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Neural correlates of familiarity across time scales and their involvement in explicit memory decisions

Haopei Yang, *The University of Western Ontario*

Supervisor: Köhler, Stefan, *The University of Western Ontario*

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Abstract

Familiarity is a type of memory signal that can support recognition of prior occurrences without retrieval of associated contextual information. It is typically probed with respect to recent laboratory exposure in recognition-memory studies involving human participants. This line of work has revealed several neural correlates including event-related potentials (ERPs) and blood-oxygenation-level-dependent (BOLD) activity in several regions. However, few studies have examined familiarity accumulated outside of laboratory settings through lifetime experience. Hence, it is currently unclear whether similar neural correlates are involved. The fluency-attribution framework decomposes familiarity judgement into automatic and decision-related processes. Since recent and lifetime familiarity are phenomenologically and experimentally dissociable for meaningful stimuli, another question is whether certain neural correlates track both types of familiarity regardless of task relevance --- as a marker of automaticity, and whether they can be distinguished from other neural correlates that are decision-related. To answer these questions, I conducted an ERP and an fMRI study using a common paradigm in which degree of recent and lifetime familiarity could be compared in both task-relevant and -irrelevant conditions. In Chapter 2, I focused on ERP (FN400/N400 and LPC) responses and found that the LPC tracked both lifetime and recent familiarity when they were relevant to the task, while the N400 tracked both types of familiarity regardless of task relevance. The FN400 was sensitive only to task-relevant recent familiarity. In Chapter 3, I focused on BOLD activity in PrC and found that the left PrC tracked both types of familiarity regardless of task-relevance, while a set of frontoparietal regions tracked only task-relevant familiarity. In Chapter 4, I attempted to further delineate the decision-related neural correlates in familiarity judgement by combining the fMRI data collected in Chapter 3 with drift-diffusion modelling (DDM). A model comparison procedure showed that familiarity effects in medial frontal regions were most strongly involved in decision-making, followed by PrC, then by medial parietal regions. Overall, these results revealed temporally (ERP) and spatially (fMRI) distinct neural correlates corresponding to the automatic and decision-related processes in both recent and lifetime familiarity judgement. Furthermore, a hierarchy exists among the decision-related neural correlates.

Keywords

Familiarity, Decision making, Task-relevance, Recognition memory, Medial Temporal Lobe, Perirhinal cortex, Frontal lobe, Parietal lobe, Object concept, fMRI, ERP

Summary for Lay Audience

We can make memory judgements on different time scales. For example, we can judge whether we have seen an apple during our last visit to the supermarket, and we can judge how familiar we are with apples in general. These two types of judgement rely on different information. Scientific studies of memory have mostly focused on the first kind. This line of research has revealed several neural correlates including electrical potentials in the brain recorded with electroencephalogram (EEG) and changes in blood oxygenation level related to neural activity recorded with functional magnetic resonance imaging (fMRI). However, two questions are unclear. First, do these neural correlates also track information supporting the second kind of memory (i.e. how familiar we are with apples in general)? And second, given that we can make both types of judgement when presented with an apple, if one is asked to make one versus the other type of judgement, do these neural correlates behave differently depending on which judgement is being made? In Chapter 2, I showed that for three brain potentials recorded with EEG, one tracked both types of memory information regardless of which judgement was required, another tracked only the information that was relevant to the judgement, and a third selectively tracked information supporting the first kind of memory judgement when a judgement of that kind was required. In Chapter 3, I showed that fMRI activity in a region called perirhinal cortex (PrC) tracked memory information supporting both types of judgement, regardless of which judgement was required. fMRI activity in other regions tracked only the information that was relevant to the judgement being made. In Chapter 4, I combined the fMRI data with a mathematical model and showed that activity in PrC and other regions contributed differently to memory decision. Overall, these results revealed temporally (EEG) and spatially (fMRI) distinct markers corresponding to automatic (i.e. present regardless of if the information is relevant to the judgement) and decision-related (i.e. only present when the information is relevant) processes in both types of familiarity judgement. Furthermore, a hierarchy exists among the decision-related neural markers.

Co-Authorship Statement

The thesis overall benefited immensely from feedbacks provided by Dr. Stefan Köhler and Dr. Ken McRae.

For the study presented in Chapter 2 which has been published in Scientific Reports (Yang et al., 2019). Dr. Stefan Köhler and I designed the experiment and wrote the manuscript. I also collected and analyzed the data. Dr. Ken McRae was involved in designing the experiment, providing the stimuli, and writing the manuscript. Dr. Geoffrey Laforge and Dr. Bobby Stojanoski helped with source localization analyses. Dr. Emily Nichols helped with setting up equipment and with data analyses. All authors reviewed the manuscript.

For Chapter 3 and Chapter 4, Dr. Stefan Köhler and I designed the experiment and wrote the chapters. Dr. Ken McRae also contributed to the conceptualization of the experimental design, providing the stimuli, and writing. Dr. Ken McRae also provided input on the modelling aspect in Chapter 4.

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Table of Contents

List of Tables (where applicable)

List of Figures (where applicable)

List of Appendices (where applicable)

Chapter 1

1 « General Introduction »

The ability to recognize previously encountered objects is an important aspect of human cognition. According to the now-dominant dual-process models of recognition memory, two processes, familiarity and recollection, can support recognition judgements. The classic example that demonstrates the different experiences of familiarity and recollection is the “butcher on the bus” phenomenon (Mandler, 1980). Imagine being on a bus and you encounter someone who seems familiar to you, in that you are sure you have met him before, but cannot recall who he is or where you have met him. This relatively deprived experience of knowing that one has encountered someone or something before without any accompanying information to pinpoint the origin of such feelings is characteristic of familiarity. Upon searching your memory further, you may recall that the familiar person was the butcher from the supermarket you visited the day before. The recovery of the contextual information is characteristic of recollection. Although a consensus on the precise characterization of familiarity has not been reached (Mandler, 2008), from this real-life example and many empirical studies to follow, familiarity can be understood in mechanistic terms by contrasting it with recollection (Jacoby et al., 1989; Mandler, 2008; Tulving et al., 1972; Yonelinas, 2002).

Several neural correlates have been identified for familiarity. For the purpose of the current thesis, I will focus on two types of neural correlates examined in humans. The first type are event-related potentials (ERPs), which reflect time-locked electrical activity recorded on the scalp using electroencephalogram (EEG). ERPs offer excellent temporal resolution while having poor spatial resolution. On the other hand, BOLD activity recorded with fMRI provides millimeter-level spatial resolution while offering poor temporal resolution. Thus, the two approaches complement and inform each other. For ERP correlates, the bulk of ERP studies in the memory literature focused on components roughly within the time window of 300 ms to 800 ms after stimulus onset. Within this time window, studies on recognition memory have revealed two dissociable components, in line with the idea that familiarity assessment is a faster process than recollection

(Boldini et al., 2004): the FN400, a fronto-centrally distributed early component peaking around 400 ms after stimulus onset; and the late-positive complex (LPC), a centro-parietally distributed late component peaking around 600 ms after stimulus onset. While both components have been found to be more positive for stimuli judged to be old compared to those judged to be new, this line of research has generally linked the FN400 to familiarity and the LPC to recollection based on paradigms that were designed to separate the two processes (Curran, 2000; Duzel et al., 1997; Rugg & Curran, 2007; Wilding & Rugg, 1996, 1997; Woodruff et al., 2006, but see Brezis et al., 2016; Ratcliff, Sederberg, et al., 2016; J. L. Voss, Lucas, et al., 2009).

The second type of neural correlates are blood-oxygen-level-dependent (BOLD) signals recorded with functional magnetic resonance imaging (fMRI). Studies on recognition memory using this technique have primarily focused on the medial temporal lobe (MTL) given that lesions in this region tend to produce pronounced amnesia that includes deficits in recognition memory (Squire et al., 2007). In this line of research, one view is that familiarity and recollection depend on distinct MTL structures. In particular, familiarity has been suggested to rely on the perirhinal cortex (PrC) while recollection has been suggested to rely on the hippocampus (Eichenbaum et al., 2007; but see Squire et al., 2007; Wixted & Squire, 2011). However, familiarity effects and more broadly recognition memory effects are often observed in regions outside of MTL as well, including in frontoparietal regions (Horn et al., 2016; Kim, 2013). There is little consensus about the functional role of these frontoparietal regions in recognition memory and how it differs from that of the MTL, in part due to their involvement in numerous other cognitive functions such as decision-making and working memory (Gillebert et al., 2012; Siegel et al., 2011), and the fact that many subdivisions exist within frontoparietal networks (Carlén, 2017; Euston et al., 2012; Ritchey & Cooper, 2020; Scalici et al., 2017; Silson et al., 2019; Simons & Spiers, 2003).

Notably, recognition memory studies typically measure participants' familiarity with respect to study exposure in a laboratory setting. That is, participants' memory judgments are not about whether in general they are familiar with the stimuli, but rather whether they find it familiar with respect to the specific experimental context (Levy, 2012). This

markedly differs from the “butcher on the bus” phenomenon, as the familiarity with the butcher is not necessarily based on a single episode of prior exposure. While most studies have focused on the distinction between familiarity and recollection guided by the theoretical framework of dual-process models, only a small number of studies have investigated lifetime familiarity accumulated over multiple exposures and compared it to recent familiarity measured in study-test paradigms (Bridger et al., 2014; Coane et al., 2011; Duke et al., 2017; Glanzer et al., 1993). What characteristics are shared or different between the two types of familiarity have not been established. And there is evidence for both overlap and dissociation in terms of behavioral and neural findings.

In recognition memory studies using meaningful stimuli such as words, judgements on either type of familiarity can be made. Thus, it is interesting to ask how they contribute differently to memory judgements depending on the task goal. From a decision-making point of view, mechanisms that can flexibly and selectively attend to only task-relevant information are necessary for accurate task performance in general. A critical question then, is whether neural correlates of the two types of familiarity display different levels of sensitivity to task relevance. Using recent exposure judgements as an example, some neural correlates of lifetime familiarity, reflecting its automatic components, may still be present even though these signals are not helpful or may be detrimental to task performance. Alternatively, some other neural correlates, reflecting decision-related processes, may only be present when lifetime familiarity is relevant to the task at hand.

The current thesis aimed to determine in the context of familiarity judgements about object concepts i) whether neural correlates of recent familiarity previously identified in the recognition memory literature are also sensitive to lifetime familiarity; ii) whether neural correlates of familiarity are sensitive to task relevance; and iii) whether the specific involvement of neural correlates of familiarity to the memory decisions can be estimated. Towards this end, I present an ERP study, an fMRI study, and a third study in which I combine the fMRI data with a mathematical model of decision-making. Finally, I discuss how these findings from these studies contribute to our broader understanding of familiarity-based memory judgements and their relationship to existing theories of recognition memory.

1.1 « Psychological and neurocognitive models of familiarity »

Before describing the goals of my thesis in more details, and how I pursued them experimentally, I provide an overview of relevant theoretical work and pertinent evidence. Research on familiarity is conducted mostly within the theoretical framework of dual-process models of recognition memory, which focus on the distinction between recollection and familiarity. Although the current thesis does not focus on such distinction, it is guided by the characterization of familiarity in this framework. In the dual-process literature, familiarity differs from recollection in several aspects. Compared to recollection, familiarity is a continuous signal (Jacoby, 1991; Mandler, 1980; Yonelinas, 1994, 1999a; Yonelinas & Jacoby, 2012; but see Heathcote, 2003; Wixted & Mickes, 2010; Kelley & Wixted, 2001; Wixted, 2007), associated with different phenomenological experience (Gardiner, 1988; Tulving, 1985; Yonelinas & Jacoby, 1995; but see W. Donaldson, 1996; Wais et al., 2008), relatively faster (Hintzman et al., 1998; Hintzman & Caulton, 1997; Hintzman & Curran, 1994; McElree et al., 1999; Gronlund & Ratcliff, 1989; but see Brainerd et al., 2019; S. A. Dewhurst et al., 2006; S. A. Dewhurst & Conway, 1994), and mainly involved in memory of single items (M. W. Brown & Aggleton, 2001; Diana et al., 2006; but see Quamme et al., 2007; Yonelinas et al., 2010). A detailed coverage of this literature is beyond the scope of the current thesis (see Yonelinas, 2002 for a comprehensive review).

Of particular relevance to the current thesis, one influential dual-process model proposes that familiarity is an automatic process while recollection is controlled (Jacoby et al., 1989; Jacoby & Dallas, 1981). Although this distinction was perhaps implied in earlier models (Mandler, 1980), it was made explicit in Jacoby and Dallas' model. This model views familiarity as a fluency-attribution process. The conscious experience of familiarity is proposed to originate from participants experiencing increased processing fluency and interpreting such fluency as a result of prior exposure. Numerous behavioral studies have provided support for this view (Jacoby & Whitehouse, 1989; Johnston et al., 1985, 1991; Macken & Hampson, 1993; Schmitter-Edgecombe & Nissley, 2000; Wolters & Prinsen, 1997; Yonelinas, 2001). For example, studies using a process-dissociation paradigm

(Jacoby, 1991) have shown that the estimation of the automatic process (i.e. familiarity) was not affected by whether participants studied the stimuli under full or divided attention while the estimation of the controlled process (i.e. recollection) was (Schmitter-Edgecombe & Nissley, 2000; Wolters & Prinsen, 1997). Although this insensitivity to an attention manipulation speaks to the automaticity of familiarity signals, a more specific link between fluency and familiarity comes from studies demonstrating that manipulating fluency can affect familiarity judgements (Jacoby & Dallas, 1981; Jacoby & Whitehouse, 1989; Johnston et al., 1985, 1991). For example, Jacoby and Whitehouse (1989) combined a repetition- priming manipulation with a recognition-memory paradigm. As in a typical recognition paradigm, participants studied a list of words, and then were asked to make old/new judgements in a test phase. The critical manipulation was that before some of the words in the test phase, a prime (i.e. "context word" in Jacoby and Whitehouse) could be presented. These primes could either be the same words as the following target words (i.e. "match") or different words (i.e. "nonmatch"), and could either be presented supraliminally or subliminally. The main finding was that when the primes were presented subliminally, new words preceded by matching primes were associated with a greater proportion of false alarms compared to those preceded by nonmatching primes, while the opposite pattern was found when the primes were supraliminal. The effect in the subliminal condition was interpreted as unconscious processing of the matching prime improving processing fluency of the following target word, which was interpreted by the participants as familiarity. The effect in the supraliminal condition could reflect recollection, which may have provided the correct contextual information to reject an "old" response based on the experimental manipulation of fluency (Rotello et al., 2000).

One may argue that the fluency effect induced with priming is still mnemonic in nature, and hence it is not entirely surprising that it affected familiarity judgements. From this perspective, perhaps the strongest evidence for the fluency-attribution account comes from studies that manipulated fluency without introducing any new mnemonic information prior to the recognition judgement. In Johnston et al. (1985), stimuli presented during the test phase of a recognition-memory paradigm were masked with visual noise, which gradually dissipated. Participants were asked to identify the word as

soon as possible and follow the identification with an old/new recognition judgement. The key finding was that words (and nonwords in their second experiment) identified as old were identified faster than those that were new, regardless of the objective old/new status. Johnston et al. (1985) concluded that participants misattributed perceptual fluency to prior exposure (but see Johnston et al., 1991; Wagner & Gabrieli, 1998). Overall, this line of research demonstrates that fluency signals, mnemonic or not, affect familiarity judgement. The current thesis focuses on the mnemonic kind.

The fluency-attribution framework put forward by Jacoby and colleagues has been incorporated in a recently developed neurocognitive model (Bastin et al., 2019), hereafter referred to as the IM (integrative memory) model. This model synthesizes current knowledge from patient and neuroimaging research to broadly characterize neural substrates supporting memory judgement into two systems. A representational core system consisting of primarily medial temporal lobe that contains the raw memory signals ("reactivated content" as called by Bastin et al.). In keeping with the line of earlier work reviewed above, for familiarity, these signals are referred to as fluency, which captures the characteristic of it being relatively automatic and not necessarily mnemonic in nature. These fluency signals can then be interpreted as and "attributed" to prior exposure by an attribution system consisting primarily of frontoparietal regions, supporting the phenomenological experience and the explicit judgement of familiarity. A critical extension of Bastin et al. (2019) from earlier versions of fluency-attribution theory is that the attribution system includes a host of cognitive and metacognitive processes generally engaged during conscious usage of any form of memory signals (e.g. familiarity or recollection) and even non-memory signals. This broad conceptualization of an attribution system and the brain regions putatively assigned to it share some overlap with other previously suggested systems that were based on the theoretical concepts of "cognitive control" (Miller, 2000; Zanto & Gazzaley, 2013) and "working-with-memory" (Moscovitch, 1992).

Inherent in the general framework of fluency-attribution are two aspects of familiarity judgement, an automatically computed fluency signal and an attribution system that act upon such signal according to task goals. This division between automatic and decision-

related processes involved in familiarity judgement provides the guiding framework for the current thesis. A novel question asked in the current thesis is whether neural correlates of familiarity can be tied to the automatic or the decision-related component. To begin to address this question, I first summarize extant research from several relevant fields using task-relevance as one organizing factor in my review. The other organizing factor is time scale (recent versus lifetime). As most research has focused on recent familiarity, research on lifetime familiarity encompasses a much smaller number of studies from several different fields. Nevertheless, I believe that a synthesis across literature with these two organizing factors in mind can provide a hint on the knowledge gaps in our understanding of familiarity.

For the following sections on neural correlates, I will focus primarily on the FN400/N400 and the LPC for ERP, and MTL, in particular PrC BOLD activity for fMRI. In the following two sections, 1.1.1 and 1.1.2, I review ERP and fMRI findings on task-relevant recent familiarity from recognition-memory literature. Studies about task-relevant lifetime familiarity is covered in section 1.2. These sections focus on neural correlates of task-relevant familiarity (i.e. explicitly judged), while section 1.3 reviews neural correlates of task-irrelevant familiarity. Section 1.4 touches on relevant findings from electrophysiological studies on non-human animals. Then in section 1.5 and 1.6, I attempt to provide a theoretical decomposition of the attribution system proposed in the IM model by drawing insights from decision-making literature.

1.1.1 ERP correlates of task-relevant recent familiarity

In ERP research of recognition memory, the FN400 and the LPC are commonly viewed as neural correlates of familiarity and recollection, respectively (Curran, 2000; Rugg et al., 1998; Woodruff et al., 2006). Results in support of this dual-process interpretation have been obtained in several behavioral paradigms that are designed to separate recollection from familiarity. For example, Curran (2000) asked participants to study a list of words which could either be singular or plural. Then in a test phase, participants were asked to make recognition judgement on a mixed list of studied, similar, and new words, with the similar words being those studied with switched plurality. The correct endorsement of stimuli with consistent plurality between study and test as old is assumed

to depend on recollection. FN400 amplitude was similar for stimuli judged to be old regardless of whether the plurality had switched and was more positive than that of correctly rejected new stimuli. On the other hand, LPC amplitude was similar for stimuli that had switched plurality and judged to be old as well as correctly rejected new stimuli, while stimuli with consistent plurality judged to be old elicited a more positive amplitude. Similar results have also been found with remember/know (RK) paradigms, which distinguish familiarity from recollection based on phenomenological experience. For example, in Woodruff et al. (2006), the response options at test included "remember", which designate successful retrieval of any contextual information pertaining to the study episode. If contextual information was absent, participants were asked to choose from four options representing a cross between old/new and confident/unconfident, representing different degrees of (recent) familiarity. The FN400 amplitude differentiated the four levels of familiarity, while the LPC amplitude differentiated between the "remember" and confident old responses, which presumably reflected recollection.

Interestingly, when comparing the effect of confidence, collapsed across the old/new judgement, Woodruff et al. (2006) found a parietal effect similar to the LPC. Although this effect appeared to be more lateralized to the right than the LPC effect associated with recollection in the same study, it suggests that LPC effects observed in other studies may be related to processes other than recollection. Indeed, several other studies have reported LPC effects that cannot be easily linked to recollection (Brezis et al., 2016; MacKenzie & Donaldson, 2007; J. L. Voss & Paller, 2007; Yovel & Paller, 2004). For example, Brezis et al. (2016) reasoned that LPC effects observed in RK paradigms were often confounded by confidence, since recollection tends to produce more confidecent recognition (Yonelinas, 2002). To eliminate the potential confound of confidence, they used a two-stage RK paradigm in which participants were first asked to make an old/new decision and indicate their confidence, then followed by a RK judgement if they deemed the stimulus old. This paradigm allowed the authors to place RK contrast, which probed for the presence of recollection, in opposition to confidence, which can be interpreted as a proxy for memory strength/familiarity. The main result was that confident-K responses were accompanied with more positive LPC amplitude than unconfident-R responses. Thus, in contrast to the dual-process interpretation which links the LPC to recollection,

this component may be more generally sensitive to the strength of memory signals, at least when probed with RK paradigms.

