variations in perceptual fluency should reveal the differences in the fluency ERP and its influence on the FN400 component. We hypothesized that if familiarity arises from assessing inconsistencies between experienced and expected fluencies (Whittlesea and Williams, 2001a, 2001b), the discrepancies between these fluencies should influence FN400 as well as the fluency ERP. Although, the pattern of our behavioural results and ERP effects provided convergent support for the view that the FN400 component is multiply determined, there are several important points worthy of careful consideration.

Our behavioural results reveal that participants took less time to respond to primed stimuli that were clear or slightly blurred images. However, the highly blurred stimuli showed slower response times when primed as compared to unprimed stimuli (see Table. 4.1). The priming effect influenced the recognition judgments only when images were not clear (i.e. F1, F2 conditions). Interestingly, no significant difference was observed between primed and unprimed conditions when it came to subsequent hit rate in response to clear images. That said, for these two filter conditions, hit rate linearly increased with each repetition (see Figure 4.2). However, this was not the case with the highly blurred images. Participants recalled fewer images that were from the high filter condition and the responses to these stimuli were the slowest. It is apparent from the behavioural results that repetition and clarity contributed to recognition judgments. Our ERP results showed that there was no recollection effect (i.e. no difference between Hits and Misses in the late positive component (LPC)) revealing that the interaction context created by the clarity and repetition conditions only contributed to the fluency and the FN400 components (Leynes & Zish, 2012; Whittlesea & Williams, 2001a, 2001b).

It is important to note that previous studies including our previous work (see Chapters 2 and 3) suggested that the FN400 component is not entirely associated with explicit memory and can be observed during encoding (Griffin et al, 2013; Reder et al., 2009). These studies have shown that FN400 during encoding was not distinct, in terms of time window or scalp localization, from the FN400 component typically observed in recognition phase.

The pattern of ERP results suggests that in some cases the FN400 ERP component was affected by conceptual priming and in other cases it was affected by familiarity (repetition based explicit memory) or even perceptual fluency. Likewise, the fluency ERP showed an interesting pattern of interactions and an effect at posterior sites, which is discussed in the following paragraphs. The fluency and FN400 effects were dissociated by location and time. The distribution of these effects is shown in the head map (see Figure. 4.3). This map reveals that the priming effect was mostly confined to the anterior and right-anterior sites, familiarity was mid-frontal based, and perceptual fluency was bilaterally distributed over parietal and occipital sites (see Figure 4.3). ERP results at the mid-frontal and central electrodes revealed that SH stimuli triggered relatively more positive FN400 potentials than SM stimuli during the first exposure of the stimuli (R1 condition) regardless of whether the stimuli were primed or not or/and blurred or clear (see Figure 4.4a and 4.4b). Additionally, it could be seen that primed highly blurred SH stimuli elicited more positive FN400 potentials for all repetitions whereas unprimed stimuli did not elicit such an effect (Figure 4.4a). Similar results were reported by other studies revealing that conceptual fluency affects behavioural measures of subsequent recognition (Wang et al., 2015; Guo et al., 2015; Paller et al., 2007). It is noteworthy that the conceptual implicit priming factor altered the behavioural responses when clarity was manipulated suggesting that when the perceptual information was altered, subjects tended to rely on conceptual priming more than repetition (Figure 4.4a and 4.4b) These findings are challenging to reconcile with either the view that "FN400 reflects familiarity" or that the "FN400 captures conceptual implicit memory", given that there was a clear distinction between the conditions (primed vs. unprimed, repetition, and filters).

FN400 Reflects Familiarity?

First of all, our results showed that the behavioural indices of recognition were altered by repetition such that hit rate went up with each repetition in all cases except for the highly blurred stimuli (i.e. F2 condition). This finding may suggest that familiarity supported recognition, however, this behavioural effect of familiarity was revealed in the FN400 component only at the mid-central electrode (CZ). However, our ERP results did show that the filter condition also affected the FN400 component. It is noteworthy that SH primed stimuli at the mid-central electrodes were more positive than the SM stimuli.

However, this effect was observed either during the first exposure of the stimulus or when the stimulus was blurred (F1 or F2 conditions) (see Figure 4a and b, also see Figure 4.3). These results indicate that the FN400 ERP is affected by perceptual fluency only under certain conditions (Voss et al., 2012). Likewise, similar observations at other electrodes (anterior and right-frontal) lead to the possibility that different sources of fluency may have interacted with the processes related to familiarity and altered the FN400 component (see Figure 4.3). Therefore, in our study the FN400 did not reflect stimulus-induced familiarity, but instead may have reflected a top-down mechanism triggered by the stimulus (Leynes et al., 2017; Bruett & Leynes, 2015; Wang et al., 2015; Gazzaley & Nobre, 2012).

FN400 Reflects Conceptual Fluency?