A mechanistic account of the LPC effect that can accommodate these divergent findings has been provided by Ratcliff et al. (2016), who used a sequential sampling model (i.e. drift-diffusion model, see section 1.6 for more details) to estimate parameters representing latent decision processes. They first classified old/new status of individual trials using single-trial EEG data from either the FN400 time window or the LPC time window. The classifier performed above chance for both time windows, replicating previous old/new effects observed in both components. However, when sorting trials according to the classifier results and separately fitting the drift-diffusion model for each half of the sorted trials, the drift-rate differed only between the two halves when the trials were sorted using data from the LPC time window. This suggests that the LPC may index decision-making processes during memory judgement rather than being an exclusive marker of recollection. Another relevant ERP component corroborating this interpretation of the LPC comes from studies on perceptual decision-making. The centro-parietal positivity (CPP) is an ERP component with a scalp distribution and polarity similar to the LPC (O'Connell et al., 2012; Twomey et al., 2016). Although its involvement in decision-making is often revealed by analyzing the data time-locked to responses, when the data were aligned with respect to stimulus onset, it occupied a similar time window as the LPC and demonstrated selectivity to task-relevant information (Twomey et al., 2016). However, differences in theoretical conceptualizations and experimental paradigms across the fields of recognition-memory and decision-making make a direct comparison of the two components difficult.

Aside from the FN400/LPC distinction, there is also an unresolved debate on whether the FN400 is different from N400, which is another ERP component mostly studied in the literature on semantic memory (Bridger et al., 2012, p. 400; Stróżak et al., 2016; J. L. Voss & Federmeier, 2011a; Wolk et al., 2004, see 1.3.1 for more details). Because the two components share similar polarity and time window, on a technical level, the distinction is based entirely on scalp distribution. Although principled ways to distinguish scalp distribution do exist (McCarthy & Wood, 1985), a lack of comparison of

topographies across studies makes it difficult to verify the reliability and generality of topographical distinctions reported in single studies. On the other hand, given that the two components can be distinguished even with such poor spatial resolution, it indicates that at least in certain scenarios, they originate from different neural substrates. For this reason, I will treat them as separate components when discussing specific studies in the following sections.

To summarize, familiarity effects have been found to modulate the FN400, the N400 to the extent that it can be distinguished from the FN400, and the LPC, but probably for different reasons. Considered within the IM model, emerging evidence suggests that the LPC may be more related to decision-making processes of the attribution system. Whether the earlier components can be linked to automatic signals (i.e. fluency) is less clear. Furthermore, the brief review above focuses on task-relevant recent familiarity. Thus it is also unclear whether these ERP components have a similar relationship to lifetime familiarity, and whether they are modulated by task-relevance which would be expected for neural correlates of the attribution system.

1.1.2 fMRI correlates of task-relevant recent familiarity in PrC

A large body of neuroimaging studies has focused on the medial temporal lobe (MTL) and has provided substantial although not unanimous support for the dual-process account of recognition memory. One prominent view is that PrC is involved in object familiarity while parahippocampal cortex carries contextual information, with both types of information being combined in the hippocampus to support episodic recollection (Hsieh et al., 2014; Kirwan & Stark, 2004; Kafkas et al., 2017; Ranganath et al., 2004; Yonelinas et al., 2001; for reviews, see Mayes et al., 2007; Eichenbaum et al., 2007; also see Squire et al., 2007; Murray et al., 2007; Cowell, 2012; Bussey & Saksida, 2007 for alternative conceptualizations of MTL functions). In an early fMRI study, Henson et al. (2003) summarized four studies showing that PrC BOLD activity distinguished whether the stimuli were presented recently or not. In two of the studies (Cansino et al., 2002; Rugg et al., 2003), the PrC effects were also shown to be insensitive to retrieval of contextual information, which provides support for its involvement in familiarity but not in recollection. Interestingly, in Henson et al. (2000), a task-irrelevant repetition

suppression effect was found in PrC as well, suggesting that its signal may reflect the automatic component of familiarity. Other studies have also reported PrC effect of recent familiarity in multiple behavioral paradigms. Montaldi et al. (2006) asked participants to make RK judgements to recently studied pictures of scenes and novel ones. Following the framework developed by Yonelinas (1994), the K responses were also accompanied by a confidence judgement. A linear contrast along levels of confidence was used to probe for a familiarity effect, while a binary contrast between R responses and K responses with the highest level of confidence was used to probe for a recollection effect. The familiarity effect was found to be significant in PrC, where no recollection effect was found. The hippocampus showed the opposite pattern. In Daselaar et al. (2006), participants were asked to make old/new responses followed by confidence ratings in response to a mixed list of words that were either studied recently or not. Based on participants' responses, this resulted in six levels of "oldness" ranging from "definitely new" to "definitely old". Consistent with the dual-process account (Yonelinas, 2002), a linear change in BOLD activity along the six levels, indicating familiarity, was found in PrC, while a nonlinear increase in activity to the highest level of "oldness", indicating recollection, was found in posterior hippocampus. However, the same linear effect was also found in anterior hippocampus, suggesting the simple picture of mapping recollection to hippocampus and familiarity to PrC may not always hold (Squire et al., 2007; Wais et al., 2006). Indeed, it has also been reported that when the behavioral task promotes unitization between pairs of individual stimuli or between stimuli and context, PrC can also support the seemingly associative memory judgement that has typically been used to index recollection (Diana et al., 2010; Staresina & Davachi, 2006).

Overall, although PrC is certainly not the only structure that is sensitive to familiarity (see Horn et al., 2016 for a review) and under some conditions there may also be recollection related signals in it, PrC has been implicated relatively consistently in fMRI studies on task-relevant recent familiarity. However, it is less clear whether PrC also tracks lifetime familiarity and whether task-relevance affects its ability to do so.

1.2 Task-relevant lifetime familiarity

Early work done by Tulving made the distinction between semantic and episodic memory and tied them to different conscious states (Tulving, 1985). Along with such a theoretical distinction, the RK paradigm now commonly used to separate recollection from familiarity was originally developed to separate these states of consciousness and by extension semantic and episodic memory. From this historical perspective, one can say that familiarity, now commonly studied in episodic recognition paradigms, has its origin in semantic memory research. Research on semantic and episodic memory has since developed into largely segregated fields with their own definition of familiarity. While research on episodic memory has studied familiarity arising from recent exposure typically confined to experimental settings, research on semantic memory has studied familiarity arising from cumulative exposure to concepts happening outside of experimental settings, and it has produced a number of normative databases that include lifetime familiarity ratings of concepts in different languages (McRae et al., 2005; Moreno-Martínez et al., 2014a; Schröder et al., 2012a). These databases have consistently shown that lifetime familiarity ratings for object concepts (i.e. words representing concrete objects) are positively correlated among people from the same cultural background, which is perhaps not surprising given that people from the same culture likely have been exposed to many common objects in similar ways. But such a positive correlation does provide some indication of ecological validity. Lifetime familiarity ratings also tend to be positively correlated with word-frequency, which has been used as a proxy for lifetime familiarity in some studies (e.g. Bridger et al., 2014).

Judgements of lifetime and recent familiarity differ in a number of ways. The most obvious difference is the time scale of experience. While recent familiarity judgement is usually confined with reference to a recent experimental study phase, lifetime familiarity judgement draws upon experience spanning years or even decades. Another potential difference is the link to semantic knowledge. When we encounter object concepts in real life, we often gain semantic knowledge. For example, routine usage of computers not only makes you acquire a sense of familiarity with computers but also leads to more knowledge, such as about their functions, their components, etc. Such gain in knowledge

usually does not occur in experimental settings where recent familiarity is built up by mere repetition with limited opportunity to acquire new pertinent knowledge. The role of episodic contextual information should also be considered. Recent familiarity signals probed with recognition memory paradigms are thought to be devoid of contextual information, while it is less clear whether lifetime familiarity shares the same characteristics. Some studies have suggested that it does (Bowles et al., 2016a; Duke et al., 2017). As Mandler (2008) puts it: "familiarity is not a well-grounded theoretical concept--- it is the best available common-language label for describing a psychological phenomenon" (p. 391).

This is perhaps even more apt for lifetime familiarity, which, relying on a more open-ended and subjective judgement, makes it more difficult to characterize it with behavioral data alone. Although it is beyond the goals of the current thesis to examine all of these differences, I hope the characterization of neural correlates of lifetime and recent familiarity can provide some helpful insight for future research to better characterize familiarity, especially lifetime familiarity.

1.2.1 ERP correlates of task-relevant lifetime familiarity

ERP studies that included explicit judgement of lifetime familiarity or similar measurement are rare. Although several studies in the face perception literature have included judgement related to lifetime familiarity, such as about fame or personal familiarity, these studies tend to focus on earlier neural correlates known to be selective to faces (e.g. N170 and N250: Caharel et al., 2006, 2014; Huang et al., 2017; Miyakoshi et al., 2008). Since the current thesis focuses on familiarity signals for other stimulus types, with a large portion of existing evidence coming from studies using object concepts probed with words and reporting later ERP components, the specialized literature on face perception and recognition will not be covered extensively (for a recent review, see Ramon & Gobbini, 2018). One particularly relevant study on task-relevant lifetime familiarity that did use face stimuli but focused on later ERP components was conducted by Nessler et al. (2005). They conducted three experiments to compare ERP correlates of lifetime (semantic) familiarity, perceptual fluency, and recent (recognition-related) familiarity with the task-relevance of each signal being manipulated across

experiments. Task-relevant lifetime familiarity was operationalized by contrasting face stimuli explicitly judged to be famous or non-famous, which revealed a widespread effect with a frontal distribution similar to the FN400. Furthermore, this effect was topographically indistinguishable from the effect of recent familiarity, defined by comparing repeated face stimuli correctly judged to be old and non-repeated face stimuli correctly judged to be new, suggesting a common set of neural substrates underlying both types of familiarity. Nessler et al. (2005) also found a marginally significant effect when comparing the lifetime familiarity under task-relevant and -irrelevant conditions across experiments, also in the FN400 time window, potentially due to recruitment of attribution processes in the task-relevant condition. However, this cross-experiment comparison was not performed in the later LPC time window. Thus, based on this and other related studies (Miyakoshi et al., 2008; Renoult et al., 2015) it is unclear whether the later component would also show a task-relevance effect for lifetime familiarity as would be expected if the LPC is involved in decision-making (Ratcliff, Sederberg, et al., 2016).

1.2.2 fMRI correlates of task-relevant lifetime familiarity in PrC

Only a few fMRI studies with a primary focus on the MTL have probed for lifetime familiarity in task-relevant conditions (Yassa & Stark, 2008; Duke et al., 2017; Gimbel et al., 2017; but see Ramon et al., 2015). In Yassa and Stark (2008), participants performed a continuous recognition task. Non-famous pictures were presented 1 to 4 times and they were asked to distinguish first presentations from later repetitions with an “old/new” judgement. Critically, stimuli also included famous pictures which were to be given the same “old” response as repeated non-famous pictures in the recognition task. Participants were also exposed to these famous pictures in a pre-scan session. A comparison of BOLD activity between famous and non-famous pictures can be thought as a contrast of lifetime familiarity. This comparison revealed the presence of lifetime familiarity signals in the right PrC and right parahippocampal cortex (PhC). Interestingly, the effect in PrC also showed an anterior/posterior difference, with famous pictures evoking lower activity in the right anterior PrC but higher activity in the right posterior PrC. Note that although the authors focused on the comparing famous pictures with the correct rejection (i.e. 1st presentations) of non-famous pictures, this was in fact confounded with the different

degree of recent familiarity because famous pictures were also presented once before the recognition task in a preexposure phase. A better-controlled comparison would be between non-repeated famous pictures and non-famous pictures that were repeated once in the recognition task, the results of which can only be inferred from the figures they provided which seem to show the same heterogeneity of PrC effects of lifetime familiarity. Another limitation is in the comparison itself. When making an "old" response towards a repeated non-famous picture, participants could rely solely on recent familiarity and lifetime familiarity signal might be irrelevant to the task. Thus, one could argue that the comparison between famous and non-famous pictures in Yassa and Stark (2008) did not represent a purely task-relevant contrast of lifetime familiarity, although in all fairness, task-relevance was never the focus of that study.

Two later studies also demonstrated the involvement of MTL in tracking task-relevant lifetime familiarity. In Gimbel et al. (2017), participants made RK judgements on non-famous faces that were either recently studied or novel. In a separate task, they also made RK judgement on famous faces and foils. A comparison between "know" (K) and "new" (N) in the latter task constituted a task-relevant contrast of lifetime familiarity, which revealed a significant effect in PhC and several frontoparietal regions, as well as a numerical trend in PrC. In a study that the current thesis builds upon, Duke et al. (2017) used words representing object concepts from a normative database (Cree & McRae, 2003; McRae et al., 2005) and asked participants to provide cumulative lifetime familiarity ratings on these concepts modelled after the judgement in those database. Similarly, recent familiarity was probed with a cumulative judgement of relative presentation frequency of old words presented for different number of times in a study phase. An increase in BOLD activity with increasing level of judged lifetime familiarity was found in PrC, but not in PhC. Moreover, the same PrC cluster showed decreasing activity with respect to recent familiarity as demonstrated by a conjunction analysis. One advantage of this study was that by using cumulative judgement, the tasks required participants to make fine-grained decisions on graded signals which minimized the effect of episodic context. Moreover, by including only studied stimuli in the recent familiarity judgement and new stimuli in the lifetime familiarity judgement, it avoided ambiguity in terms of which signal contributed to the memory judgement. In contrast, in Yassa and

Stark (2008), because of the pre-scan exposure to the famous pictures, there remained the possibility that participants could use either lifetime or recent familiarity to arrive at a correct judgement.

Although results from these few studies were not in full agreement, likely due to use of different stimulus material (faces versus object concepts) as well as different experimental markers of lifetime familiarity (fame versus normative familiarity ratings), they converge on highlighting the involvement of PrC in tracking task-relevant lifetime familiarity. A limitation of these studies is that the analyses were done only for task-relevant conditions, whether PrC also tracks task-irrelevant familiarity remains unclear, which is the focus of the next section.

1.3 Behavioral and neuroimaging findings of task-irrelevant familiarity

According to the fluency-attribution model reviewed above, judgements of recent familiarity can be explained by attributing the increased processing fluency to prior exposure (Jacoby, 1991; Jacoby et al., 1989). This idea of processing fluency is also the basis of priming effects, a form of implicit memory (Henson, 2003). Behaviorally a priming effect typically is operationalized as increased speed and/or accuracy in indirect memory tasks, which differs from recognition-memory paradigms since they require no judgement about prior occurrences. Perceptual fluency was emphasized in early conceptualization of the fluency-attribution model (Jacoby & Dallas, 1981). The contribution of perceptual fluency could be demonstrated with paradigms that visually masked the test stimuli and manipulated the clarity of the mask (Johnston et al., 1985; Whittlesea, 1993). It was later shown that both perceptual and conceptual processes can result in fluency signals that form the basis of familiarity judgement (Duke et al., 2014; W. Wang et al., 2015) and their relative contribution depends on task instructions and the type of stimuli used (Lanska et al., 2014), although under standard conditions, conceptual processes tend to be the main contributor (Nessler et al., 2005; see Wagner & Gabrieli, 1998; Yonelinas, 2002 for reviews). For example, in Wang and Yonelinas (2012), interindividual differences in familiarity, as estimated with ROC or RK paradigm, were positively correlated with interindividual differences of conceptual priming effect, as

measured with free-association tasks. It is worth noting that research on priming is a complex field of its own right and not all of its topics are relevant to the discussion of familiarity (see Henson, 2003; Schacter et al., 2004 for reviews). Hence, studies reviewed in the current thesis, which emphasized intersections between priming and recognition memory, represent only a subset of the vast priming literature. In terms of neural correlates, I focus primarily on repetition priming in which the target stimuli themselves serve as the prime. To the extent that repetition priming effects are due to prior exposure happening either within the same trial or shortly before in an experimental study phase, it can be interpreted as task-irrelevant recent familiarity.

Another relevant phenomenon is the word-frequency mirror effect. It is commonly observed that low-frequency words are associated with higher hit rate and lower false alarm rate in recognition-memory paradigms (Glanzer & Adams, 1990). This phenomenon can be explained by a dual-process account (Diana et al., 2006; Reder et al., 2000). It interprets the hit rate portion of the effect as reflecting contribution of recollection since low-frequency words are associated with fewer number of encoding episodes, resulting in a higher probability of recovering the correct study episode during retrieval. On the other hand, high-frequency words would have been encountered in a larger number of pre-experimental episodes, thus the probability of retrieving the correct study episode is lower. The increased false-alarm rate of high-frequency words is explained by the higher degree of familiarity participants had with these words (Hoshino, 1991; Joordens & Hockley, 2000). In a series of RK experiments conducted by (Reder et al., 2000), high-frequency words elicited more false-alarm associated with K responses than low-frequency words while false-alarm rate of the R responses were not modulated by word-frequency.

Notably, in the typical dual-process framework, familiarity is considered a unidimensional signal with both lifetime experience and recent laboratory exposure contributing to this common familiarity signal. A more recent study by Coane et al. (2011), however, has shown that there may be two types of familiarity signals that drive behavioral decisions. They adopted a process-dissociation approach in which participants studied two lists of words, one presented visually and the other auditorily. In a later test

phase when stimuli on both lists and new stimuli were presented, participants were asked to only endorse stimuli on the auditory list as old while treating all other stimuli as new. The two types of familiarity can be measured by two types of errors in this paradigm. First, failure to excluded visually studied stimuli from old responses (i.e. exclusion error) captured the contribution of recent (relative) familiarity without recollection. Second, false alarms to new stimuli captured the contribution of lifetime familiarity. Coane et al. also manipulated response time and found that for faster responses, low-frequency words produced more exclusion errors, while the false alarm rate for new stimuli were higher for high-frequency words regardless of response time. The heightened exclusion error rate for low-frequency words implied the presence of a fast-acting relative familiarity mechanism that is sensitive to recent changes of familiarity, and the increased false alarm rate for high-frequency new words implied the presence of a lifetime familiarity mechanism that is more diffuse in its time course. In general, if we treat word frequency as a proxy for lifetime familiarity, the false alarm portion of the mirror effect can be thought as a case where task-irrelevant lifetime familiarity intrudes and impedes people's decision on recent occurrences.

There is also evidence suggesting that the effect of task-irrelevant lifetime familiarity is not always impeding. In other types of decision, lifetime familiarity can play a faciliatory role. For example, lexical decisions (Chee et al., 2003) and access to autobiographical memory (Gurguryan, Yang, Köhler, & Sheldon, in preparation) are faster with word cues denoting object concepts of higher lifetime familiarity.

Given that signals underlying repetition priming effects can be thought as a form of task-irrelevant recent familiarity and those underlying word-frequency effects can be thought as a form of task-irrelevant lifetime familiarity, it is interesting to ask whether they are indexed by a similar set of neural correlates as task-relevant familiarity.

1.3.1 ERP correlates of task-irrelevant recent familiarity effects

Studies on priming, in particular repetition priming are particularly relevant to questions about task-irrelevant familiarity, given that they often involve prior exposure in indirect tasks. Since repetition priming is often thought as a type of conceptual priming (Henson,

2003; Vaidya et al., 1995; but see J. L. Voss & Paller, 2008), it is perhaps not surprising that modulation of N400, a component extensively studied in psycholinguistic research, is commonly reported (Doyle et al., 1996; Holcomb et al., 2005; Misra & Holcomb, 2003; Kutas & Federmeier, 2011; Rugg, 1985). In Rugg (1985), participants made lexical decision on a list of words and pseudowords. The words included semantically associated pairs as well as repetitions of the same words. Starting from 250 ms, repetitions evoked more positive potentials as compared to the first presentations. This effect lasted through all analysis windows ending at 600 ms. With a slightly later onset from 350 ms to 450 ms, the "targets", namely the second words in semantically associated pairs evoked more positive potentials than the "primes", namely the first words in associated pairs. A topography comparison did not reveal any different between the associative and the repetition priming effect, with both effects having a centroparietal maximum. The time window and topography of these effects are largely consistent with the N400 component. There was also a repetition effect in a later time window of 450 ms to 600 ms. It is possible that this effect was related to the LPC, although the time window of this effect did not cover the full duration of the LPC, which often extends to about 800 ms.