Displaying a name or concept before a conceptually related image was expected to evoke a robust FN400 effect. Although conceptual priming affected behavioural responses (i.e. quicker response times to primed stimuli), this effect was not captured by the FN400 component. This observation is contrary to the claim that conceptual memory co-varies with the FN400 component more than familiarity (Paller et al., 2012; Voss et al., 2012). However, our results do support the claim that the FN400 amplitudes do not always correlate with the behavioural measures of conceptual priming (Mecklinger et al., 2012; Stenberg et al., 2009), suggesting that conceptual implicit memory may contribute to FN400 in some cases but not always. The question then becomes what possible system could the FN400 reflect that sometimes involves implicit memory, but not always? Reder and colleagues (2009) argued that the proposed distinction between implicit and explicit memory as two isolated and distinct systems is not valid due to the fact that some implicit and explicit memory tasks share the same memory representations (see a comprehensive review by Reder et al., 2009; also Turk-Browne et al., 2006). They further argued that the distinction is likely task-driven, and that some tasks will involve implicit memory or explicit, or both, depending on the nature of the task (Griffin et al., 2013; Reder et al., 2009; Roediger & McDermott, 1993; Roediger et al., 1990)).

Interestingly, in our study, FN400 values were slightly more positive at the mid-frontal and central electrodes for primed stimuli than unprimed stimuli during the first exposure or when the stimuli were filtered, however, this effect was reversed at the fronto-polar sites (see Figure 4.3). This interaction between the perceptual fluency of the stimuli and conceptual priming has been noted previously by Mollison and Curran (2012), who found that the FN400 amplitudes vary when perceptual information is manipulated and conceptual information is held constant (Mollison & Curran, 2012). This finding supports the idea that different forms of implicit memory (perceptual and conceptual fluency) contribute to familiarity through a discrepancy attribution framework revealing that familiarity is a multiply determined phenomenon (Lucas & Paller, 2013; Mecklinger et al, 2012; Mollison & Curran, 2012).

Fluency Effect and Recognition Judgments

Last but not the least, our results also indicate that perceptual fluency influenced recognition judgments (see Figure 4.2). A fluency ERP driven by an image clarity interaction was observed bilaterally at posterior regions; however, the interaction between fluency ERP and priming occurred more towards central occipital and left parietal regions, whereas the filter conditions interacted with repetition at the right parietal sites (see Figure 4.3). Assessment of the fluency ERPs at the PO7 and PO8 electrodes revealed that this effect was more pronounced for the stimuli that were presented three times, irrespective of whether they were primed or not (see Figure 4.7). Interestingly, the fluency ERP effect suggested graded levels of perceptual fluency such that clear images (F0 condition) showed the least positive voltages (F0 < F1 < F2). However, it is not clear why no such effect was observed during the first and second presentation of the stimuli (R1 and R2 conditions). These results yet again confirm that the fluency ERP is closely linked to perceptual fluency and F0 images being the most fluent used the least neuronal resources, and hence exhibited the least positive amplitudes of all (Lucas & Paller, 2013; Voss et al., 2012; Paller et al., 2007).

Likewise, a similar fluency ERP effect was observed at occipital sites. Additionally, occipital electrodes (particularly O1 electrode) also showed a repetition effect; however, this effect captured an effect of repetition only for the F0 images (see Figure 4.8). Interestingly, the fluency ERP at occipital sites revealed graded levels based on repetition (i.e. R1 > R2 > R3). When the images were blurred the effect of repetition was diminished. Similar results were observed in our previous studies and in other studies that revealed that repetition helps create a context for fluency (i.e. old seem more fluent) (Bruett & Leynes., 2015; Leynes & Zish., 2012). As mentioned earlier, the fluency effect is a cognitive experience that results from interpretive processes (Bruett & Leynes, 2015; Whittlesea & Williams, 2001a; 2001b). Moreover, the interpretive process that underlies fluency is instantaneous and relative to the context; and mostly based on the perceptual features of the stimulus (Lucas & Paller, 2013; Voss & Paller, 2010). Therefore, the different levels of perceptual fluency across the trials produced a norm and expectations based on this norm. These expectations may have been violated upon exposure with clear fluent images (F0) in comparisons with the non-fluent blurred images (F1 or F2),

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suggesting that this effect may have integrated into a feeling of familiarity (Lucas & Paller, 2013; Voss & Paller, 2010; Whittlesea & Williams, 2001a; 2001b). So collectively, these results add support for the notion that perceptual fluency is capable of influencing recognition judgments in certain cases (Whittlesea and Leboe, 2003).

So What Does FN400 Reflect?

The above stated results indicate that neither of the perspectives regarding FN400 completely account for the effects we observed in our study (see Leynes et al., 2017 for similar arguments). However, one cannot ignore the fact that there is substantial evidence in favour of both views.

One possible resolution to the conflicting pattern of results for the FN400 in our study and in the literature may come from the classic "discrepancy attribution hypothesis" (Whittlesea & Leboe, 2003; Whittlesea, 2002; Whittlesea & Williams, 2001a, 2001b). As mentioned earlier, when unexpected fluency is experienced while encountering a stimulus, the violation of expectation is unconsciously attributed to the illusion of familiarity (Whittlesea & Williams, 2001a; 2001b), particularly, when the source of enhanced fluency is not known (Whittlesea & Leboe, 2003; Jacoby & Whitehouse, 1989). If the discrepancy between the experienced and expected fluency is violated, it gets noticed and the participants look for a source to explain the unexpected ease of processing. More likely, the source is attributed to prior experience if the participant is uncertain about the source of the unexpected fluency (Whittlesea & Williams, 2000). However, the feeling of familiarity may not arise if an alternative explanation is available, as there would still be a discrepancy between the experienced and expected fluency but the source of discrepancy would be explainable (Whittlesea & Leboe, 2003). Therefore, it is possible that the discrepancy between different sources of fluencies (highly fluent in terms of perceptual, conceptual or explicit memory) of the stimuli and the complexity of the less-fluent stimuli (blurred images) gave rise to an experience of ‘relative familiarity’ that is observed in the ERP differences -- reflected not only in the FN400 component, but also in the fluency ERP (200 – 400 ms) (Whittlesea and Williams, 2001a, 2001b; Lucas & Paller, 2013; Voss et al., 2012; Paller et al., 2007).

In our study there were multiple sources of fluency (perceptual manipulation, repetition and conceptual priming). The presentation of novel (R1) and familiar (R2 and R3) images, clear (F0) and blurred (F1 and F2) images, and primed and unprimed images may have created a scenario where bottom-up and top-down mechanisms were pitted against each other. These variations may have increased the discrepancies between expectations and actual experiences, which eventually would lead to different levels of familiarity depending upon the stimulus and the relative manipulation associated with it (Whittlesea and Leboe, 2003; Whittlesea and Williams, 2001a, 2001b). For instance, since priming enhances fluency unconsciously, the participant would be uncertain of the source of fluency of these stimuli relative to the less fluent unprimed stimuli. This discrepancy between experienced and expected fluencies could lead to the feeling of familiarity. It is noteworthy that this discrimination of primed and unprimed stimuli was observed only for the FN400 at the frontopolar sites (see Figure 4.6). On the other hand, the ease of processing of a clear image (F0) among a pool of blurred stimuli may also have created a violation of expectations. However, in these cases the source of fluency was not uncertain (image clarity), therefore, this effect was attributed to perceptual fluency, which was reflected in the fluency ERP at parietal sites. Likewise, the ease of processing offered by a stimulus repeatedly seen among stimuli that were only presented once may also create a discrepancy between expected and experienced fluencies. The source of this discrepancy is also not uncertain and therefore reflected only in the fluency ERPs. However, for this to happen, this ERP should discriminate stimuli on the basis of repetition. Indeed, we did observe a discrimination based on repetition in the fluency ERPs at the occipital sites of the scalp (see Figure 4.8).

Although we found that the fluency ERP captured perceptual fluency (Leynes & Zish, 2012; Voss & Paller, 2010), the fluency component captured graded levels of perceptual fluency mostly when stimuli were presented for the third time.

On the other hand, the fluency ERP seemed to be drawn from the repetition effect at occipital sites and even more interestingly, this effect was observed for the clear images mostly (F0) (see Figure 4.8). In this case, R3 images were the least positive in voltage than the other repetition conditions supporting the idea that fluent stimuli use fewer neuronal resources to be processed (Whittlesea & Williams, 2001a; Jacoby & Dallas, 1981). It is interesting to note that the fluency ERP driven by perceptual fluency and the same ERP driven by repetition are separated by scalp location but not time. These results suggest that the processing underlying these different fluencies may overlap ((Lucas & Paller, Reder et al., 2009), interact or even interfere with each other.

4.6 Conclusion

In sum, the fluency ERP co-varied with the behavioural indices revealing that perceptual fluency influences recognition judgments in cases when other sources of familiarity are uncertain (Bruett & Leynes, 2015; Leynes & Zish, 2012). Our results also reveal that manipulation of perceptual fluency alters the recognition judgments even if other sources of fluency are available (i.e. conceptual fluency or repetition). These observations further strengthen the idea that implicit and explicit memory systems do not work in isolation from each other. Depending on the task and stimulus, either of the memory processes could be recruited. The current study suggests that the FN400 is "multiply determined" and is capable of reflecting familiarity (explicit memory driven) or conceptual fluency depending on the task and stimulus (Mecklinger et al., 2014; Paller et al., 2012; 2007). Perceptual fluency is not reflected by the FN400 component, however, it plays a crucial role in shaping the FN400 component. Although our results support the *discrepancy attribution hypothesis framework,* further research is needed to better examine these processes.

Results from these studies suggest that the processes of recognition are closely linked to the processes of encoding. This means that when we attempt to explore these two different memory processes, using electrophysiological indices, one process could be interacting with the other. Findings from our current research indicate that familiarity emerges from the interaction of different forms of implicit memory (perceptual and conceptual fluency) as well as explicit memory (absolute familiarity) and that these processes may originate from different and in some cases shared mechanisms. These findings also indicate that familiarity is more complicated than *single-process*or *dual-process* models of recognition may suggest. Interactions between different sources of fluency and familiarity should be taken into consideration when designing experiments to capture these processes separately. Additionally, we believe that the *Discrepancy Attribution Hypothesis* provides a better understanding of the interactions between familiarity and other co-varying phenomena and therefore new studies should consider this framework in their experimental design (Whittlesea and Williams, 2001a, 2001b).

5 Chapter: General Discussion and Conclusion

The general aim of this thesis was to understand the basic framework of memory encoding and recognition and to investigate whether these two processes share the same neural mechanisms. However, the nature of the association between the processes that lead to encoding and the processes that lead to recognition remains unclear. Few studies have directly investigated whether the encoding strategies during encoding contribute to recognition (Richter & Yeung, 2016; Ritter, 1996). The basic question that we asked in these studies is: what is the role of implicit and explicit memory in setting up the encoding strategies and how do these encoding strategies influence retrieval? Memory models support the idea that familiarity and recollection are largely a subjective experience, however, the association between these processes remains disputed.