Similarly, in a later study, Rugg et al. (1998) attempted to separate effects of implicit and explicit memory in a single recognition-memory paradigm. An effect of implicit memory was operationalized as a contrast between misses and correct rejections of the recognition judgement, with the rationale that if the participants failed to endorse a stimulus as old, then they must have no conscious experience of its prior occurrences. This contrast revealed an N400 effect. In addition, they conducted two experiments using similar designs with the only difference being that participants were asked to make animacy judgement instead of recognition in the test phase. A comparison between old and new stimuli in this indirect task also revealed an N400 effect. Aside from the putative marker of implicit memory, Rugg et al. (1998) also found a more frontally distributed effect in the same time window that was only present when comparing hits versus correct rejection. As they have suggested, this effect may be an FN400 linked to explicit familiarity signals.

However, distinctions between the FN400 and the N400 are not always reliable and some have argued for a unification of the two components (Paller et al., 2007; J. L. Voss & Federmeier, 2011a; J. L. Voss & Paller, 2007, 2008). For example, J. L. Voss and Paller (2007) demonstrated a conceptual priming effect on the FN400 instead of the N400. They used squiggles (Groh-Bordin et al., 2006), which are artificially constructed line drawings with no intrinsic meaning. Nevertheless, participants may still perceive different levels of meaningfulness among the squiggles, which was captured by meaningfulness ratings in their experiment. A conceptual repetition priming effect was found behaviorally, with repeated exposure leading to faster meaningfulness judgement only for squiggles rated high in meaningfulness. ERP data were collected in a separate RK experiment using these squiggles as stimuli. Supporting the view that the FN400 indices (conceptual) implicit memory, a comparison between meaningful and meaningless squiggles while controlling for explicit memory strength revealed an FN400 effect, whose magnitude was also positively correlated with behavioral measurement of priming across participants.

These findings suggest that the N400 tracks task-irrelevant recent familiarity. Whether the FN400 is distinguishable from the N400 in that regard is less clear. It is also not well-established whether task-irrelevant recent familiarity would be reflected in the LPC.

1.3.2 fMRI correlates of task-irrelevant recent familiarity effects in PrC

fMRI studies using repetition priming have reported left inferior frontal, fusiform, lateral middle temporal, and occipital effects (Ganel et al., 2006; Henson, 2003; Vuilleumier et al., 2002). Critically, several fMRI studies have also reported priming effects in PrC (Heusser et al., 2013; J. L. Voss, Hauner, et al., 2009; W.-C. Wang et al., 2014). In J. L. Voss et al., (2009), participants made living/non-living judgement on word concepts in a study and a test phase. A behavioral priming effect, measured as shorter response latencies, was observed in the test phase for studied words, along with reduced activity in bilateral PrC anatomically defined a priori. Moreover, the activity reduction in the left PrC was significantly correlated with interindividual differences of behavioral priming effect. Similar results have been reported by Heusser et al. (2013). They asked participants to make natural/manmade judgement on concepts presented continuously.

Concepts were presented twice, and the two presentations could either be in the same or different modalities (i.e. pictures, written words, or spoken words). Comparing first and second presentations, reduced activity was found again in left PrC for second presentations, although only for within-modality repetition of pictures. However, this PrC effect did appear to generalize to between-modality repetitions, as revealed by a correlation analysis, in which the group-averaged activity reduction in the PrC was found to the significantly correlated with the group-averaged behavioral priming effect across all the conditions with different modality pairing. Critically, this behavior-fMRI correlation remained significant in PrC even when only between-modality conditions were included, suggesting contribution of conceptual processes that were not limited by specific perceptual features. From a fluency-attribution point of view (Jacoby et al., 1989), a common set of neural mechanisms is expected to support both priming and explicit recognition. Interestingly, such neural mechanisms might be located in PrC as demonstrated by Wang et al. (2014). Participants were first presented with an abstract/concrete judgment task of word concepts, followed by a free association task to measure conceptual priming effect, and lastly an "old/new" recognition memory task with six levels of confidence. PrC BOLD activity reduction in relation to behavioral priming effects was observed in the free association task. But more importantly, PrC voxels showing this priming effect overlapped with voxels showing a familiarity effect in the recognition memory task, which was probed with a linear contrast across levels of confidence. Overall, these studies suggest that PrC activity is sensitive to recent familiarity regardless of whether the task requires judgements of this dimension.

1.3.3 ERP correlates of task-irrelevant lifetime familiarity

ERP studies investigating task-irrelevant word-frequency effects (as a proxy for lifetime familiarity) in recognition memory tasks often report an impact on the N400 component. In Bridger et al. (2014), participants first studied a list of words of varying normative frequencies. Then in a test phase, they made old/new recognition judgements on a mixed list of studied and novel words. When comparing hits with correct rejections, more positive potentials in the frontal regions were observed for hits for both high- and low-frequency words about 300 ms after stimulus onsets, replicating the typical FN400 effect

reported before (Curran, 2000; Rugg & Curran, 2007; Woodruff et al., 2006). This effect reflected differences in task-relevant recent familiarity. In the same time window, a comparison between correct rejections associated with high- and low-frequency new words revealed a parietally distributed effect that was more positive for high-frequency words, similar to the N400 effect (Kutas & Federmeier, 2011), which reflected differences in task-irrelevant lifetime familiarity. An analysis of the scalp distributions of the recent and lifetime familiarity effects demonstrated that they were dissociable. Interestingly, this contradicted an earlier report of a common FN400 effect observed for both types of familiarity (Nessler et al., 2005), perhaps due to the different types of stimuli (words vs. faces) and task structures. In studies with tasks requiring no judgement of prior occurrences, similar N400 effects of task-irrelevant word-frequency have also been reported (Grainger et al., 2012; Rugg, 1990; Van Petten & Kutas, 1990). To the extent that word frequency can be treated as a proxy for lifetime familiarity, these small number of studies suggest that N400 is a neural correlate of task-irrelevant lifetime familiarity. Whether and under what conditions the FN400 and the LPC may be sensitive to task-irrelevant lifetime familiarity remain to be explored.

1.3.4 fMRI correlates of task-irrelevant lifetime familiarity

Although word-frequency mirror effect is a prominent phenomenon in recognition-memory literature which often implicates MTL, its neural correlates have not been found in MTL so far. Instead, studies on word frequency have revealed sensitivity to this dimension in several other regions, including left frontal, left lateral temporal, and fusiform gyrus (Chee et al., 2003; de Zubicaray et al., 2005a, 2005b; Protopapas et al., 2016; Rundle et al., 2018). In searching for potential neural substrates of a mirror effect, de Zubicaray et al. investigated task-irrelevant word-frequency effects separately during study and test phases in a recognition memory paradigm. Participants studied a list of words and made simple “old/new” judgements in the test phase. When comparing fMRI data in the study phase associated with subsequent hits for the low-frequency words with high-frequency words, the only significant effect was found in the left inferior prefrontal cortex, showing higher activity for low-frequency words (de Zubicaray et al., 2005a). On the other hand, fMRI data in the test phase showed that hits on low-frequency words were

associated with higher activity in left occipital, fusiform, and middle temporal regions, as compared to hits on high-frequency words (de Zubicaray et al., 2005b). Chee et al. (2003) replicated the study-phase effect and found a similar left-dominant inferior frontal region showing higher activity for low-frequency words. However, they also found several other regions with similar effects, such as anterior cingulate and fusiform gyrus. Notably, no study to my knowledge has reported word-frequency effect in PrC. In fMRI, this region is known to suffer from signal dropout and distortion due to tissue interfaces causing inhomogeneity in the local magnetic field (Olman et al., 2009). Since few neuroimaging studies have investigated word-frequency effects in general, it is currently unclear whether this is merely due to signal dropout in the PrC region or that PrC is not sensitive to word-frequency manipulation. The latter possibility may stem from the limitation of using word frequency as a proxy for lifetime familiarity. Aside from the obvious lack of consideration of interindividual differences when using word frequencies extracted from corpus norms, word frequency is about the words themselves while lifetime familiarity is about the concepts represented by the words. Thus, the latter captures much more diverse experience than the former as it is not restricted to exposure to printed text. Behaviorally the two measurements are positively correlated but only moderately so (Cree & McRae, 2003) and their effects can be dissociated (Chedid et al., 2019). It is possible that PrC activity is modulated by lifetime familiarity of concepts rather than words per se.

1.4 Familiarity signals in PrC revealed by non-human electrophysiological studies

Familiarity, or recognition memory more generally, has also been studied in a large literature on non-human animals (see M. W. Brown & Banks, 2015 for a review). Although not the main focus of the current thesis, some electrophysiological studies in this literature have also provided converging evidence on the involvement of PrC in tracking both recent and lifetime familiarity. In these studies, animal subjects were familiarized with the stimuli through numerous presentations over weeks or months. Familiarity signals resulting from such repeated exposure over an extended period of time could be considered as a, albeit somewhat deprived, proxy for lifetime familiarity. Meanwhile, whether a stimulus, which can either be familiar or unfamiliar, has been

recently presented to the subject would mainly modulate recent familiarity. Neurons that were sensitive to either and both types of familiarity have been found in MTL including PrC (Fahy et al., 1993; Xiang & Brown, 1998; reviewed by Brown & Xiang, 1998), typically with decreased firing rating with increasing level of familiarity (but see Hölscher et al., 2003), although the distinction between PrC and surrounding inferior temporal (IT) regions was not always clear in some research.

Critically, it has also been found that PrC neuronal activity tracked familiarity regardless of task-relevance. Fahy et al. (1993) trained monkeys to perform a serial recognition task using 2D images. The stimuli could either be highly familiar to the monkeys or unfamiliar through manipulation of presentation frequencies in a passive fixation task. Stimuli could also have been presented recently or not. The monkeys were trained on a visual discrimination task, of which the authors provided few details, but it presumably did not involve any memory component. In a separate task, they were also trained to distinguish unfamiliar and familiar stimuli, as well as repeated unfamiliar stimuli which were to be given the same response as familiar stimuli. Reduction in firing rate in response to either increased recent or lifetime familiarity were found in several MTL regions including PrC not only during recognition, but also when such signals were irrelevant to the task such as during fixation or visual discrimination task. Although this is only one study, the findings do suggest that at a regional level, PrC may track both recent and lifetime familiarity regardless of task-relevance. Whether the same pattern can be observed in human PrC remains to be explored.

1.5 Role of decision making in familiarity judgement

The review so far suggests that MTL regions signal familiarity regardless of task-relevance. An important question thus emerges as to where such signals are processed for the purpose of making task-relevant memory decisions. One possibility is that such computation is handled by frontoparietal regions, as neuroimaging studies have consistently observed familiarity effects in these areas (Daselaar et al., 2006; Horn et al., 2016; Montaldi et al., 2006; Skinner & Fernandes, 2007; Vilberg & Rugg, 2007). Their functions are less agreed upon and do not easily fall into the recollection/familiarity distinction of the dual-process framework. Note that here I am using the term

"frontoparietal" in a broad sense. Many subregions with diverse functionalities are covered by this term and a detailed coverage is beyond the scope of the current thesis (for reviews, see Euston et al., 2012; Kim, 2010; Ritchey & Cooper, 2020; A. R. Vaidya & Badre, 2022). It is also worth noting that much of the theoretical consideration has been placed on the lateral aspects of frontoparietal regions (Fletcher & Henson, 2001; Simons & Spiers, 2003; Vilberg & Rugg, 2008a; Wagner et al., 2005), yet familiarity effects in medial regions are also commonly reported (Horn et al., 2016; Skinner & Fernandes, 2007). With these complexities in mind, I would like to highlight that many of these regions are linked to decision-related processes (i.e. attribution) in the IM model proposed by Bastin et al. (2019) and reviewed in section 1.1. According to that model, during familiarity-based retrieval, PrC contributes entity-level fluency signal which can then be interpreted by the frontoparietal attribution system as due to prior occurrences and lead to an "old" judgement. Interestingly, a parallel hierarchy can be found in the literature of perceptual decision-making, where a distinction is made between evidence and decision variable. Evidence refers to any source of information that is relevant to the decision at hand and individual pieces of evidence are thought to be noisy and fleeting. The decision variable is the combination and accumulation of all sources of evidence, as well as other information such as prior believes and value (Gold & Shadlen, 2007). Thus, in the context of familiarity-based memory decision, the fluency signal, which is automatic and insensitive to task-relevance manipulation, can be thought as a source of evidence during familiarity-based decision. The attribution system, which operates based on task goals, can be thought as encompassing the decision variable. This conceptualization is also similar to the dual-process model proposed by Wixted and Stretch (2004), in which familiarity and recollection signals (evidence) are combined into a memory strength signal (decision variable) to be evaluated against some criteria.

However, a notable feature of the attribution system proposed in Bastin et al. (2019) is the multitude of processes it encompasses, which are involved in different stages of decision-making. Broadly speaking, these processes can be classified into two categories. The first category is related to the experiential aspects of memory such as metamemory (Baird et al., 2013; Ye et al., 2018) or vividness (Richter et al., 2016). To the extent that metamemory or metacognition in general can be considered a post-decision process

(Yeung & Summerfield, 2012) and dissociable from the primary decisions (Fleming & Dolan, 2012), which suggests that signals in these regions may be less predictive to performance of memory judgement compared to MTL regions. The other category is related to decision-making processes that produce the ensuing behavioral report (D. I. Donaldson et al., 2009; Euston et al., 2012; Wagner et al., 2005). These processes suggests that signals in frontoparietal regions would be more predictive to performance of memory judgment compared to MTL regions. Thus, a more detailed understanding of these regions and more generally, networks involved in memory decisions may be gained by considering formal models of decision-making.

1.6 Modeling of decision processes and their neural correlates in memory judgements

Sequential-sampling models (SSMs), which formalizes decision-making as accumulating noisy evidence over time towards a threshold, can provide a quantitative framework to interrogate neural correlates of familiarity in terms of their contribution to the memory decision. In fact, one version of SSMs, the drift-diffusion model (DDM), was initially proposed to explain memory retrieval (Ratcliff, 1978; Ratcliff, Smith, et al., 2016). In this model, the presentation of a memory probe evokes a parallel comparison process between the probe and all items stored in memory. These comparisons were construed to take the form of diffusion processes, with noisy evidence accumulating over time towards either a "match" boundary or a "nonmatch" boundary. If the "match" boundary is crossed, a "match/old" response is produced. Or, if all diffusion processes terminated at the "nonmatch" boundary, a "nonmatch/new" response is produced. There are three key advantages of this model and other SSMs. First, they can simultaneously account for both response-choice data such as accuracy and response time. Thus, from an experimental point of view, they provide more efficient usage of behavioral data. Second, the model fitting procedure produces a number of parameters, which represents latent processes involved in decision-making (A. Voss et al., 2004). Third, beyond the explanatory power on behavioral data, neural correlates that resemble processes indexed by these parameters have also been observed, providing further validation of the SSMs framework (Gold & Shadlen, 2007; O'Connell et al., 2018).

Recent developments in the field of decision-making have allowed for the incorporation of neuroimaging data into SSMs in a unified framework to estimate the involvement of various neural correlates in decision-making (Turner et al., 2015; Wiecki et al., 2013). This approach has been adopted in a memory study by Mack and Preston (2016). Participants were first exposed to pictures of famous faces and places (pre-exposure phase). They subsequently learned to associate those pictures with other pictures of common objects. Then in a delayed-match-to-memory (DMTM) task, those pictures of objects were used as cues to retrieve the associated pictures of famous faces or places during a delay period, followed by either the correct target picture or a foil of the same category to verify retrieval. Trial-level item reinstatement was estimated in hippocampus, PrC, and occipitotemporal regions. This was done by calculating the similarity of multivariate voxel patterns between the pre-exposure phase and each trial of the DMTM phase. This item reinstatement index was entered into the fitting process of DDMs as a trial-level regressor on different parameters in separate model instances, separately for each region of interest. The relative goodness-of-fit of these neurally-informed DDMs provided evidence for the different involvement of representational content in those regions, which revealed that PrC reinstatement effect was mostly involved in memory decisions when the targets were faces, while hippocampal reinstatement was mostly involved when the targets were places. On the other hand, occipitotemporal regions, despite showing face and place reinstatement effects, did not contribute to memory decisions as shown by inferior model fit compared to a baseline model without any neural data. Relating to a decision-hierarchy, these results suggest that at least for associative memory judgement on pictures, MTL regions are more involved in decision-making processes. Given the associative nature of their task, it likely mainly involved processes underlying recollection instead of familiarity. A question that has not been addressed by extant research is whether a similar decision-hierarchy can be identified with this approach among MTL, more specifically PrC, and frontoparietal attribution regions during familiarity-based judgement.

1.7 Knowledge gaps in current research on familiarity

Given that familiarity is conceptualized as an acontextual memory signal (Yonelinas, 2002), recent familiarity as operationalized in recognition-memory paradigms has its limitation in that it is nonetheless a contextual judgement, because participants' recognition judgements, even when it is based on familiarity, refer to a study phase in the experimental context (Levy, 2012). From this perspective, lifetime familiarity, which develops from a large number of episodes spanning an extended period of time, is arguably a more ecologically valid measurement of familiarity. However, much less research has been done on lifetime familiarity compared to recent familiarity, especially on the characterization of neural mechanisms underlying lifetime familiarity, and how they differ or overlap with those supporting recent familiarity.

Motivated by the distinction between automatic and attribution components underlying familiarity judgement proposed in the IM model (Bastin et al., 2019), another question that has not been systematically investigated is whether neural correlates of familiarity can be distinguished based on their sensitivity to task-relevance. Together with the question regarding time scale (recent versus lifetime), they form a two-by-two matrix representing the conceptual space in which neural correlates of familiarity can be characterized (Figure 1.1). The literature review in previous sections was based on many cross-study comparisons and almost none of the studies examined all four cells. The only exception may be Nessler et al. (2005) who examined (proxy of) lifetime familiarity and recent familiarity together with task-relevance manipulation using faces in an ERP study. Currently, no study has attempted to characterize, with both factors, neural correlates of familiarity for object concepts. Neither was there any fMRI study that included manipulation of both factors.

A separate question concerns the attribution system, which encompasses a wide variety of cognitive processes. Whether different neural correlates of familiarity can be linked to different subcomponents of the attribution system is also largely unexplored. And considering the degree of involvement of these neural correlates in decision-making processes may be helpful in providing a common axis to distinguish these subcomponents.

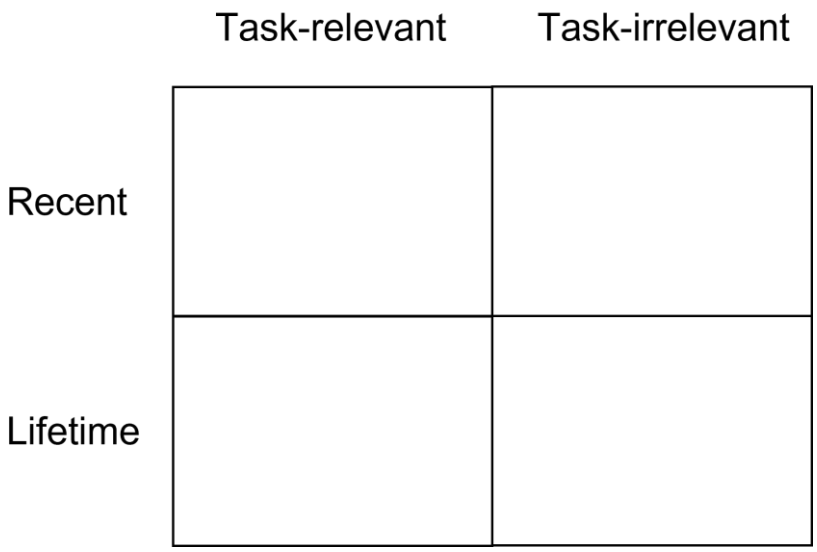

Figure 1.1. Schematic of conceptual space used to characterize neural correlates of familiarity

1.8 Summary of thesis goals and main hypotheses

The current research was conducted with two main goals in mind. Informed by the IM model and decision-making literature, the first goal is to characterize ERP and fMRI correlates of familiarity for object concepts with direct comparison of the two factors of interest (Figure 1.1) in a common paradigm. The second goal is to explore whether the contribution of different neural correlates to familiarity judgement could be estimated by considering formal models of decision-making, which could potentially provide a more detailed account of the attribution system in the IM model. In order to pursue these goals, I conducted three experiments using the same behavioral paradigm adopted from Duke et al. (2017). Object concepts with different degree of lifetime familiarity were extracted from a normative database (McRae et al., 2005) to be used as stimuli. Participants made animacy judgements on half of the stimuli in a study phase, in which the stimuli were presented for different number of times to manipulate the degree of recent familiarity. Then in a test phase, participants performed two tasks in alternating blocks. In one task, they rated relative frequencies of presentation on studied stimuli as a measurement of task-relevant recent familiarity. In the other task, they rated degree of lifetime familiarity on the other half of the stimuli which were not presented in the study phase. For Chapter

3, participants also rated lifetime familiarity on studied stimuli at the end of the experiment.