The dual-process signal detection (DPSD) model supports the idea that recognition memory relies on two explicit memory processes, familiarity and recollection which are linked to two distinct ERPs; the FN400 and the LPC effect (Rugg et al., 2008; Yonelinas et al., 2002; Friedman et al., 2000; Rugg et al., 1998). This model suggests that the FN400 effect is produced by familiarity-driven recognition and the LPC effect is the reflection of a threshold-based recollection process (Rugg & Curran, 2007; Curran & Cleary, 2003; Curran, 2000). On the other hand, the univariate signal detection (UVSD) model or simply the ‘single-process’ model, proposes that recognition is assessed by the strength of a continuously varying unitary signal, of which, familiarity and recollection lie at the two hierarchical ends (Berry et al., 2008; Squire et al., 2007; Wixted, 2007). Specifically, the model assumes that recognition memory relies on the strength of a continuously varying neural signal that may not rely solely on explicit memory but also may get support from implicit memory (Paller & Voss, 2012; Wilding & Ranganath, 2011; Wixted, 2007; Nessler et al., 2006; Schott et al., 2005; Donaldson, 1996; Tulving & Schacter, 1990). A large body of research has shown that although implicit and explicit memory mechanisms are dissociable, it is difficult to disentangle them during a recognition task. To understand the mechanisms that support recognition memory, its reliance on explicit or implicit memory, and how encoding is linked to recognition, we conducted three studies. Significant results from these studies are discussed below.

5.1 Significant Findings

5.1.1 Experiment 1

Experiment 1 examined the role of the mid-frontal FN400 effect in regards to familiarity-driven recognition. According to the DPSD model, recognition memory relies on two distinct processes; familiarity and recollection. The mid-frontal FN400 effect reflects familiarity-driven recognition, whereas the late positive component (LPC) reflects a threshold-based all-or-none process all known as recollection. In contrast, our ERP results indicated that the FN400 component during encoding may have indexed conceptual fluency (implicit memory) and not familiarity (explicit memory) (Voss & Paller, 2010a; 2007). This finding is in agreement with the classic view of Jacoby and Dallas (1981) that familiarity stems from conceptual attributions based on previous experiences (Jacoby & Dallas, 1981). Additionally, we observed that during the encoding phase, subsequent recognition was related to a “fluency effect” such that subsequently-remembered stimuli elicited less positive amplitudes than subsequently-not-remembered stimuli at parietal electrodes during the 200–400 ms interval. We called this a fluency ERP effect because previous studies have linked this ERP difference to the perceptual fluency of stimuli (Bruett & Leynes, 2015; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007). Perceptually more fluent stimuli or more easily perceived stimuli use less neurocognitive resources to process and hence generate less positive ERP amplitudes (Leynes et al., 2015; 2012; Voss & Paller, 2010). The participants in this study did not perform well and perhaps the reason behind our participants' weak performance on subsequent memory is that they were expected to remember 800 pictures and they were tested on only 300 from that pool. Also, studies showed that perceptually too fluent (very common objects) do not leave a strong memory trace (Guo et al., 2015; Beskin & Mulligan, 2013; Paller & Wagner, 2002). Moreover, a shallow task engages a low level of processing, which yields relatively low SM performance as compared to a deep level of processing (Craik et al, 2002; 1972). Interestingly, a similarity in the patterns of encoding and recognition ERPs were observed, suggesting that the process of recognition is closely linked to the process of encoding (Craik, 2007; Craik & Lockhart, 2002). Furthermore, according to the *discrepancy attribution hypothesis*, for a stimulus to be remembered in a shallow task, it has to violate expectations and that violation must be noticed (Whittlesea & Leboe, 2003).

Collectively, we showed that the FN400 does not reflect familiarity exclusively; rather this effect may also reflect conceptual fluency and/or relative familiarity depending upon the context (Bruett & Leynes, 2015; Lucas & Paller, 2013; Paller et al., 2007). These findings are in support of other recognition studies, which have shown that conceptual implicit memory contaminates the neural measures of familiarity when familiarity and conceptual implicit processing co-occur (Paller et al., 2012; Voss et al., 2012; Voss & Paller, 2010a). However, with our paradigm and the type of stimuli, we were not able to disentangle familiarity and conceptual memory from each other. There is evidence that the repetition of a stimulus may initiate several cognitive processes such as perceptual fluency, conceptual fluency, and familiarity because all three of these concepts appear to co-vary with repetition (Lucas & Paller, 2013; Leynes & Zish, 2012; Voss et al., 2012; Paller et al., 2007). Therefore, for our next study, we chose stimuli with no attached meanings to rule out the possibility of pre-existing conceptual memory associated with these stimuli.