In Chapter 2, I explored whether ERP correlates observed in recognition memory paradigms that focused on recent exposure also tracked lifetime familiarity, and whether they were sensitive to a task-relevance manipulation. I analyzed FN400/N400 and LPC responses to varying degree of lifetime and recent familiarity either when participants made explicit judgements along the corresponding time scale or not. I predicted that if the LPC does indeed track the strength of multiple types of memory signals in a decision-dependent manner, it should be sensitive to the degree of lifetime familiarity when participants were making lifetime familiarity judgements, but not when participants were judging the degree of cumulative recent familiarity. Similarly, it should be sensitive to the degree of cumulative recent familiarity when a judgement of that dimension was required but not during the semantic judgements in the experimental study phase. ERP components in the FN400/N400 time window were analyzed as well to determine the specificity of the predicted LPC results.

In Chapter 3, I attempted to replicate the conjunctive effect of lifetime and recent familiarity in PrC reported in Duke et al. (2017) and extend it by asking whether the PrC effects were sensitive to task-relevance. A similar procedure was used as in Chapter 2. To demonstrate the automaticity of PrC familiarity signal, I also included analyses of task-irrelevant lifetime familiarity effects during judgement of recent familiarity as well as during animacy judgement, using participants' individual ratings collected at the end of the experiment. Task-irrelevant recent familiarity effects were probed with an analysis of repetition effects during animacy judgements. I hypothesized that PrC activity would track both types of familiarity regardless of task-relevance. Specifically, I predicted that both recent and lifetime familiarity effects would be present in PrC not only when participants were making familiarity judgement on the corresponding time scale, but also when they were making familiarity judgement on a different time scale and when they were not making familiarity judgement at all (as in the study phase).

In Chapter 4, I explored whether a decision hierarchy exists among regions showing familiarity effects (i.e. PrC and frontoparietal regions), which would allow me to link these regions to subcomponents of the IM model in a more detailed manner. To achieve this, I reanalyzed fMRI data of recent familiarity judgement collected in Chapter 3. Specifically, I fit neurally-informed DDMs with single-trial BOLD activity from different regions. I then performed Bayesian model comparisons to estimate the relative positions of PrC and frontoparietal regions along the decision hierarchy based on their goodness of fit, with the assumption that a region more involved in decision-making processes would have its activity explaining more variance in the DDM parameters thus resulting in a better model fit. I predicted that trial-by-trial BOLD activity in PrC would contribute to the decision-making processes during judgement of recent familiarity, resulting in a superior fit of the DDM compared to the baseline model without neural information. Following the IM model, raw mnemonic signals in PrC are expected to undergo further processing in the attribution system. For frontoparietal regions, if their activity indexed the decision-making aspects of the attribution system, DDMs that included such activity are expected to fit the behavioral data better than those that included PrC activity. Otherwise, if activity in these regions indexed experiential aspects of the attribution system (e.g. metacognition) which can be considered post-decision, their activity might provide an inferior fit relative to the PrC model.

Chapter 2

2 « Late positive complex in event-related potentials tracks familiarity signals when they are task-relevant »

This chapter aims to examine if ERP correlates of recent familiarity also tracks lifetime familiarity, and if they are sensitive to task-relevance manipulation. This work is now published in the journal Scientific Report with the title “Late positive complex in event-related potentials tracks memory signals when they are decision relevant” (Yang et al., 2019). The version included below has been slightly modified from the publication to fit better in the overall thesis structure.

2.1 « Introduction »

Recognition memory refers to the ability to recognize that a stimulus has been encountered previously. Due to its broad functional significance in cognition, it has been studied in laboratory settings with a variety of behavioral and neuroimaging methods, including a rich body of literature focusing on event-related potentials (ERPs; for a review see (Rugg & Curran, 2007)). Most of the studies have employed variants of study-test paradigms that require discriminating items that had been previously encountered in a study phase from non-studied novel stimuli. Two ERP components have been identified that have been shown to track the outcome of participants’ memory judgements in many studies. First, the late positive complex (LPC) is a positive-going ERP that peaks around 600 ms after stimulus onset with a central posterior topography. Stimuli judged as old (i.e., previously encountered in an experimental study phase) typically elicit a more positive LPC than do those judged as new (Woodruff et al., 2006). The second ERP component is the mid-frontal FN400, characterized by an earlier peak at 400 ms, with a more positive deflection for stimuli judged to be old. These two ERP components have often been interpreted in the context of the dual-process model of recognition memory, with the LPC marking recollection of episodic details about the prior stimulus encounter, and the FN400 marking item-based familiarity assessment (devoid of episodic context). This popular interpretation of the two ERP components of recognition memory has, however, been questioned in recent years, and the exact processes that underlie them

remain a contentious issue (Bridger et al., 2012; J. L. Voss & Federmeier, 2011b). The current research addresses the functional significance of the LPC in light of recent evidence that ties it to aspects of decision making during memory judgements, rather than a unique role in episodic recollection (Brezis et al., 2016; Ratcliff, Sederberg, et al., 2016). We examine this idea in the context of two memory tasks not frequently employed in prior research, which focus on assessment of different types of cumulative familiarity, rather than discrimination between previously studied and novel stimuli.

Results from a recent study called into question the classic interpretation of the LPC as a specific marker of episodic recollection by suggesting that the LPC tracks the perceived strength of memory (reflected in confidence) even when participants cannot recollect episodic detail pertaining to the stimulus encounter (Brezis et al., 2016). Brezis et al. (2016) employed a variant of the Remember/Know (RK) procedure, commonly used in recognition-memory experiments to distinguish familiarity from recollection. In a RK paradigm, participants are asked to not only indicate whether they have encountered the stimuli in the study phase, but also to specify whether they can recollect episodic details of that encounter ('Remember') or not ('Know'). They added a component to the memory judgement by asking participants to provide confidence ratings of their old/new responses prior to indicating the basis of recognition of old items by choosing "Remember", "Know", or "Guess". Their core analyses showed that high confidence Know responses elicited a more positive LPC than low confidence Remember responses. This result suggests that, while tied to the outcome of the memory decision, the LPC is not an exclusive marker of episodic recollection. Instead, it may be a broader marker of the strength of the signal that drives the decision as measured by expressed confidence. From this perspective, the LPC may indeed also track other types of memory signals, to the extent that they are relevant to the memory decision.

Evidence that favors an interpretation of the LPC as a marker of signal strength for the memory decision at hand also comes from a recent EEG-based study that fitted a drift-diffusion model to single-trial data from a recognition-memory experiment that required participants to make old/new judgements about items from a list of words (Ratcliff, Sederberg, et al., 2016). The drift-diffusion model simulates decision-making processes

as an accumulation of noisy evidence. Studies using this model typically estimate its parameters using reaction time and accuracy data, and then examine the estimated parameters as markers of the underlying mechanisms of decision making. Ratcliff et al. (2016) first trained classifiers to label individual trials as “studied” or “unstudied” based on objective item status, using EEG data from multiple time windows (approximately FN400 or the LPC time windows). They found that only the classifier trained on the LPC time window predicted later behavioral performance on a trial-by-trial basis. Specifically, the drift rate, a parameter that corresponds to the speed of evidence accumulation, differed significantly only when the drift-diffusion model was fitted with the classifier output from this time window. Ratcliff et al. concluded that the LPC tracks evidence accumulation, and that it is the only electrophysiological component that contains information that drives memory judgements.

In the studies outlined above, as well as in the ERP literature at large, the memory judgements required discrimination of previously studied from non-studied items. In such a study-test paradigm, participants always make memory judgements with respect to an experimentally controlled study phase. However, when meaningful stimuli such as object concepts (i.e., the concrete object to which a word or picture refers (Duke et al., 2017; A. Martin, 2016)) are used, participants also have varying degrees of pre-experimental familiarity that can lead to different memory strengths. Indeed, it has been argued that recognition-memory studies conducted with meaningful stimuli and with memory judgements that probe exposure in an experimental study phase tap into the degree of recent change in memory strength rather than absolute cumulative strength (Duke et al., 2017; Mandler, 1980). Behavioral findings suggest that humans can also judge cumulative familiarity to object concepts accrued over their lifetime outside the laboratory. For example, people can easily judge whether they have had more lifetime familiarity to apples or tangerines. Such judgements display considerable consistency across participants within a given culture (Cree & McRae, 2003; Moreno-Martínez et al., 2014b; Schröder et al., 2012b), and engage brain structures in the medial temporal lobe that are known to play a critical role in recognition memory (Bowles et al., 2016b; Duke et al., 2017).

In the present study, we employed judgements of lifetime familiarity to determine whether and how the LPC is tied to decision-making in memory judgements. Specifically, we asked whether the LPC can flexibly track the strength of multiple types of memory signals to the extent that they are task-relevant. For this purpose, we also used relative frequency judgements that assess cumulative recent item familiarity, which was directly manipulated in an experimental study phase with an incidental semantic encoding task. We predicted that if the LPC does indeed track the strength of multiple types of memory signals in a decision-dependent manner, it should be sensitive to the amount of cumulative lifetime familiarity when participants are making lifetime familiarity judgements, but not when participants are judging the relative frequency of cumulative recent familiarity. Similarly, it should be sensitive to the degree of cumulative recent familiarity during frequency judgements but not during the semantic judgements in the experimental study phase. Because the LPC has previously been linked to left ventral lateral parietal cortex in intracranial electrocorticography (ECoG) and recordings from depth electrodes in humans (Gonzalez et al., 2015b; Rugg & King, 2017; Rutishauser et al., 2018b), we hypothesized that cortical source activity in this region would show a similar effect during the LPC time window. To determine whether these predicted results are specific to the LPC, we also analyzed the FN400/N400 ERP component.

2.2 Method

2.2.1 Participants

Sixty-five participants (38 females) were recruited through posters or an online recruitment tool (*Psychology Research Participation Pool*, n.d.). All participants were 18 to 35 years old, right handed, native English speakers who had lived in Canada since childhood. None of them reported any known psychiatric or neurological disorder. Seven participants were excluded from final analyses due to technical problems with EEG equipment. One additional participant was excluded because they failed to follow instructions. Other analysis-specific exclusions were applied, such that participants with less than 10 trials in any of the experimental conditions were not considered in corresponding ERP analyses. Depending on the phases, the exclusion criteria removed 9 or 10 of 57 participants, resulted in 47 participants for analyses of the test phase, and 48

participants for the study phase. However, for analyses including the within-participant experiment phase (i.e. study or test) factor, only 43 participants whose data from both phases passed the criteria were included.

The study was approved by the Western University Non-Medical Research Ethics Board (NMREB). Informed consent was acquired from each participant before the experiment. Participants were given course credit or monetary compensation. All experiments were performed in accordance with the approved guidelines and regulations.

2.2.2 Material

Stimuli were 250 concrete English nouns selected from a normative database collected from Canadian participants (McRae et al., 2005). They were divided into 10 bins of 25 words (Table 2.1). Five bins were randomly selected to be used in the study phase and the cumulative recent-familiarity task (i.e. relative frequency-judgement), and the other 5 bins were used in the lifetime familiarity task (see Procedure). This assignment was counterbalanced across participants to create two versions of the experiment. Word length, number of phonemes, number of syllables, word frequency, and normative lifetime familiarity ratings were matched across bins as verified by an ANOVA. Stimuli were selected to cover a wide range of lifetime familiarity ratings in the database. On the 9-point scale of lifetime familiarity provided by the database, the two versions of the experiment had mean ratings of 5.44 and 5.52, and ranges of 7.00 and 6.90.

Table 2.1: Average normative lifetime familiarity, concreteness, natural log of word frequency, number of letters, and number of phonemes for the ten bins selected as stimuli. Concreteness ratings were taken from Brysbaert et al. (2014). Other measurements were taken from McRae, Cree, Seidenberg, & McNorgan (2005)

	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5	Bin 6	Bin 7	Bin 8	Bin 9	Bin10

Normative lifetime familiarity	5.20	5.85	5.64	5.01	5.49	5.19	5.44	5.57	5.61	5.81
concretenes s	4.84	4.83	4.73	4.82	4.88	4.80	4.87	4.85	4.87	4.84
ln(KF)	1.85	1.76	1.63	1.79	1.48	1.35	1.65	1.62	1.66	1.66
Number of letters	6.12	5.92	6.28	5.68	6.00	6.00	5.84	6.36	5.88	5.60
Number of phonemes	4.64	5.00	5.24	4.72	4.96	5.00	4.80	5.08	4.80	4.92

2.2.3 Procedure

After acquiring informed consent, participants were seated in front of a monitor in a soundproof booth. Oral instructions were given to participants regarding the general structure of the study phase. Participants were instructed to minimize movements and remain vigilant throughout the experiment. Written instructions about response-key mappings were displayed on the monitor for participants to read at their own pace. E-prime (Psychology Software Tools, n.d.) was used to present the stimuli and log behavioral responses. For the study phase, a list of 125 unique concrete nouns (i.e. 5 bins) appeared on the monitor one at a time following a fixation cross. The stimuli were presented at different frequencies (i.e., number of repetitions) across bins, such that items were presented either one (bin 1), three (bin 2), five (bin 3), seven (bin 4), or nine times (bin 5). In sum, this resulted in 625 randomized trials in the study phase. For each trial, a fixation cross was presented for 1000 milliseconds, and became bolded for 1000 milliseconds to indicate the imminent presentation of a stimulus. A stimulus and the

response options then were presented for 1000 milliseconds, and participants were asked to judge the animacy of each word by pressing one of two keys (Figure 2.1). They were not told about the ensuing memory test phase.

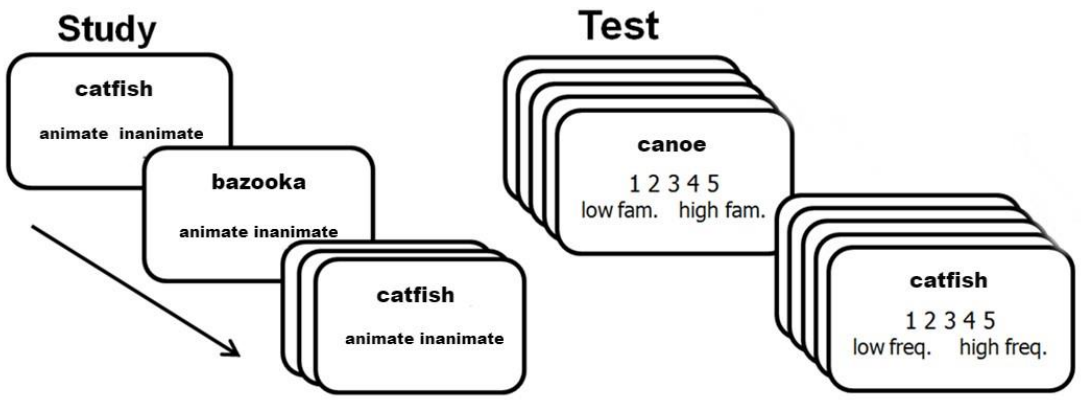

Figure 2.1: Experimental procedure. Note that the text below the scale in the test phase is only for illustrative purposes, they were not shown to participants in the actual experiment.

Immediately after the study phase, participants were given oral instructions about the structure of the test phase. Written instructions regarding response key-mappings were displayed on the monitor for participants to read at their own pace. The test phase consisted of two types of trials: recent and lifetime familiarity judgements. For the recent familiarity task, participants judged the relative presentation frequency of each word in the study phase on a 5-point scale. For the lifetime familiarity task, participants were presented with unstudied stimuli (i.e. the other 5 bins) and were asked to judge how familiar each corresponding concept was based on their lifetime experience, on a 5-point scale. There were 125 trials per task. The two tasks alternated in blocks every 5 trials. A message indicating the task type for the next 5 trials was shown for 2000 milliseconds prior to every alternation. The presentation order of items was randomized for each task. For both tasks, each trial started with a fixation cross, which was presented for 1000 milliseconds and was subsequently bolded for 1000 milliseconds to indicate the imminent presentation of a stimulus. Then a stimulus and the response options were presented for 2500 milliseconds during which participants' responses were registered. Participants

were asked to use all 5 keys and both hands. The mapping of the keys was counterbalanced across participants such that for approximately half of the participants, "5" was mapped on the left of the monitor and the keyboard, while for the other half, "5" was mapped on the right. Each key was mapped onto one finger. From left to right, participants used their left middle finger, left index finger, right index finger, right middle finger, and right ring finger to press corresponding keys.

2.2.4 Behavioral data collection and preprocessing

To quantify participants' behavioral performance, their ratings in the recent and lifetime familiarity tasks were correlated with the actual presentation frequencies in the study phase and the normative lifetime familiarity ratings from the database by McRae et al. (2005), respectively. On trials in which a participant failed to provide a response, the participant's averaged response for the corresponding judgement type (i.e. recent/lifetime familiarity) was used.

2.2.5 ERP data collection and preprocessing

EEG data were collected using a Biosemi ActiveTwo 64-channel system. Electrode placements followed the international 10-20 system ("Biosemi Headcaps"). Two extra electrodes were applied on bilateral mastoids to be used in offline re-referencing. Another four extra electrodes were applied to the lateral corners of both eyes, above and below the left eye, to capture eye movements. Electrode offsets were kept below 20 mV. The data were originally sampled at 2048 Hz, and were down-sampled to 512 Hz to be imported into EEGLAB (Delorme & Makeig, 2004), a free toolbox for MATLAB (MATLAB-R2015a, The MathWorks, Inc.). Data for malfunctioning electrodes were interpolated from neighboring electrodes using the spherical interpolation algorithm provided in EEGLab. For study phase data, four participants had one electrode interpolated, and one participant had two electrodes interpolated. For the test phase data, five participants had one electrode interpolated, and one participant had two electrodes interpolated. All other participants had no interpolated electrodes. Data were bandpass filtered between 0.1 to 30 Hz. An independent component analysis (ICA) was applied to identify and remove ocular artifacts (Jung et al., 1998). The data were then re-referenced to linked mastoids. Epochs

were extracted from -199 ms to 998 ms with reference to stimulus onsets. A moving window with a width of 200 ms, a step size of 100 ms, and a threshold of 100 μV was used to mark remaining artifacts in the epoched data. Data were then averaged with respect to trial types (i.e., experimental task and response selected) to extract ERPs. All marked epochs were excluded from the averaging process. After artifact rejection, participants with less than 10 trials in any condition were excluded from statistical analyses. On average 43 trials contributed to each ERP, which corresponds to a rejection rate of 13%.

To probe for any experimental effects in the ERP recordings, four regions of interest (ROI) were selected. These ROIs were Left Anterior (Fp1, AF3, AF7, F1, F3, F5, F7, FC1, FC3, FC5, FT7), Right Anterior (Fp2, AF4, AF8, F2, F4, F6, F8, FC2, FC4, FC6, FT8), Left Centroposterior (C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, P9, PO3, PO7, O1), and Right Centroposterior (C2, C4, C6, T8, CP2, CP4, CP6, TP8, P2, P4, P6, P8, P10, PO4, PO8, O2). ERP data were averaged across electrodes within each ROI before being submitted to statistical analyses. Following extant research (e.g. (Rugg et al., 1998; Woodruff et al., 2006)), the LPC and FN400/N400 time windows were chosen a priori to be 500-800 ms and 300-500 ms, respectively. Omnibus ANOVAs were carried out with the mean amplitude within each time window as the dependent variable, violations of the sphericity assumption were corrected by the Greenhouse-Geisser procedure. Multiple comparisons were corrected using the Bonferroni procedure in all tests following the omnibus ANOVAs. All p-values are reported following these corrections, unless otherwise specified. Effect sizes are reported using generalized eta squared: $\hat{\eta}_G^2$ (Bakeman, 2005) and Cohen's d for F-tests and t-tests, respectively.