5.1.2 Experiment 2

Our main finding from Experiment 2 was that the neural correlates of the conceptual implicit memory process could influence the decisions driven by explicit memory. Experiment 2 investigated whether familiarity is an expression of explicit memory or implicit memory using the same protocol but with different stimuli, i.e. meaningless novel stimuli (fractals) were used instead of pictures of common objects. Our ERP results during encoding showed that the frontal FN400 ERP component that is elicited in the time window (300-500 ms) is distinct from a fluency ERP, which is linked to perceptual fluency and elicited at left parietal sites during the time window (200-400 ms) post-stimulus. Most importantly, no FN400 effect was detected at frontal sites during the recognition test; however, an FN400-like effect was observed which discriminated Hits from Miss significantly but the difference between CR and Hit was not significant. Additionally, a fluency ERP was elicited at right parietal sites. This finding suggests that participants relied on perceptual fluency and not repetition based familiarity to assist their decision-making process for recognition (Leynes et al., 2017; Whittlesea & Leboe, 2003). In other words, a fluency ERP was found to influence the behavioural indices of recognition. Last but not the least, early encoding and recognition ERPs were similar, revealing that the processes during encoding and recognition were linked. Collectively, and in agreement with previous findings, the conceptual and perceptual implicit memory processes influenced the decisions driven by explicit memory.

In sum, these results are compatible with previous findings that showed that the FN400 amplitudes result from a number of processes, which could include familiarity and/or conceptual implicit memory processing depending upon the context (Bruett & Leynes., 2015; Lucas & Paller, 2013; Voss et al., 2012; Paller et al., 2007). It is clear from the findings listed above that recognition judgments relied on perceptual fluency rather than familiarity (Leynes & Zish, 2012; Paller et al., 2012; Rugg et al., 2007; Whittlesea and Price, 2001). The question becomes then how and when recognition relies on fluency and how is fluency linked to familiarity? Therefore, we conducted another experiment to study the link between fluency and familiarity and to better understand these complex processes, which appear to co-vary in the same time window.

5.1.3 Experiment 3

Our previous studies raised several questions concerning the role of perceptual fluency, familiarity and conceptual fluency regarding how and when these processes influence recognition judgments. A subsequent-memory design was used in Experiment 3 to examine the contribution of these processes to recognition judgments. Participants' responses were quicker for clear images (i.e. F0 and F1 condition) that were primed, however, subsequent hit rates for clear images were not affected by conceptual priming. Repetition on the other hand, for the F0 and F1 filter conditions, significantly affected hit rate in a graded manner (i.e. R3 > R2 > R1). Participants recalled fewer images that were from the high filter condition (F2) and the responses to these stimuli were the slowest. It is apparent from the behavioural results that all three conditions i.e. priming, repetition, and clarity affected recognition judgments.

Our ERP results indicated that perceptual fluency, conceptual fluency, and repetition-driven familiarity were distinguishable from each other in terms of the scalp location of their related ERPs during encoding. Conceptual priming (FN400) was significant over anterior and right frontal electrodes, perceptual fluency (fluency ERP) was observed over the posterior sites, and the repetition-driven familiarity effect (FN400) was detected at the central electrode sites. Apart from that, our behavioural and ERP results provided convergent support for the view that the FN400 component is multiply determined and may reflect a number of processes depending upon the stimulus and task. Results from Experiment 3 also validated our previous observations that implicit and explicit memory processing may share at least some neuronal mechanisms.

5.2 Conclusion

Collectively, we found that conceptual priming affected the FN400 but not always; in other cases it was affected by familiarity (repetition based explicit memory) and/or perceptual fluency. Additionally, results from all three studies support the idea that recognition judgments were influenced more by perceptual fluency than familiarity (in this particular paradigm). The question arises what does it mean that the FN400 is elicited by a manipulation in some contexts, but is not elicited by the same manipulation in other contexts? And, how does the fluency of a stimulus influence the mechanisms reflected by the FN400? We believe the Discrepancy-Attribution Hypothesis can best account for these conflicting results (Whittlesea & Williams, 2001a, 2001b).

The *discrepancy attribution hypothesis* proposes that familiarity emerges from the evaluation of discrepancies between the experienced and the expected fluency of processing of a stimulus based on recent events (Whittlesea & Williams, 2001a, 2001b). Thus, key to understanding the processing of these discrepancies is resolving the relationship between fluency and familiarity (Whittlesea & Leboe, 2003; Whittlesea & Williams, 2001a, 2001b; Jacobi & Whitehouse, 1989). Whittlesea and Williams (1998) proposed that familiarity results not only from absolute fluency but also can emerge erroneously when items are processed more fluently than expected relative to recent events.

The discrepancy between expected and experienced fluency is attributed to sources that are either in the past or the present (Whittlesea, 1993). On facing a discrepancy or surprise, people look for the source. If the participant knows the source of discrepancy, the attribution will be registered accordingly. However, an unexplainable discrepancy will more likely be attributed to familiarity (erroneously), which the authors termed 'relative familiarity' (Whittlesea & Leboe, 2003). For instance, in our first study, we found that almost all participants recognized the image of Buddha during recognition. The semantic richness of the Buddha image among all other common objects made it stand out and it was therefore noticed. The discrepancy between the expected degree of fluency when viewing a common object (e.g. a cup) and the experience of the more fluent processing of the picture of Buddha, may have triggered a surprise. Based on participants' performance, it appears that the participant knew the source of their surprise. Hence the discrepancy was attributed to the conceptual fluency associated with Buddha, which was reflected by the amplitude of the FN400. Conversely, in the cases where the source of discrepant fluency not known, the participant may have attributed it to relative familiarity.