2.2.6 LPC source localization

The exploratory source localization was carried out using the Brainstorm MATLAB toolbox (Tadel et al., 2011). We used default anatomy that is based on Colin 27 atlas (Holmes et al., 1998) for all participants. The electrode locations were imported from BioSemi 64 10-10 cap file provided by the Brainstorm. The forward model was estimated using OpenMEEG BEM (Gramfort et al., 2010; Kybic et al., 2005). The inverse solution was estimated using Tikhonov-regularized minimum-norm (Baillet et al., 2001), with

current density as the measurement. The estimated dipole orientations were constrained to be normal to the cortex. For each participant, noise and data covariance matrices used in the inverse solution were computed from the epoched EEG data separately for the study and the test phase, using pre-stimulus baseline (-199.20 ms to -2.00 ms) and roughly the first second of stimulus presentation (0.00 ms to 998.00 ms). The source localization was performed on the binned ERPs in each condition (high vs. low, see Results), and the difference in absolute current densities between the high and low bins were extracted for inferential statistics. We focused on the left dorsal and ventral lateral posterior parietal lobe, which were defined using the Desikan-Killiany atlas (Desikan et al., 2006) offered in the Brainstorm Scout module.

2.3 Results

2.3.1 Behavioral results

To quantify participants' memory performance in the recent familiarity task, we correlated participants' judged relative frequency in the test phase with the actual number of repetitions in the study phase. Significant positive correlations (at $p < .05$) were observed in 53 out of 57 participants, with a mean $r(123) = .41$, $p < .001$, indicating sensitivity of these judgements to our exposure manipulation (Figure 2.2). To quantify performance in the lifetime familiarity task, we followed a procedure employed in our prior work (Duke et al., 2017). We correlated participants' ratings with those reported in a normative database (McRae et al., 2005). Significant positive correlations were observed in 54 out of 57 participants, with a mean $r(123) = .51$, $p < .001$, again indicating sensitivity to the memory dimension of interest (Figure 2.3).

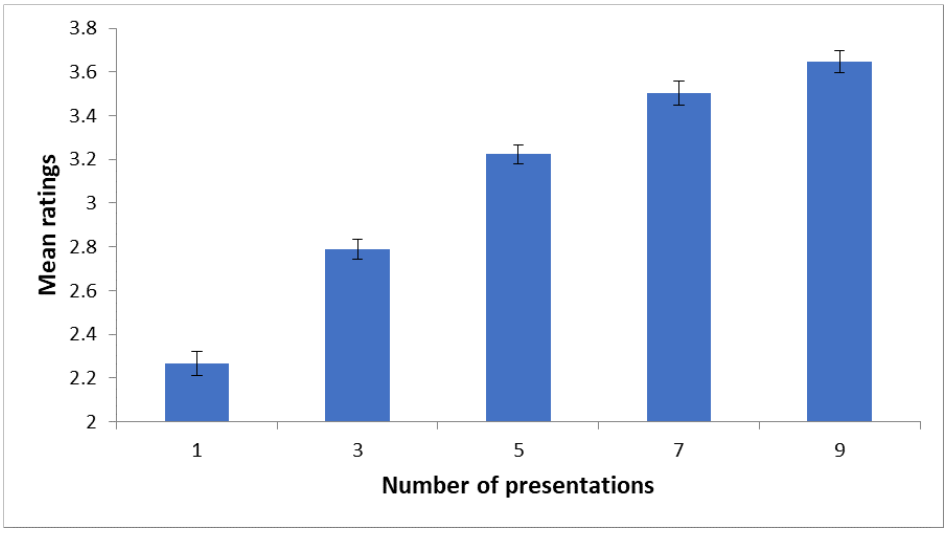

Figure 2.2: Mean ratings given to each presentation frequency bin in the test phase for recent familiarity. Error bars represent standard errors of the means across participants

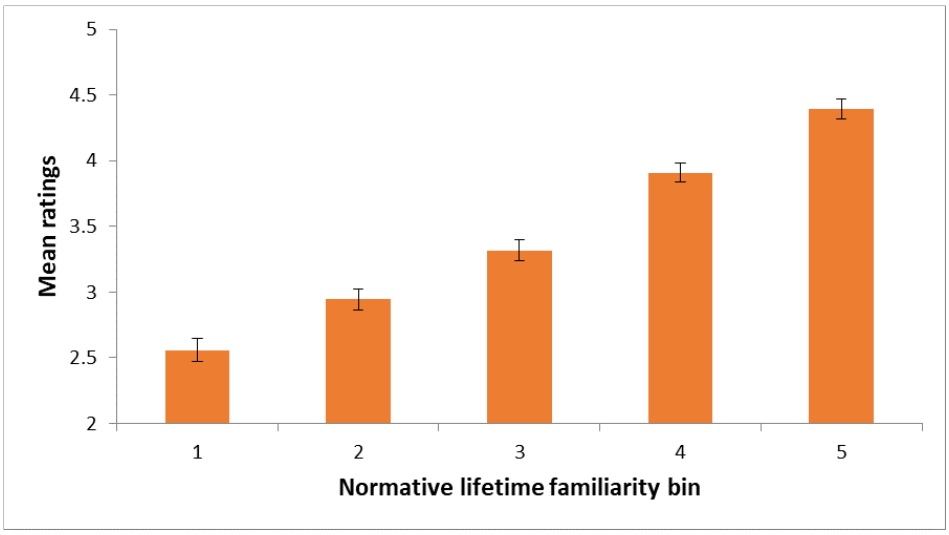

Figure 2.3: Mean ratings given to each normative lifetime familiarity bin in the test phase. Bins are defined based on normative data reported by (McRae et al., 2005). Error bars represent standard errors of the means across participants.

It is evident that the mean response time (RT) was shorter for the study phase (Table 2.2) as compared to the test phase (

). However, when comparing the RT differences calculated according to the ERP contrasts ("high" – "low", see below) using permutation tests, we found that these RT differences related to degree of familiarity were closely matched across the two tasks in the test phase, and between study and test phase, all ps > .7.

Relative frequency judgement					Lifetime familiarity judgement				
1	2	3	4	5	1	2	3	4	5
1356.29 (30.79)	1436.70 (30.64)	1397.65 (46.09)	1346.00 (30.47)	1222.37 (30.56)	1324.25 (30.59)	1475.17 (33.91)	1476.00 (51.05)	1437.82 (36.06)	1188.44 (31.37)

Table 2.2: Response times in milliseconds in the study phase (Means and Standard Errors*)*

	Numbers of presentation								
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
Bin 1	683.78 (9.84)								
Bin 2	683.87 (9.04)	657.09 (10.12)	644.58 (10.08)						
Bin 3	691.04 (10.08)	649.82 (10.68)	649.95 (9.36)	645.54 (11.16)	628.28 (10.25)				
Bin 4	694.66 (9.30)	656.47 (9.10)	643.89 (9.05)	642.03 (10.78)	635.38 (10.85)	628.34 (9.92)	627.33 (11.13)		
Bin 5	691.99 (8.98)	652.53 (10.15)	640.34 (10.34)	639.03 (10.69)	631.95 (9.67)	624.44 (11.40)	627.01 (10.03)	620.77 (10.52)	618.30 (10.65)

Table 2.3: Response times in milliseconds in the test phase (Means and Standard Errors)

Relative frequency judgement					Lifetime familiarity judgement				
1	2	3	4	5	1	2	3	4	5
1356.29 (30.79)	1436.70 (30.64)	1397.65 (46.09)	1346.00 (30.47)	1222.37 (30.56)	1324.25 (30.59)	1475.17 (33.91)	1476.00 (51.05)	1437.82 (36.06)	1188.44 (31.37)

2.3.2 Does the LPC track perceived familiarity in cumulative memory judgements?

To obtain a sufficient number of trials for critical comparisons along the memory dimensions in the two types of memory judgements, and to maximize stability of the corresponding waveforms, we computed weighted ERP averages for high- versus low-familiarity bins. Specifically, responses for the upper most response levels (i.e. 4 and 5) were contrasted with those for the lower most response levels (i.e. 1 and 2). For the recent-familiarity task, the high and low combined levels had on average 43 and 38 trials, respectively, corresponding to average rejection rates of 13% for both levels. For the lifetime familiarity task, the high and low combined levels had on average 53 and 35 trials, corresponding to average rejection rates of 15% and 13%, respectively. ANOVAs were conducted on the four ROIs. For the LPC time window (500 – 800 ms), we first conducted an omnibus repeated measures ANOVA on the ERPs with anteriority (2 levels), laterality (2 levels), task (2 levels), and response (2 levels) as factors.

The omnibus test yielded significant main effects of anteriority, $F(1, 46) = 49.81$, $p < .001$; $\hat{\eta}_G^2 = 0.14$; and laterality, $F(1, 46) = 14.28$, $p < .001$, $\hat{\eta}_G^2 = .01$. Significant two-way interactions were observed for anteriority × response, $F(1, 46) = 18.96$, $p < .001$, $\hat{\eta}_G^2 = .005$; laterality × task, $F(1, 46) = 8.97$, $p = .004$, $\hat{\eta}_G^2 < .001$; and anteriority × laterality, $F(1, 46) = 4.04$, $p = .050$, $\hat{\eta}_G^2 < .001$. All other effects were non-significant, $F < 4.04$, $p > .1$, $\hat{\eta}_G^2 < .005$.

Because our primary interest is in effects related to the memory judgements, we performed simple-effect post hoc tests on the anteriority × response interaction. Results showed that ERPs corresponding to high ratings in both recent and lifetime familiarity tasks were more positive than those of low ratings of both tasks on the centroposterior ROIs, t (46) = 1.96, p = .028, d = 0.29, one-tailed, but not on the anterior ROIs, t (46) = -1.19, p = .88, d = -0.17, one-tailed.

A quantitative comparison of the topographies with a range-normalization method (McCarthy & Wood, 1985) revealed no statistical difference between the two tasks. For each participant, we first computed the difference ERPs between high and low responses within each task, then range-normalized these difference ERPs across all electrodes within each task. An ANOVA on range-normalized LPC voltage differences with factors anteriority, laterality, and task showed that the topographies were not significantly different between the two tasks: anteriority × task F (1, 46) = 0.58, p = .45, $\hat{\eta}_G^2$ = .002; laterality × task F (1, 46) = 1.85, p = .18, $\hat{\eta}_G^2$ = .003; anteriority × laterality × task F (1, 46) = 2.01, p = .16, $\hat{\eta}_G^2$ = .001.

In summary, ERPs associated with high ratings in both recent and lifetime familiarity tasks were more positive than those associated with low ratings in the 500ms to 800ms time window on the centroposterior ROIs. The direction and the topography of these ERP effects were consistent with the LPC component previously described in the literature on old–new effects in the recognition-memory literature (see (Rugg & Curran, 2007) for a review).

2.3.3 Does the LPC track only task-relevant memory signals?

First, we tested whether the LPC effect for cumulative recent familiarity is present only when judgements of this dimension are required. If that was the case, it should not track the amount of recent familiarity during the study phase during which this dimension was irrelevant for the judgement at hand (i.e., about animacy). For the critical comparison in the study phase, we binned the last presentation of each stimulus that was presented once or three times (low) versus seven or nine times (high). This process resulted in an average of 43 trials entering the ERPs for both binned levels. The corresponding trial rejection

rates were 13% for the “low recent-familiarity” condition and 14% for the “high recent-familiarity” condition. When these data were analyzed using an ANOVA, we observed an effect in the 500-800 ms time window related to the degree of recent familiarity, namely a significant anteriority × laterality × presentation frequency interaction; $F(1, 47) = 6.82$, $p = .012$, $\hat{\eta}_G^2 < .001$. Post hoc t-tests on the interaction revealed, however, that unlike the LPC effect observed in the test phase in posterior ROIs, the effect in this time window at study showed a right-lateralized frontal distribution: right anterior ROI, $t(47) = 2.39$, $p = .02$, $d = 0.35$, one-tailed; right centroposterior ROI, $t(47) = 1.00$, $p = .16$, $d = 0.14$.

For a formal comparison of the topography of the effect in this time window between the two experimental phases (study versus test), we also conducted an ANOVA on the range-normalized difference ERP in the LPC time window with factors anteriority, laterality, and phase (study versus test). Critically, there was a significant interaction between anteriority and phase: $F(1, 42) = 10.18$, $p = .003$, $\hat{\eta}_G^2 = .04$, in line with the idea that the ERP component captured in this time window is not the same in both phases of the experiment (Figure 2.4). In summary, the LPC we observed in relation to cumulative recent familiarity was present only when such signal was relevant to the current task.

In the next set of analyses, we tested whether the LPC effect we observed in relation to judgements of cumulative lifetime familiarity was also present only when the task required consideration of this dimension. We compared the influence of cumulative lifetime familiarity on ERPs during judgements of lifetime versus recent familiarity. For the latter, we used normative estimates of lifetime familiarity and the same binning with two levels (high versus low) as described previously. This process resulted in an average of 46 trials entering the ERPs for the “low lifetime-familiarity” condition and 38 trials for the “high lifetime-familiarity” condition. On average both conditions had 14% of the trials rejected. Critically, an ANOVA comparing the effect in the LPC time window between both tasks revealed a significant three-way interaction of anteriority × lifetime familiarity × task, $F(1, 46) = 4.76$, $p = .034$, $\hat{\eta}_G^2 = .001$. Follow-up analyses of this three-way interaction in the LPC time window showed that a anteriority × lifetime familiarity interaction during judgements of lifetime familiarity, $F(1, 46) = 15.37$, $p < .001$, $\hat{\eta}_G^2 = .008$, where the differences in ERP amplitude between high versus low lifetime

judgements were numerically more positive on the centroposterior ROIs, although the differences did not reach significance when tested using separate t-tests, all ps> .1. During judgements of recent familiarity, no effect involving the factor “lifetime familiarity” was significant, all ps > .1.

We also examined the issue of task relevance in a similar comparison but focusing on the effect of lifetime familiarity in the study phase (rather than presentation frequency; Figure 2.5). The pattern of results was comparable to that of the previous analyses. When comparing the normative lifetime familiarity ratings of first presentations in the study phase, we found a marginally significant main effect of lifetime familiarity in the LPC time window, F (1, 42) = 3.94, p = .054, $\hat{\eta}_G^2$ = .007. Importantly, this effect differed topographically from the LPC effect observed in the test phase when participants made judgements on lifetime familiarity, as indicated by a significant anteriority × laterality × phase interaction when tested using the range-normalization method described previously, F (1, 42) = 7.86, p = .008, $\hat{\eta}_G^2$ = .007. In summary, these analyses suggest that the LPC we observed in relation to lifetime familiarity was present only when this dimension was relevant to the task.

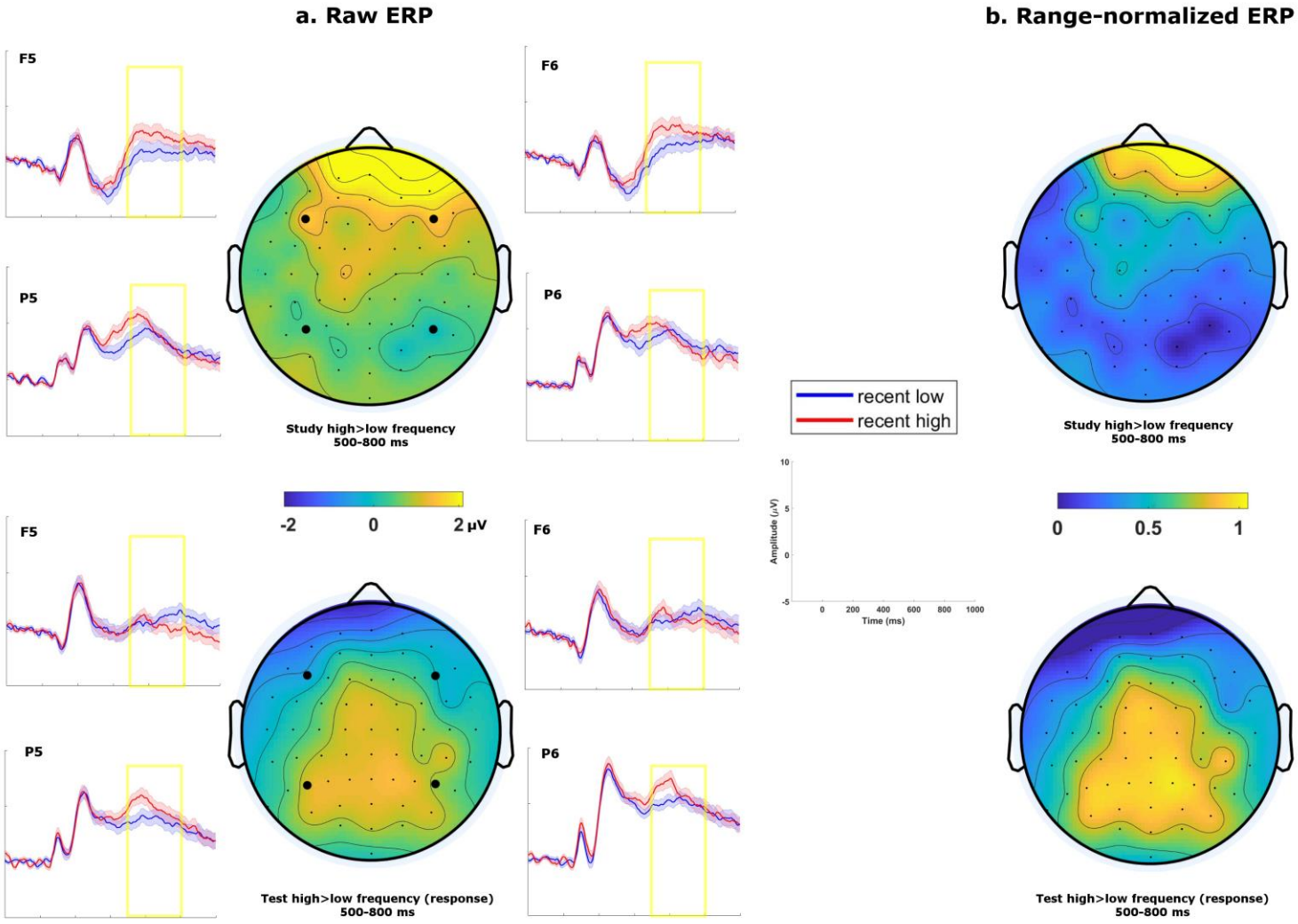

Figure 2.4: (a) Grand average topographies and ERP traces for recent familiarity in the 500-800 ms time window. Traces are plotted for 4 representative electrodes, with shaded areas representing standard errors of the mean. Study phase contrasts (top) were generated with actual presentation frequency. Test phase (bottom) contrasts were generated with participants' frequency responses. (b) Grand average topographies range-normalized across electrodes (i.e. values ranging from 0 to 1) of the same contrasts.

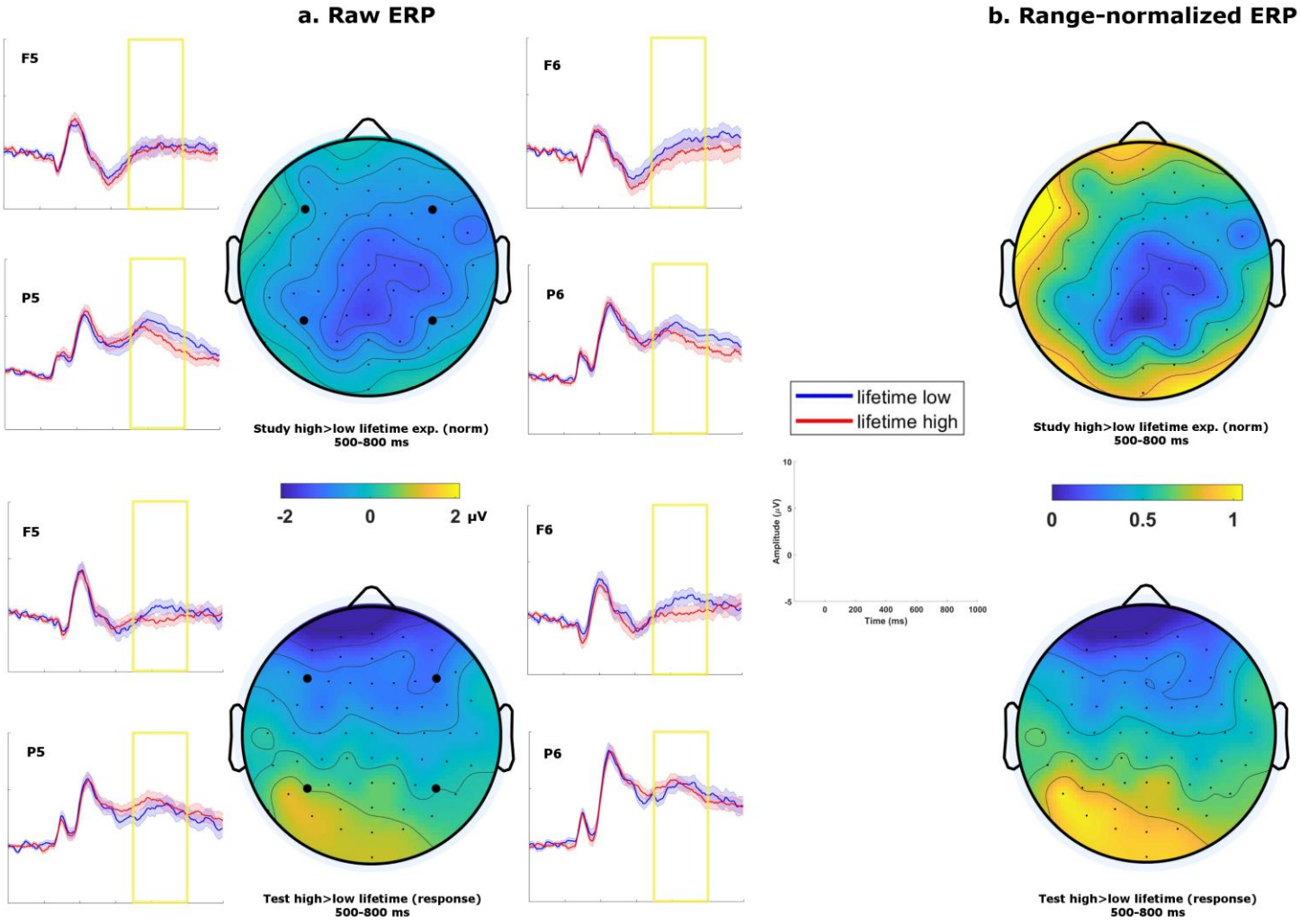

Figure 2.5: (a) Grand average topographies and ERP traces for lifetime familiarity in the 500-800 ms time window. Traces are plotted for 4 representative electrodes, with shaded areas representing standard errors of the mean. Study phase contrasts (top) were generated with normative score. Test phase contrasts (bottom) were generated with participants' responses on lifetime familiarity. (b) Grand average topographies range-normalized across electrodes (i.e. values ranging from 0 to 1) of the same contrasts.

2.3.4 Could the LPC effects be explained based on differences in response times?

To examine whether the shifts in topography we report for the LPC, and interpret in relation to task relevance, could be explained by differences in RTs across trials or conditions, we conducted several additional sets of analyses. First, we added single-trial ERP analyses with a model comparison approach, separately for the recent and lifetime familiarity effect, using the lme4 package in R (Bates et al., 2015) (see (Payne et al., 2015) for a similar approach). In these single-trial analyses, the mean amplitude in the 500-800 ms (LPC) time window was spatially averaged across electrodes in each ROI and was the dependent variable. The corresponding dataset includes all trials from the study and the test phase in which a response was made. The fixed factors were anteriority (frontal, centroparietal), laterality (left, right), task (animacy, frequency, lifetime), frequency (5-point), lifetime familiarity (5-point), and RT (continuous). Random intercepts of participants and words were also modeled. Frequency of recent familiarity was modeled as the actual presentation frequency, re-coded into 5 levels, in the study phase and in the lifetime familiarity task; in the frequency task it was modeled as judged frequency on the 5-point scale employed. Lifetime familiarity in the study phase and in the frequency judgement task was modeled based on normative data, while in the lifetime familiarity task it reflects perceived degree of lifetime familiarity judged on a 5-point scale. The resulting model comparisons were evaluated in terms of fits with χ^2 tests among models. Critically, these analyses revealed that models with the factor frequency (Model 2) or lifetime familiarity (Model 3) fit the data significantly better than a model that included only RT (Model 1), $\chi^2(51) = 194.76$, $p < .001$; and $\chi^2(67) = 97.22$, $p < .001$, respectively. These results suggest that the LPC effect we report cannot be explained solely by RT.

Second, we examined the role of RT in our topography ANOVA results. For each participant, we computed the average RT difference between high and low frequency trials, as well as the average RT difference between high and low lifetime familiarity trials, separately for the study and the test phase. Subsequently, we used these RT differences as a covariate in the two relevant analyses that compared LPC topography of

the frequency effect and lifetime familiarity effect between the study and the test phase. Critically, the anteriority × phase (study or test) interaction remained statistically significant with inclusion of this covariate, F(1,42) = 10.18, p = .003; F(1,42) = 13.21, p < .001, for frequency and lifetime familiarity, respectively. Again, these results suggest that the LPC effect we report cannot be explained solely with respect to differences in RT.

2.3.5 Does source activity in the left lateral posterior parietal lobe follow the pattern of the LPC effect?

To examine cortical regions linked to the decision-dependent LPC effect, we performed source localization on the binned ERP data (i.e. high vs. low). A recent review of a large number of fMRI studies suggests a critical role of ventral lateral parietal cortex in making memory decisions (Rugg & King, 2017). Meanwhile, two electrophysiological studies also point to the potential contribution of surrounding areas, such as intra-parietal sulcus and superior parietal lobule (Gonzalez et al., 2015b; Rutishauser et al., 2018b). These effects are typically left-lateralized. In light of these findings, we focused on two ROIs in the left lateral posterior parietal lobe, the ventral lateral parietal region which includes the angular gyrus, and the dorsal lateral parietal regions which includes the superior parietal lobule. The omnibus test was a repeated-measures ANOVA (n = 43). We extracted differences in absolute current densities between high and low bins, then averaged each difference across sources in each ROI and across the LPC time window (500 to 800 ms). These spatially and temporally averaged difference source measurements were used as the dependent variable, while task-relevance, task, and ROIs were used as within-participant independent variables. Significant main effects of task-relevance and ROIs were observed, F (1, 42) = 6.88, p = .012, $\hat{\eta}_G^2 = 0.014$, F (1, 42) = 5.31, p = .026, $\hat{\eta}_G^2$ = .006, respectively. A two-way interaction between ROIs and task-relevance was also observed, F (1, 42) = 9.48, p = .004, $\hat{\eta}_G^2$ = .004. We performed follow-up tests on this interaction, focusing on the effect of task-relevance within each ROI. Larger differences in source activity for the task-relevant compared to the task-irrelevant contrast was observed in the left ventral lateral parietal ROI, t (42) = 3.58, p < .001, d = 0.55, but not

in the left dorsal lateral parietal ROI, t (42) = 1.09, p = .28, d = 0.17 (Figure 2.6 & Figure 2.7).

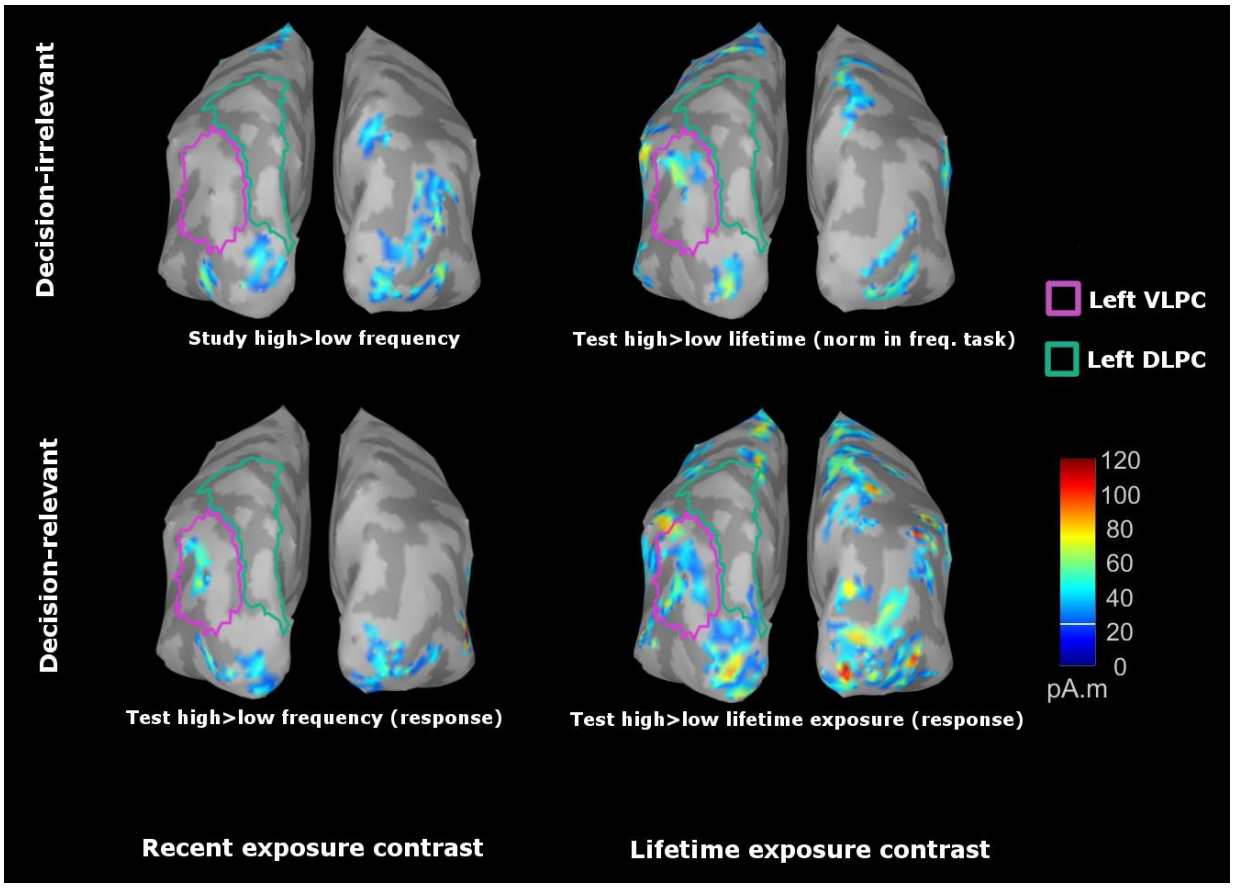

Figure 2.6: Grand average current density maps during the LPC time window for the contrasts of recent and lifetime familiarity. Boundaries of left ventral and dorsal lateral parietal cortex are marked in purple and green, respectively. Maps were plotted with amplitude threshold of 20% and size threshold of 20 in Brainstorm.

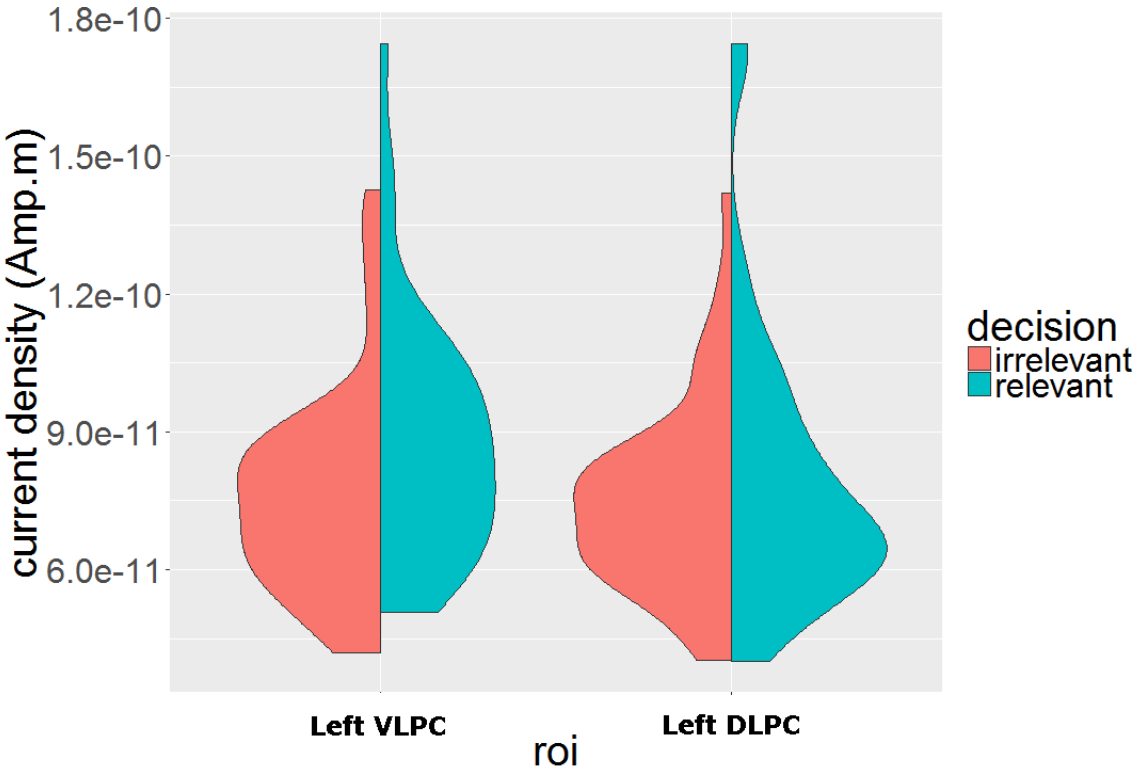

Figure 2.7: Violin plot on the effect of decision-relevance in the two ROIs (i.e. left ventral and dorsal lateral parietal cortices).

2.3.6 Does the FN400 also track perceived familiarity in a decision-dependent manner?

To determine whether the pattern of LPC effects was specific to this ERP component, we conducted a similar set of analyses to examine the time window of the FN400, that is, the other ERP component that has sometimes been reported to distinguish between perceived old and new items in recognition-memory judgements (although this remains controversial; see (Bridger et al., 2012; Ratcliff, Sederberg, et al., 2016; J. L. Voss & Federmeier, 2011b). Starting with the omnibus ANOVA for recent- and lifetime-familiarity judgements during the test phase, we found a trend similar to the effect in the LPC time window, as indicated by a two-way anteriority × response interaction, F (1,46) = 4.04, p = .050, $\hat{\eta}_G^2$ < .001. We also found a 4-way interaction of anteriority × laterality × task × response, F (1, 46) = 7.08, p = .011, $\hat{\eta}_G^2$ < .001. We further tested the 2-way interaction with simple-effect tests and the 4-way interaction with range-normalized topography comparison between the two tasks. Post-hoc tests on the anteriority ×

response interaction showed that the ERPs corresponding to the high response category were significantly more positive than those corresponding to the low response category on the centroposterior ROIs, t (46) = 2.22, p = .031, d = 0.32, one-tailed, but not on anterior ROIs, t (46) = 0.14, p = .44, d = 0.02. Topography comparison between the two tasks revealed a 3-way anteriority × laterality × task interaction, F (1, 46) = 5.73, p = .021, $\hat{\eta}_G^2$ = .003. While the direction of the effect in this time window is consistent with previously reported old-new effects (Bridger et al., 2014; Rugg et al., 1998), we note that the scalp distribution in the lifetime familiarity task was more posterior than a typical FN400 effect and more similar to an N400 as reported in studies on semantic memory (Kutas & Federmeier, 2011).

To determine whether the effect observed in the FN400/N400 time window (300—500 ms) for recent familiarity was tied specifically to a condition in which this dimension is task-relevant, we examined whether the effect was also present in the study phase. We observed a significant anteriority × presentation frequency interaction, F (1, 47) = 4.45, p = .040, $\hat{\eta}_G^2$ = .001; and a significant anteriority × laterality × presentation frequency interaction, F (1, 47) = 6.74, p = .013, $\hat{\eta}_G^2$ < .001. Post hoc t-tests on the 3-way interaction showed that the recent-familiarity effect during the study phase was significant on the left centroposterior ROI, t (47) = 2.67, p = .010, d = 0.38, but not in the anterior ROI, t (47) = 1.04, p = .15, d = 0.15. A topography comparison of the recent-familiarity effect between the study and the test phase revealed a significant three-way interaction, anteriority × laterality × phase, F (1, 42) = 8.23, p = .006, $\hat{\eta}_G^2$ = .005. The effect of cumulative recent-familiarity in this time window appeared to be more pronounced on the left centroposterior ROI during the study phase (Figure 2.8).

In our final analysis, we addressed whether effects of lifetime familiarity on the FN400/N400 are task relevant, first by comparing ERPs for judgements of lifetime familiarity with ERPs for normative lifetime familiarity during frequency judgements of recent familiarity. Critically, unlike for the LPC, there was no significant interactions involving lifetime familiarity × task in the 300-500 ms time window, all ps > .08. We also examined task-relevance in a similar comparison but focusing on the effect of lifetime familiarity in the study phase (rather than presentation frequency). The pattern of

results was comparable to that of the previous analyses. When comparing the ERPs elicited by first presentations of stimuli in the study phase, we found a significant three-way anteriority × laterality × normative lifetime familiarity interaction, F (1, 42) = 6.61, p = .014, $\hat{\eta}_G^2$ < .001. However, a topography comparison showed that this effect did not differ significantly from the ERPs for judgements of lifetime familiarity in the test phase (Figure 2.9), anteriority × phase, F (1, 42) = 0.14, p = .71, $\hat{\eta}_G^2$ < .001, laterality × phase, F (1, 42) = 1.07, p = .31, $\hat{\eta}_G^2$ = .002, and anteriority × laterality × phase, F (1, 42) = 0.31, p = .58, $\hat{\eta}_G^2$ < .001.

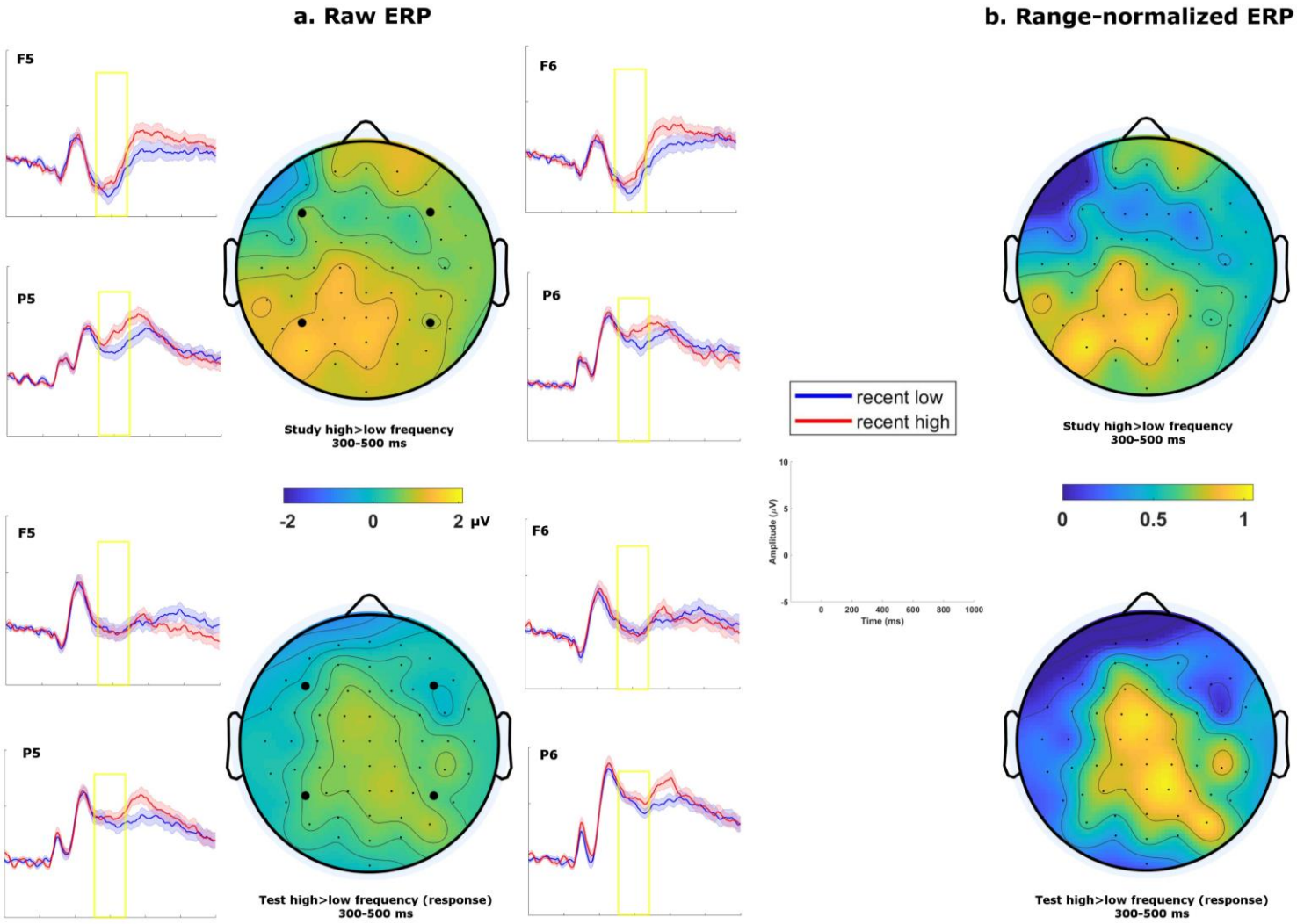

Figure 2.8: (a) Grand average topographies and ERP traces for recent familiarity in the 300-500 ms time window. Traces are plotted for 4 representative electrodes, with shaded areas representing standard errors of the mean. Study phase contrasts (top) were generated with actual presentation frequency. Test phase (bottom) contrasts were generated with participants' frequency responses. (b) Grand average topographies range-normalized across electrodes (i.e. values ranging from 0 to 1) of the same contrasts