Here, we present a model, which takes into account both *the level of processing framework* (Craik et al, 2002; 1972) and *the discrepancy attribution hypothesis* (Whittlesea & Williams, 2001a; 2001b) (see Figure 5.1). The model suggests that memory retrieval varies as a function of the depth of neural processing that takes place at the time of encoding. The "depth" of an encoding process ranges between the shallowest to the deepest level of processing (Craik, 2002). The shallowest level refers to the perceptual processing such as the physical and sensory characteristics of the stimulus and the deepest level is the semantic processing such as comprehension and pattern recognition. Based on this model we speculate that the most "shallow" level of processing would be the task that is capable of activating a neural mechanism capable enough to encode a memory item that is recognizable during the retrieval phase as a familiar item. Whereas, a "deep" level of encoding would be a task that is capable of activating multiple levels of processing that involve multiple neural mechanisms and result in successful recollection when all contextual details are available at the time of retrieval.

In general, meaningful pictures or pictures with names can generate both kinds of fluency as it may generate perceptual fluency for the visual attributes and conceptual fluency for meaning in case of repetition (Voss et al 2010a). In this case, perceptual and conceptual implicit memory co-occurs and the interaction of these processes collectively generates a feeling of familiarity (Paller et al., 2012; 2007; Rugg et al., 2007). In an ideal world, if subjects are presented with a nameless stimulus that has no meanings attached, they are likely to rely on perceptual characteristics of the stimulus only. The repetition of such a stimulus would give rise to perceptual fluency that would be reflected in the fluency ERP.

However, when encountering a series of such events, participants adopt a '*norm'* or an expectation based on the processing of events. As mentioned previously, the processing of discrepancy must be noticed, and expectations must be violated to generate relative familiarity. This means that with every ongoing event, relative familiarity is continuously re-assessed (e.g., ''norms on the fly", Whittlesea & Leboe, 2003). One could assume then that both fluency (e.g., the fluency attribution model, Lucas et al., 2012; Jacoby & Whitehouse, 1989) and familiarity (e.g., the discrepancy attribution hypothesis, Whittlesea and Williams, 2001a, 2001b) are assessed on a trial-by-trial basis.
In fact, participants unconsciously set an actuarial value or "a norm" to assess discrepancies driven by stimuli as well as task and context (Whittlesea and Leboe, 2003; Jacoby & Whitehouse, 1989; Kahneman & Miller, 1986). This generation of a norm is purely subjective and one's pre-experimental associations specific to events may contribute to set up this norm (Kahneman & Miller, 1986).

In our second study (Chapter 3) a fluency ERP at parietal sites was observed during recognition when all the stimuli were meaningless fractals. In that experiment, fluency varied on the basis of repetition, as it was the only source of fluency. It appears from our behavioural and ERP results that random variations in fluency on the basis of repetition produced a fluency effect, which was reflected in the fluency ERP (Leynes & Zish, 2015; Whittlesea and Leboe, 2003; Whittlesea and Williams, 2001a, 2001b). However, in our third study, an FN400 was observed when perceptual fluency was manipulated by presenting both clear and blurry images during the first presentation of the stimuli (Chapter

4). In that case, when perceptual fluency was intentionally varied across trials, the enhanced fluency of some images (in comparison to others) was perceived to be the result of previous experience with the stimulus and experienced as relative familiarity (Jacoby & Dallas, 1981), eliciting the FN400 effect (see Figure 5.1).

On the other hand, we found fractals that were remembered by almost all participants, even though no concept was associated with them (Chapter 3). Thus, the "norm" while encountering these events may have derived from the sum of the subjective expectations generated through processing the perceptual features of the geometrical shapes hidden in these stimuli (fractals). Failing to name the fractal may have caused the participants to focus more on the features of each fractal instead holistically processing the image. It is likely that a familiar shape within each fractal may have triggered richer associations in terms of perceptual or even conceptual fluency. A fractal, which was different in shape from the majority of the stimuli (Julia set) may have caused a violation of the "norm" and triggered an associated neural process. Note that for an experience of familiarity to be assessed, the processing of discrepancy must be noticed, and expectations must be violated (Leynes et al., 2017; Whittlesea & Leboe, 2003). Therefore, fractals, which violated the expectations based on the "norm" that evolved or trials for each individual participant, triggered a discrepancy strong enough to be revealed in the FN400 component during encoding (see Figure 5.1). Perhaps, this is the reason that in some cases the FN400 component has been observed when participants were presented with nameless objects or pseudo words (Stróżak et al., 2016; Groh-Bordin et al., 2006). During recognition, the discrepancy between experienced and expected fluencies was apparently attributed to relative familiarity. This could be one of the reasons that we had a large number of false alarm rates (Whittlesea & Leboe, 2003).

Normally, meaningful images can generate both kinds of fluency as they may generate perceptual fluency for the visual attributes, and conceptual fluency for a meaning or associated concept (Voss et al 2010a). In such cases, perceptual and conceptual implicit memory co-occur and collectively these processes can formulate familiarity (Paller et al., 2012; 2007; Rugg et al., 2007). The question arises how familiarity is assessed when there are multiple sources of fluency? In conjunction with the *discrepancy attribution hypothesis*, Leynes and colleagues (2017) argued that familiarity could emerge from any source that could alter the processing of the "norm". Given that there were multiple sources of fluency in our third experiment (perceptual manipulation, repetition and conceptual priming), the variations in these fluencies may have increased discrepancies between expectations and actual experiences, which eventually may have led to different perceptions depending upon the stimulus and the relative manipulations associated with it (Whittlesea and Leboe, 2003; Whittlesea and Williams, 2001a, 2001b). Although, there was substantial variability in our ERP results, the relative familiarity or unexpected fluency of performance likely arose when there was a violation of expectation (unexplainable ease of processing) and the source of the fluency was uncertain. If true, one would hypothesize that the FN400 potentials for false alarm rates would go up due to relative familiarity. And indeed our behavioural results from Experiment 2 (fractals) did show that false alarm rates were higher than those in Experiment 1 (pictures) revealing that relative familiarity was integrated into an FN400 effect elicited by FA stimuli (see Figure 5.2; also Figure 3.2).

Similarly, relative fluency was reflected by the fluency ERP elicited by FA stimuli at parietal and occipital sites (Whittlesea and Leboe, 2003).

We reported in Experiment 3 (Chapter 4) that primed and unprimed stimuli did not differ in terms of subsequent hit rates in response to clear images. However, for the same stimuli, hit rates increased with each repetition. Strangely, this effect did not get reflected in the FN400 ERP. Instead, the fluency ERP at parietal and occipital electrodes was observed to be associated with this behavioural effect. These results suggest that repetition and perceptual fluency contributed to recognition judgments. It seems that during the 250 ms exposure time of each image (the time the stimulus was on the screen) gave participants only enough time to setup a norm based on the perceptual features of the stimuli and no information beyond that. We suspect that the brief time of exposure made participants rely more on the perceptual features and expectations based on this norm were violated each time they encountered either a clear image (F0) or an image that was repeated multiple times. Since the source of fluency in these cases was known (perceptual fluency and repetition), this effect was integrated into a fluency ERP rather than a FN400 revealing that fluency driven by perceptual features or repetition is capable of influencing recognition judgments under certain restrictions (Whittlesea & Leboe, 2003; Jacoby & Whitehouse, 1989).

Collectively, our findings from all three studies are consistent with the discrepancy attribution hypothesis and support the idea that different forms of implicit memory are capable to influence behavioural judgments of recognition (Voss & Paller, 2017; Mecklinger et al., 2012; Paller et al., 2007). Guided by the discrepancy attribution hypothesis we found evidence that perceptual fluency is linked to familiarity and the role of the fluency is crucial to understanding the heuristics of familiarity (Leboe et al., 2000). Our findings also indicate that familiarity and fluency are two different perceptions that are assessed fluidly relative to other events, and their electrophysiological indices are distinguishable in time and scalp locations. These findings also extend support for the notion that the FN400 is “multiply determined” revealing that familiarity could be driven by multiple sources such as perceptual or conceptual fluency and/or repetition (Voss & Paller, 2017; Voss et al., 2012).

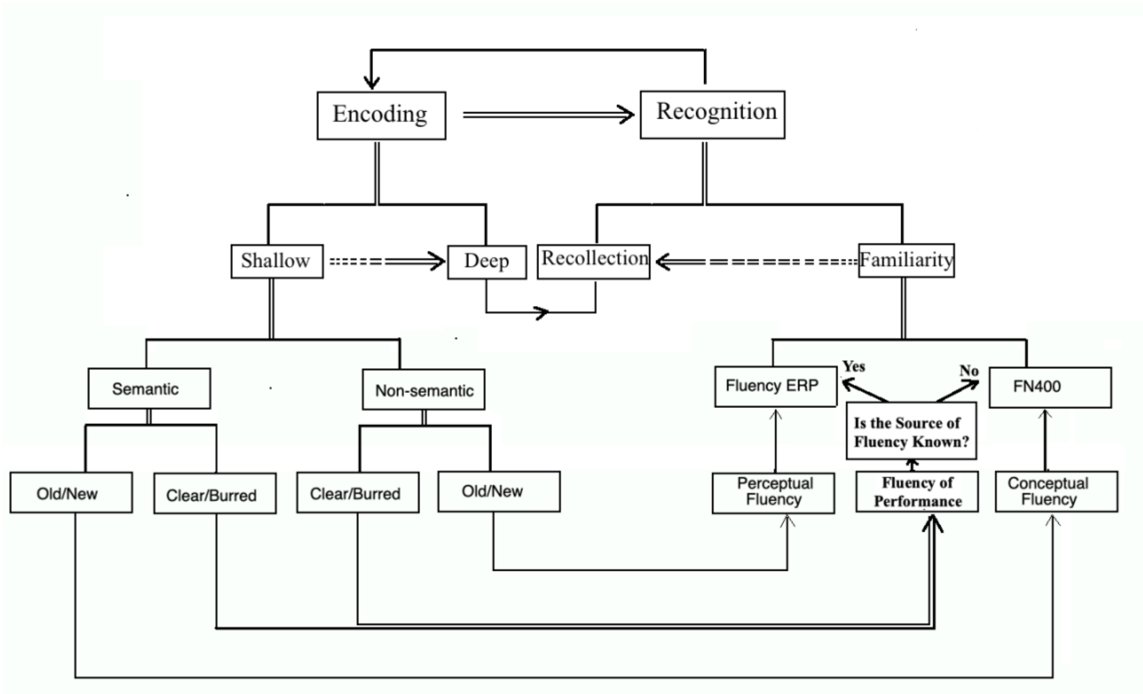

Figure 5.1**:** A schematic diagram of the process of encoding and recognition and the role of level of processing at encoding in terms of the discrepancy attribution hypothesis regarding familiarity.