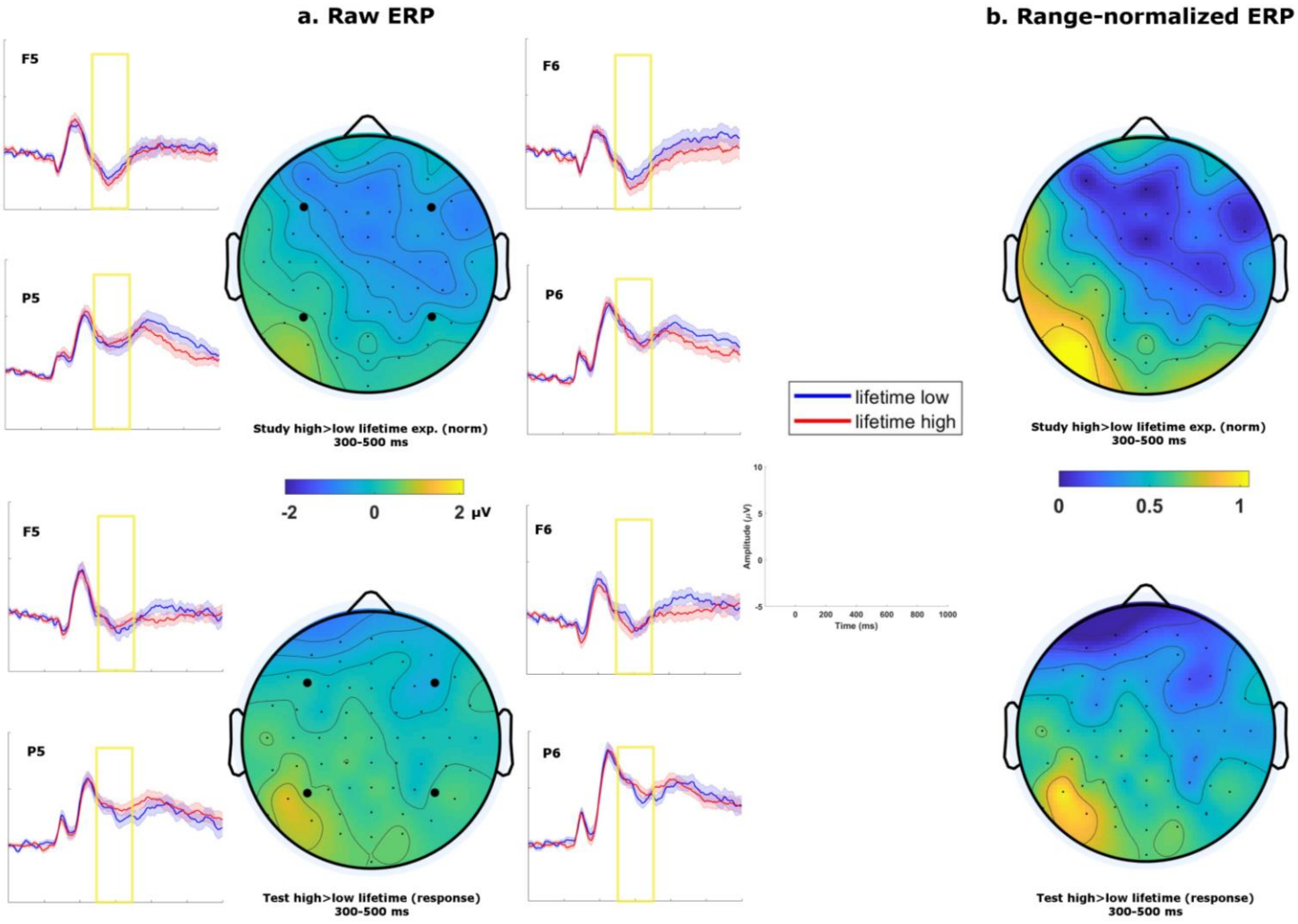

Figure 2.9: (a) Grand average topographies and ERP traces for lifetime familiarity in the 300-500 ms time window. Traces are plotted for 4 representative electrodes, with shaded areas representing standard errors of the mean. Study phase contrasts (top) were generated with normative score. Test phase contrasts (bottom) were generated with participants' responses on lifetime familiarity. (b) Grand average topographies range-normalized across electrodes (i.e. values ranging from 0 to 1) of the same contrasts.

2.3.7 Peak-based analyses

We performed exploratory peak-based analyses on effects reported above. In sum, the peak-based results, based on local peak amplitudes as well as two-step PCA, are largely consistent with what we reported (see Appendix A for more details).

2.4 Discussion

We investigated whether the LPC is linked to memory judgements and tracks the strength of multiple types of memory signals in a flexible decision-dependent manner. Participants made memory judgements either on relative frequency of item exposure in a study phase or based on cumulative lifetime experience. We showed that the LPC tracks cumulative familiarity regardless of whether the accumulation happened recently in the laboratory or over the lifetime. Critically, this effect is decision-dependent. It was present only when the memory judgement at hand required consideration of the relevant dimension. Moreover, source localization analyses revealed decision-dependent activity in left ventral lateral parietal cortex. Finally, we observed two topographically distinct components in an earlier time window that showed differential sensitivity to task-relevance. The FN400 produced a pattern of activity similar to the LPC for recent cumulative familiarity but not for lifetime familiarity. Namely, it tracked recent cumulative familiarity only when it was relevant to the task. A related ERP component, the N400, tracked both recent and lifetime cumulative familiarity, but it did so regardless of task-relevance.

2.4.1 Judgements of recent familiarity to object concepts

Most prior research on the LPC has focused on some form of memory judgement about recent laboratory exposure in study-test paradigms. This research has shown that the LPC robustly distinguishes hits from correct rejections in recognition memory judgements (Rugg & Curran, 2007). A significant body of research suggests that the LPC is linked specifically to the contribution of episodic recollection to recognition memory judgements. Evidence supporting this interpretation comes from studies adopting a variety of paradigms designed to (more or less) selectively manipulate recollective processes, including source memory judgements (Wilding & Rugg, 1996), associative recognition memory (D. I. Donaldson & Rugg, 1998; Tsivilis et al., 2001), and the Remember/Know paradigm (Curran, 2004; Woodruff et al., 2006). Specifically, the LPC has been shown to increase in size for correct versus incorrect source recognition judgements, for Remember as compared to Know responses, and for intact versus rearranged pairs in associative recognition. Some findings, however, have questioned the

specific link between the LPC and recollection, and instead point to a broader role of the LPC that is tied to decision making in memory judgements.

Finnigan, Humphreys, Dennis, and Geffen (Finnigan et al., 2002) analyzed the LPC amplitude in relation to the accuracy of old/new decisions in a recognition-memory paradigm, contrasting with the more common practice of focusing only on correct responses (i.e. Hit vs. Correct Rejection). They showed that the LPC was significantly more positive for correct than incorrect recognition responses not only when old but also when new items were considered. Moreover, correct rejections elicited a more positive LPC than did false alarms, indicating that this decision effect is not solely driven by general differences between old and new items (i.e., the old/new effect). More recently, as reviewed in the Introduction, a study based on drift-diffusion modeling of behavioural data revealed that the EEG amplitude in the time window coinciding with the LPC predicts participants' reaction time and accuracy of recognition-memory decisions on a trial-by-trial basis (Ratcliff, Sederberg, et al., 2016). Based on this finding, the authors suggested that the LPC tracks evidence accumulation in memory decisions. In other recent research directly focusing on familiarity and recollection, it has been reported that the LPC tracks confidence ratings when controlling for the relative proportion of Remember and Know responses (Brezis et al., 2016). Moreover, high-confidence Know responses elicited a more positive LPC than low-confidence Remember responses, a finding that the authors interpreted with reference to memory strength. Although no formal modeling of decision making was involved, this notion of memory strength can also be thought of as the evidence that drives memory decision. Findings from the current study are consistent with the idea that the LPC tracks memory signals when they are task-relevant. Critically, they also suggest that it is not sensitive to just one type of memory signal, but instead it can track multiple signals in a flexible manner depending on the specific demands of the memory task at hand.

In the present study, we employed frequency judgements to show that the LPC tracks memory signals in judgements about recent laboratory exposure in a decision-dependent manner. We manipulated the task-relevance of frequency information by comparing the effect of frequency in the test and study phases. When comparing stimuli judged to have

been presented with high versus low frequency, we observed the classic LPC during test. By contrast, when comparing the final presentation of stimuli presented 7 or 9 times in total versus once or 3 times in total, we did not observe an LPC in the study phase. In the earlier time window (i.e. 300-500 ms), a contrast based on judged presentation frequency in the test phase elicited a different effect compared to the contrast of actual presentation frequency in the study phase. This effect is comparable to the FN400 effect reported for old-new effects in other recognition paradigms that has been linked to relative familiarity (Bridger et al., 2014). As such our findings suggest that not all ERP components that have previously been linked to memory judgements are equally tied to decision processes.

Evidence from computational modeling and behavioral research on retrieval dynamics suggests that under many experimental conditions, familiarity is the primary basis for accurate frequency judgements (Hintzman & Curran, 1994). The FN400 effect on frequency judgements observed in the current study is consistent with this view. We manipulated item exposure at study in small increments over a substantial range of presentations and, at test, we included no novel lures. With this design, we minimized the likelihood that contextual information (underlying recollection) would allow for differentiation of the frequency of recent exposure. Thus, we maximized the need to rely on graded signals that code for recent incremental changes in familiarity in our frequency judgements. Nevertheless, it has been proposed that recollection may also contribute to frequency judgements through recursive reminding (Hintzman, 2004). Hintzman (2004) has argued for an account in which the repeated presentation of an item reminds participants of prior conscious experiences with that item. Consequently, both the current presentation and the recollected experiences are encoded, allowing for a recursive process. Frequency judgements are proposed to be sensitive to the depth of reminding, which naturally tracks the amount of cumulative recent exposure. Critically, the recursive reminding mechanism would operate not only when frequency is relevant to the task as in the test phase, but it would also occur spontaneously at study. The fact that we observed the LPC during frequency judgements in the test phase but not at study suggests that it does not reflect recollection-related recursive reminding. Findings from patient-based research also argue against an interpretation of the LPC in the current task as being

uniquely tied to recollection. We have previously reported that a focal anterior temporal-lobe lesion that includes left perirhinal cortex, but spares the hippocampus, produced impairments in making frequency judgements on this task in an individual (NB) with documented familiarity impairments but preserved recollection abilities (Bowles et al., 2016b).

2.4.2 Judgements of lifetime familiarity to object concepts

To our knowledge, the current study is the first to directly probe the LPC in memory judgements about cumulative lifetime familiarity to concepts (but see (Bridger et al., 2014) for related research on effects of word frequency). Mirroring our results for cumulative recent familiarity, we observed an LPC effect when comparing stimuli judged to have high versus low lifetime familiarity and the dimension was, thus, task-relevant. In contrast, when comparing stimuli with high versus low normative lifetime familiarity during recent familiarity or animacy judgements (in the study phase), the LPC effect was absent. Thus, these findings provide further support for the notion that the LPC tracks memory signals only to the extent that they are task-relevant.

A variable related to cumulative lifetime familiarity of concepts that has also been examined in the psycholinguistics- and recognition-memory literature is word frequency, that is, the frequency of words as measured in linguistic corpora. High frequency words tend to elicit faster and more accurate responses in linguistic paradigms (Rugg, 1990). In recognition paradigms, however, high frequency words tend to elicit more incorrect responses (i.e. more misses and false alarms as often described as mirror effect) (Bridger et al., 2014). This behavioral effect, in particular the increase in false alarms for words with high frequency, has been suggested to reflect a reliance on absolute memory strength (or cumulative lifetime familiarity) when no recent change in strength was introduced in a study phase (Coane et al., 2011; Mandler, 1980).

ERPs in both the FN400/N400 and the LPC time windows have been shown to be sensitive to word frequency across a range of tasks. Several studies have shown that high frequency words elicit a smaller N400 (Bridger et al., 2014; Polich & Donchin, 1988; Rugg, 1990; Young & Rugg, 1992). The literature on the LPC effect of word frequency is

more complex, in part due to inconsistencies in terminology (sometimes also referred to as P300 (Polich & Donchin, 1988), P530 (Rugg, 1990), or P600 (Rugg & Doyle, 1992; Young & Rugg, 1992)) and choice of time window. Rugg (Rugg, 1990), for example, used words of different frequencies with a concurrent manipulation of experimental repetition in a lexical decision task. He reported a word frequency effect on the LPC that interacted with repetition, in that the LPC was more positive for high frequency words during the first presentation, but switched polarity and was more positive for low frequency words during the second presentation. Differing somewhat from those results, we observed that the ERPs in the LPC time window were more positive for words with low degree of lifetime familiarity for the first presentation during the study phase. However, it is difficult to tell whether this subtle difference could be attributed to the selection of electrodes (Rugg reported a reversed polarity on the electrode Pz during the first presentation), differences between how word frequency and lifetime familiarity are represented in the brain, or differences between tasks (lexical decision vs animacy judgements).

In the context of our conclusion that the LPC marks decision-dependent memory processes, it also is interesting to ask whether word frequency would affect the LPC amplitude in memory tasks that require no judgement of word frequency or lifetime familiarity. Extant results in the literature are mixed. On one hand, some studies have shown that word frequency interacts with study status (old/new) in modulating the LPC amplitude in recognition paradigms (Rugg et al., 1995; Rugg & Doyle, 1992). On the other hand, a recent study (Bridger et al., 2014) that focused on old/new recognition judgements reported no effect on the LPC when comparing correct rejections of words with high versus low frequency. Similarly, when we compared stimuli with high and low degree of lifetime familiarity during the frequency judgement in the test phase, we observed no effect in the LPC time window. Although some caution is warranted when interpreting this negative finding, we note that it is in line with the idea that the LPC tracks memory signals only when they are task-relevant. On a more general level, it is also worth keeping in mind that experience with words and lifetime familiarity to concepts are correlated but only moderately so (Cree & McRae, 2003). In the lifetime familiarity task, we specifically instructed participants to make their judgement based on

the concepts a word refers to rather than word itself. While increases in lifetime familiarity of concepts tend to be tied to variability in episodic context, and typically go hand in hand with increases in concept knowledge (Duke et al., 2017, p. 201), it is unclear whether the same holds for increases in exposure to words in a more restricted reading context.

Although the structure of the task we employed to probe lifetime familiarity did not require any reference to a specific episodic encounter, it is interesting to consider whether episodic recollection may still have impacted performance. This possibility deserves consideration in light of prior evidence that implicates episodic recollection and hippocampal functioning in ostensibly semantic tasks, such as object naming or conceptual fluency, that is, the speeded generation of exemplars from different semantic categories (Greenberg et al., 2009; Klooster & Duff, 2015; Ryan et al., 2008; Sheldon & Moscovitch, 2012; Westmacott & Moscovitch, 2003; Whatmough & Chertkow, 2007). Such evidence has led to the suggestion that episodic and semantic memory may interact even on tasks that do not require recollection, and that recollection of a pertinent autobiographical episode can help generate or retrieve semantic information (see (Sheldon & Moscovitch, 2012) for detailed discussion). Behaviorally, ratings of degree of lifetime familiarity, as used in the current study, are positively correlated with perceived ease of recovering a pertinent unique autobiographical episode (Bowles et al., 2016b). However, we previously reported that a patient (HC) with severe hippocampal damage and documented impairments in recollection (Kwan et al., 2010; Rosenbaum et al., 2011) performed similarly to healthy controls on the same paradigm (Bowles et al., 2016b). Furthermore, patient NB, an individual with well documented deficits in assessment of familiarity based on recent exposure, but preserved recollection abilities, showed abnormal performance in judging lifetime familiarity to concepts (Bowles et al., 2016b). This pattern of results suggests a functional distinction between the recollection of the time and place of particular autobiographical instances of object encounters, and the assessment of degrees of experience over hundreds or thousands of encounters throughout a lifetime. Critically, it also suggests that contributions of recollection to assessing cumulative lifetime familiarity are neither necessary nor sufficient.

2.4.3 Source localization of ERP effects and the role of the parietal lobe

The electrodes that were selected to represent the LPC in the current study are broadly sensitive to source activity in the posterior lateral parietal cortex and surrounding regions (Mitka & Riecansky, 2018). Recent studies have linked left posterior lateral parietal cortex to recognition memory decisions with intracranial electrocorticography (ECoG) and recordings from depth electrodes in humans (Gonzalez et al., 2015b; Rugg & King, 2017; Rutishauser et al., 2018b). To explore whether the decision-dependent LPC effect could be linked to activity in this region, we employed source localization to estimate the current densities in the left ventral and dorsal posterior lateral parietal lobe. Because we observed the decision-dependent effect on the LPC in both types of cumulative memory judgements, we examined the data for both tasks in the same analysis. When contrasting high versus low familiarity stimuli across tasks, source activation in the left ventral lateral parietal cortex was indeed stronger for the task-relevant contrast than the task-irrelevant contrast during the LPC time window. This effect was not present in dorsal parietal cortex. While caution is necessary when interpreting our source localization results in relation to specific anatomical structures, we note that the findings from numerous fMRI studies point to a role of the left angular gyrus in aspects of decision making during memory judgement (see (Rugg & King, 2017) for a review), and that the interpretation of this angular gyrus involvement mirrors that of the LPC in ERP studies. To the extent that source activity in the left angular gyrus during the LPC time window was found to be sensitive to the task-relevance of information in the current study, our findings provide initial evidence that links these sets of findings across the two imaging methodologies. Future research can build on these initial source-localization findings with an approach that combines both imaging modalities with the tasks employed in the present study.

Chapter 3

3 « Perirhinal cortex automatically tracks recent and lifetime familiarity regardless of task-relevance»

Recognition memory, the ability to track past occurrences of objects or other aspects of the environment, plays an important role in our everyday life. There is strong evidence that the perirhinal cortex (PrC) contributes to recognition memory, especially for familiarity-based recognition. Familiarity is a sense of oldness that typically arises effortlessly. It has been proposed to rely on rapid, automatic retrieval that is independent of the more effortful recollection of contextual information about a pertinent prior episode (M. W. Brown & Aggleton, 2001; Eichenbaum et al., 2007; Jacoby & Dallas, 1981; Mandler, 1980; Mayes et al., 2007; Yonelinas, 2002). In experimental settings with human participants, recognition memory is generally probed with study-test paradigms, in which participants are presented with a list of stimuli in an initial study phase and are subsequently asked to distinguish those studied stimuli from novel unstudied stimuli in a test phase. Various study-test paradigms can be used to separate familiarity from recollection, based on theoretical assumptions made about their distinctions. For example, the remember/know paradigm (Tulving, 1985) relies on participants' introspection of the presence or absence of contextual information at retrieval, with "know" responses representing recognition based on familiarity. Source memory paradigms (Yonelinas, 1999b), by contrast, rely on participants' ability to make accurate memory judgments about specific contextual information that characterized the study phase (e.g. which list stimuli were in, or in which modality stimuli were presented). The process-dissociation procedure (Jacoby, 1991) provides a means to distinguish between familiarity and recollection based recognition, building directly on the idea that familiarity is an automatic process that dominates response output when controlled recollection processes fail. Another way to probe familiarity is to ask participants to rate the frequency of stimulus occurrences in a study phase. It has been suggested that when such judgements are made for stimuli previously encountered at different frequencies (at least once) in the study phase, it is supported mainly by familiarity. Arguably, this is the case because such judgements require probing of fine-grained variations in memory

strength of items encountered in the same episodic context (Anderson et al., 2021; Bowles et al., 2016b; Duke et al., 2017; Hintzman, 2004; Hintzman & Curran, 1994). Although frequency judgments have also been linked to contributions from perirhinal cortex in cognitive neuroscience research, the extant evidence is limited and the exact mechanisms that underly PrC contributions remain poorly understood (Bowles et al., 2016; Duke et al., 2017). A question of particular theoretical importance is whether PrC tracks cumulative levels of familiarity induced by variations in prior exposure automatically, regardless of whether the signal is relevant for the task at hand.