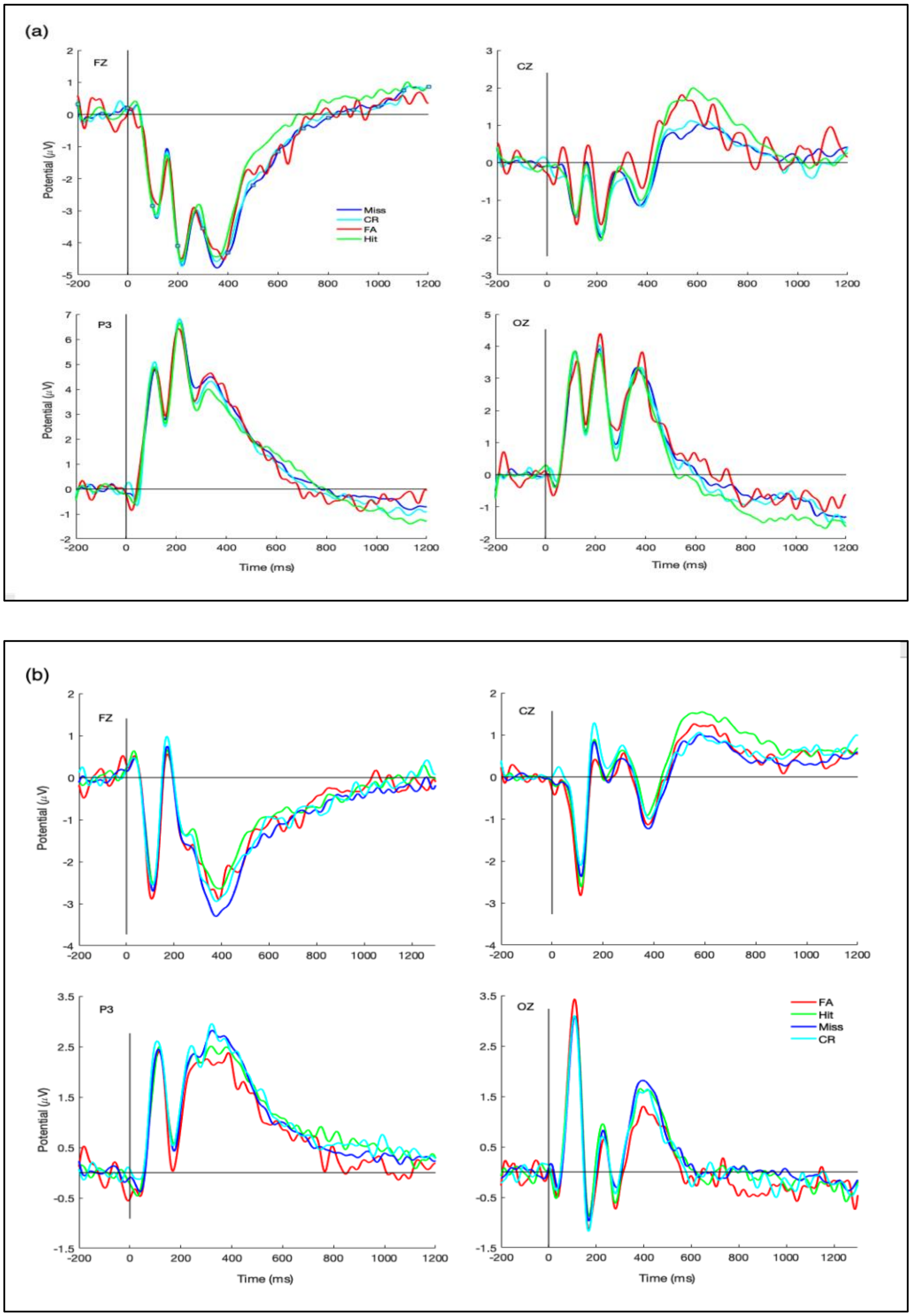

Figure 5.2. Grand average ERPs from (a) Experiment 1 using pictures of common objects and (b) Experiment 2 using pictures of abstract objects (fractals).

A.1 Appendix: Schematic design of stimuli used in Experiment 3

Filter	Repetition	Priming
(F0, F1, F2)	(R1, R2, R3)	(Primed, Unprimed)
Clear Images	36 Images (1 exposure)	18 Primed
		18 Unprimed
	36 Images (2 exposures)	18 Primed
		18 Unprimed
	36 Images (3 exposures)	18 Primed
		18 Unprimed
Lightly Blurred Images	36 Images (1 exposure)	18 Primed
		18 Unprimed
	36 Images (2 exposures)	18 Primed
		18 Unprimed
	36 Images (3 exposures)	18 Primed
		18 Unprimed
Highly Blurred Images	36 Images (1 exposure)	18 Primed
		18 Unprimed
	36 Images (2 exposures)	18 Primed
		18 Unprimed
	36 Images (3 exposures)	18 Primed
		18 Unprimed

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