Another important issue to consider when probing familiarity for meaningful stimuli is that stimuli presented in a study phase would have typically been countered hundreds or thousands of times outside of the experimental context prior to the study phase. Mandler (1980) incorporated the distinction between familiarity changes due to study-phase presentations and the absolute familiarity based on lifetime experience in a dual-process framework, in which the familiarity-based recognition in a study-test paradigm relies on the ratio of recent familiarity changes to the absolute level of familiarity. While most research on recognition memory focused on recent/relative familiarity, one can also ask participants to judge the absolute magnitude of familiarity they have with respect to concrete concepts (i.e. lifetime familiarity). Critically, on the phenomenological level, people generally can distinguish lifetime familiarity (e.g. How familiar are you with mangosteen?) from recent changes of familiarity (e.g., Have you seen an apple in the study phase?), although in certain experimental settings, it is possible to confuse the two (more on this point later). Judgements of lifetime familiarity also demonstrate reliability and external validity, as people from the same cultural background tend to agree on their lifetime familiarity ratings, and their ratings tend to correlate with objectively measured word frequency (Cree & McRae, 2003; Moreno-Martínez et al., 2014a). The current study aimed to address the role of PrC and other cortical regions in these two types of familiarity, with a particular focus on whether PrC tracks both types of familiarity automatically.

Behavioral evidence on the mirror effect in recognition memory speaks to the relationship between lifetime familiarity versus recent changes of familiarity (Glanzer &

Adams, 1990; Reder et al., 2000). Generally speaking, this research suggests that both types of familiarity can be distinguished in recognition-memory judgments, but that they are also prone to be confused in some circumstances. In this line of research, word frequency is typically employed as a marker of lifetime familiarity of the corresponding concept. The mirror effect reflects a pattern of recognition performance in a study-test paradigm in which high-frequency words tend to be associated with lower hit rates but higher false alarm rates than low-frequency words. For example, Coane et al. (2011) used a two-list exclusion paradigm combined with response deadline manipulations to separate recent (relative) familiarity from lifetime (absolute) familiarity. Participants studied two lists of words, one visually and the other auditorily. They were then asked to only assign "old" response to words presented auditorily in the study phase and respond "new" to both visually presented old words and novel words. They found that high-frequency new words showed the heightened false alarm rate compared to low-frequency new words, replicating the typical mirror effect attributed to higher degree of lifetime familiarity of high-frequency words. However, with a respond deadline short enough to eliminate recollection processes, low-frequency old words resulted in significantly more list-exclusion error, suggesting a familiarity signal that was stronger for low- compared to high-frequency old words. These findings demonstrated that both types of familiarity simultaneously contributed to memory decisions. Moreover, given that they diminished participants' ability to accurately perform the task, it suggests that both familiarity signals were automatically activated and to some extent beyond participants' cognitive control. In terms of neural correlates, ERP studies have shown that topographically distinct ERP components were sensitive to recent and lifetime familiarity, suggesting the involvement of different neural substrates (Bridger et al., 2014; Yang et al., 2019). Though informative in demonstrating the existence and separability of familiarity signals on different time scales, these findings do not speak to the involvement of PrC.

Most fMRI studies that have implicated PrC in familiarity for meaningful stimuli have focused on recent changes in familiarity introduced in a study phase (see Eichenbaum et al., 2007, for review). For example, Daselaar et al. (2006) asked participants to make old/new and confidence judgement on words and found that PrC blood oxygenation level dependent (BOLD) activity decreased continuously from the lowest (high-confidence

new) to the highest level of familiarity (high-confidence old). Similarly, Montaldi et al. (2006) found a linear decrease of PrC BOLD activity with increasing level of familiarity measured with a remember/know paradigm using real-world scene stimuli. Although there are a few studies in which increasing BOLD activity with increasing levels of familiarity was reported in PrC (Gimbel et al., 2017; Yassa & Stark, 2008), the typical finding is a decrease in BOLD activity with recent familiarity during retrieval. Note that although the mapping between BOLD activity and neuronal firing is complex (Henson & Rugg, 2003), it has been suggested that this decrease in BOLD signal with increasing familiarity may reflect what is typically referred to as repetition suppression in neurophysiological studies in non-human species (Xiang & Brown, 1998).

On the other hand, only limited evidence exists in humans that links lifetime familiarity of object concepts to PrC. An fMRI study from our lab has identified a region in the left perirhinal cortex that tracked judged degree of recent and lifetime familiarity (Duke et al., 2017). Participants made cumulative memory judgment on concrete concepts (e.g. apple) presented as words in a modified study-test paradigm. One judgement concerned the relative presentation frequency during the study phase as a measure of recent familiarity. For words shown only in the test phase, participants judged lifetime familiarity of the concepts that those words denote. BOLD activity in the PrC tracked participants' ratings in both types of judgement but in opposite directions. The signal increased with increasing degree of lifetime familiarity but decreased with increasing degree of recent familiarity. Critically, PrC was the only region to show this pattern, demonstrating its unique involvement in tracking familiarity across time scales. Furthermore, several studies on patient NB, who had a lesion in the left anterior temporal region that included much of PrC but spared the hippocampus, provided converging evidence. NB was impaired in judging recent familiarity while demonstrating preserved recollection in numerous paradigms (Bowles et al., 2007; Köhler & Martin, 2020). Critically, she was also impaired in judging lifetime familiarity, suggesting a causal role of PrC in both types of familiarity (Bowles et al., 2016b).

In the dual-process model proposed by Jacoby and colleagues, familiarity is explicitly treated as an automatic process while recollection is a controlled process (Jacoby &

Dallas, 1981; Yonelinas & Jacoby, 2012). In particular, the basis of familiarity is thought to be a fluency signal which refers to the relative ease of processing the stimuli. Prior exposure of the stimuli is one way to increase fluency even when such exposure is not directly relevant to task goals. The conscious experience of familiarity is thought to rely on an attribution system that interprets the fluency to be mnemonic in nature (Jacoby et al., 1989; Jacoby & Dallas, 1981). A more recent model mapped these processes onto different brain regions (Bastin et al., 2019). In this model, memory relies on a core system and an attribution system, with the former playing a foundational role in building the memory trace while the latter playing a supplementary role to interpret and reflect on the memory trace. The core system can be further divided into two specialized systems based on content: one for entities and the other for context. Of particular relevance, PrC is proposed to be one of the key regions in the entity core system that codes for entity-level fluency.

One limitation of Duke et al. (2017) was that the PrC effects with respect to recent and lifetime familiarity were analyzed only when they were task-relevant. As such, it is not clear whether PrC automatically tracks either or both types of familiarity regardless of a person's goals. In humans, two lines of memory research speak to the automaticity of familiarity signal. The first one is the research on priming effects, which can be though as a marker of fluency. Thus, this signal may be of the same kind as the one that underlies familiarity as proposed in attribution models (Bastin et al., 2019; Jacoby et al., 1989). Priming effects are often probed with indirect memory tasks. Participants are first exposed with either the entire primed target or association/feature of it and are asked to make some non-mnemonic judgement (e.g. animacy judgement). Memory signals resulted from the recent exposures in this type of paradigms is by definition task-irrelevant. fMRI studies using this type of paradigms have found signal reduction in PrC for primed versus unprimed stimuli, and the magnitude of such reduction was correlated with behavioral priming effect (e.g. faster response) (Voss, Hauner, & Paller, 2009; Wang, Ranganath, & Yonelinas, 2014). The other line of research, largely unexplored in neuroimaging literature, is the word-frequency mirror effect. Whereas neural priming effect could be conceptualized as task-irrelevant signals of recent familiarity, a word-frequency effect in a recognition paradigm could be conceptualized as task-irrelevant

signals of lifetime familiarity. Of the limited number of neuroimaging studies we could find that investigated mirror effect (de Zubicaray et al., 2005a, 2005b), no PrC effect of word-frequency was reported.

To the best of my knowledge, no study has investigated whether the PrC automatically tracks familiarity on both short (e.g. through recent experimental exposure) and long (e.g. through lifetime exposure) time scales regardless of task relevance. Following the fluency attribution framework of familiarity (Bastin et al., 2019; Jacoby et al., 1989), prior exposure automatically leads to enhanced processing fluency, which can be interpreted as familiarity. In the current study, we participants judged recent and lifetime familiarity in a paradigm that closely matched task structures and stimulus characteristics between the two dimensions. We hypothesized that PrC activity would track familiarity on both short and long timescales regardless of task relevance. Specifically, we predicted that both recent and lifetime familiarity effects would be present in PrC not only when participants were judging familiarity on the corresponding time scale, but also when they were making familiarity judgement on a different time scale, and when they were not judging familiarity at all.

3.1 « Methods »

The behavioral paradigm was identical to Chapter 2 except that I also collected participants' lifetime familiarity ratings on object concepts used in the recent-familiarity task at the end of the experiment.

3.1.1 Participants

Thirty-one right-handed participants (24 females), aged between 18 and 40 years old (mean age = 27) were recruited from the Western campus community through OurBrainsCAN and were compensated for CAD $20 per hour. Participants were fluent in English, had grown up in North America, and reported no history of psychological or neurological disorder. One participant was excluded from all analyses due to excessive motion during scanning. All procedures were approved by the Western University Health Sciences research ethics board.

3.1.2 Materials

Stimuli were nouns in English representing 180 concrete concepts selected from a database based on Canadian norms (McRae et al., 2005). These words were selected to cover a wide range of familiarity based on the normative data (Mean = 5.9, Rang = 7.2 on a 9-point scale). They were divided into 10 sets of 18 words, matched on mean and range of feature overlap with respect to the entire database, normative lifetime familiarity, log word frequency, number of letters, and number of syllables. This was done using the "Match" software which sampled from the initial sets of stimuli (10 in our case) to create another set of stimuli (10 in our case) with matched dimensions in terms of mean, median, standard deviation (van Casteren & Davis, 2007). The match among the output sets was confirmed with a MANOVA in R (Pillai's trace = 0.17, F (45, 850) = 0.68, p = .94). Five sets of stimuli were chosen to be used in the study phase and for judgement of recent familiarity, while the other 5 sets were used for judgement of lifetime familiarity. This assignment was counterbalanced across participants.

3.1.3 Procedure

The experiment consisted of three phases with the first two carried out inside the scanner (Figure 3.1). For the two scanned phases, stimuli were presented on a projector screen inside the scanner. For the final phase (outside of the scanner), stimuli were presented on a laptop.

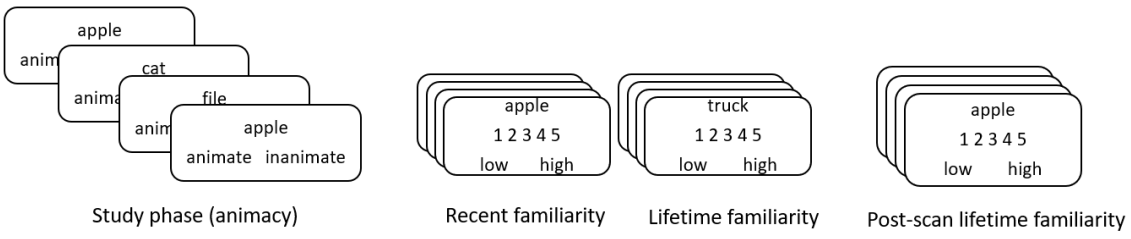

Figure 3.1: Behavioral paradigm. Participants completed a study phase (animacy judgement, left) and a test phase (recent and lifetime familiarity judgement, middle) in the scanner. Afterwards, they also rated lifetime familiarity on stimuli used in the study phase outside of the scanner (right).

Participants began with a study phase in which they incidentally encoded 5 sets of stimuli (i.e. 90 unique concepts in total) while making animacy judgements. Critically, stimuli from each of the 5 sets were presented once, three times, five times, seven times, or nine times, respectively, resulting in a total of 450 study trials. Each trial began with a fixation cross, whose duration was jittered across trials with a minimal duration of 1 second, maximal duration of 4 seconds, and a mean duration of 1.5 seconds. Following the fixation cross, a stimulus appeared on the screen for 1.5 seconds. Participants were asked to judge whether the word represented an animal or not by pressing their left or right index finger on two MR-compatible button boxes. The finger assignment was counterbalanced across participants. The first response made within 1.5 seconds of stimulus onset and during the fixation screen following the presentation of the stimulus was registered. The presentation order was pseudorandomized with the constraint that the same stimulus could not reappear within 3 trials. Participants were instructed to disregard the repetitions and make their judgement as usual.

After participants were familiarized with the use of button boxes in a practice session (see below), they were given verbal and written instructions for the test phase. This phase consisted of two tasks in alternating blocks of 5 trials. One task involved judging recent familiarity, in which participants were presented with stimuli that they had seen in the study phase and were asked to judge relatively how frequently they had experienced each of them on a 5-point Likert scale with 5 being most frequent. The other task involved judging lifetime familiarity, in which participants were presented with stimuli that they had not seen in the study phase (i.e. the other 5 sets of stimuli, see Materials) and were asked to judge how familiar they were with the thing that the word represents based on their lifetime experience, again on a 5-point Likert scale with 5 being most familiar. Before the tasks switched, a prompt was shown on the screen to let participants know what the next block would be. Participants indicated their ratings using the key mapping they had learnt in the practice phase. Regardless of the task, each trial started with a fixation cross of jittered length, with a minimal duration of 2.5 seconds, maximal duration of 10 seconds, and a mean duration of 4 seconds. The first response made during the presentation of the stimuli and the fixation cross following that was registered.

Participants were instructed to rely on their intuition and refrain from spending too much time on each trial when making the judgement.

After the scanning session, participants judged lifetime familiarity on stimuli used in the study phase and during recent familiarity judgements during scanning. These ratings allowed us to probe signals correlated with lifetime familiarity when such information was irrelevant to the participants' tasks (i.e. recent familiarity and animacy judgement). All 90 stimuli were presented in a random order in one block on a laptop, while the instruction and the finger mapping were the same as in the test phase.

Following the study phase, participants completed a practice session in the scanner to familiarize them with the button boxes and finger mapping for the test phase. The finger mapping was set up that 1 and 2 mapped onto the middle and index fingers on one hand, while 3, 4, and 5 mapped onto the index, middle, and ring fingers on the other hand, respectively. The hand assignment was counterbalanced across participants. On each trial participants were asked to respond as quickly and accurately as possible to an integer randomly chosen within the range of 1 to 5 by pressing the corresponding button. They had on average 3 seconds to respond. Participants proceeded to the test phase after consecutively making 45 correct button presses.

3.1.4 Behavioral analyses

To assess the accuracy of participants' recent familiarity judgements, we correlated each participant's frequency ratings with objective presentation frequencies. To assess the accuracy of participants' lifetime familiarity judgements, we correlated each participant's lifetime familiarity ratings (in test and post-scan phases) with normative ratings from McRae et al. (2005). These correlations across participants were tested against zero with t-tests.

For task-irrelevant familiarity signals, we conducted two sets of behavioral analyses. First, we investigated an effect analogous to the typical mirror effect. Specifically, we calculated, on a trial-by-trial basis, the overestimation error of participants' recent familiarity judgements, defined as judged minus actual presentation frequency (both were

scaled from 1 to 5). Then for each participant, we conducted a linear regression with this overestimation measurement as the dependent variable and the post-scan lifetime familiarity ratings as the independent variable. Finally, we tested the slopes of this regression model against 0 across participants with a one-tailed t-test seeking a positive slope, with the assumption that higher lifetime familiarity would lead to overestimation of recent familiarity, mimicking the increased false-alarm rate observed in typical mirror effect studies.

Second, we investigated a task-irrelevant familiarity effect when participants were not making memory judgements (i.e. during animacy judgement). We probed for a priming effect of recent and lifetime familiarity simultaneously. Within each participant, we z-scored the response latency and number of presentations (i.e. 1^{st} to 9^{th}) during animacy judgements, as well as post-scan lifetime familiarity ratings. Then we fit a linear regression model on these *z*-scores with response latency as the dependent variable, and the other two factors as independent variables. Slope estimates of the two independent variables were extracted and tested against 0 with two-tailed t-tests across participants.

3.1.5 fMRI scanning protocol

The scanning was conducted using a Siemens Prisma 3 Tesla scanner. We acquired T1-weighted (MPRAGE, 208 slices; TR 2400 ms; TE 2.28 ms; flip angle 8 degrees; FOV 256*256 mm; 0.8 mm isotropic voxels) and T2-weighted (SPC, 208 slices; TR 3200 ms; TE 564 ms; FOV 256*256 mm; 0.8 mm isotropic voxels) anatomical scans for each participant. For the functional scans, the study phase was divided into 5 runs of about 5 minutes each, with short breaks in between. The practice session was scanned for 1 run of 10 minutes or until participants reached the accuracy criteria. The test phase was divided into 4 runs of about 5 minutes each, with short breaks in between. The total scanning time including preparation was about 1 hour and 20 minutes. All functional runs used the same echo-planar imaging (EPI) protocol, with 2 mm isotropic voxels covering the whole brain. Slices were oriented perpendicular to the hippocampal long axis. Multiband factor of 2 and GRAPPA factor of 3 were used. The TR was 2.5 seconds. To reduce susceptibility artifact in the PrC region, we acquired our functional data with 3 echoes at 12.00 ms, 29.94 ms, and 47.88 ms (Kundu et al., 2017) which were later combined into

one image at the preprocessing stage. We also acquired fieldmaps for denoising purposes at the end of the scanning session.

3.1.6 fMRI preprocessing

fMRI data were preprocessed with fMRIPrep 1.5.4 (Esteban et al., 2019), which is based on Nipype 1.3.1 (Gorgolewski et al., 2011). The detailed preprocessing pipeline (automatically generated by fMRIPrep) can be found in Appendix B.

3.1.6.1 Anatomical data preprocessing

The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU), then skull-stripped with a Nipype implementation of the antsBrainExtraction from ANTs. The brain mask was further refined with a custom procedure in fMRIPrep. The anatomical scans and the brain masks were normalized to FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model (MNI152NLin6Asym). Brain masks in this MNI space from all participants were added together to form a group-level explicit mask used in the first-level general linear model (see fMRI analyses).

Bilateral PrC masks was created for each participant using Automatic Segmentation of Hippocampal Subfields (ASHS) (Yushkevich et al., 2015) in their native space. These masks were registered to the MNI space using ANTs and voxels labelled as PrC in 75% of the participants were included to form a group-level mask. To investigate if other regions showed similar response profile as PrC, we also conducted ad hoc analyses on anterior and posterior inferior temporal cortex, as well as hippocampus and entorhinal cortex. The entorhinal and hippocampal masks were generated with ASHS in the same way as the PrC mask. IT was defined directly in the MNI space using WFUPickAtlas (Maldjian et al., 2003, 2004) in SPM. Anterior and posterior IT were separated at the coronal slice that divides the IT into two halves of equal volume. If any non-PrC mask had overlapping voxels with the PrC mask, such voxels were assigned to PrC. Unless otherwise specified, the statistical results regarding regional activity were controlled for peak-level family-wise error rate within each group mask.

3.1.6.2 Functional data preprocessing

For each functional run, a reference volume and its skull-stripped version were generated using a custom methodology in fMRIPrep. Susceptibility distortion was corrected using the fieldmaps. The functional scan was then co-registered to the T1w image using bbregister (FreeSurfer) with 6 degree of freedom. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) were estimated before any spatiotemporal filtering using mcflirt (FSL). Slice-time correction was performed using AFNI. The BOLD time-series were then resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions (preprocessed BOLD). A T2* map was estimated from the preprocessed BOLD by fitting to a monoexponential signal decay model with log-linear regression. For each voxel, the maximal number of echoes with reliable signal in that voxel were used to fit the model. The calculated T2* map was then used to optimally combine preprocessed BOLD across echoes following the method described in (Posse et al., 1999). The optimally combined time series was carried forward as the preprocessed BOLD. These BOLD time-series were resampled into MNI152NLin6Asym. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA) was performed on the preprocessed BOLD on MNI space time-series after removal of non-steady state volumes and spatial smoothing with an isotropic, Gaussian kernel of 6mm FWHM (full-width half-maximum). These resulted in “non-aggressively” denoised fMRI data, in the sense that shared variance between presumed data and presumed noise was retained. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al., 2007).

3.1.7 fMRI analyses

The fMRI analyses used SPM12 version 7771 (Penny et al., 2011) and custom scripts in MATLAB R2018a. Unless otherwise specified, all analyses were performed on the “non-aggressively” denoised data (see functional data preprocessing) in the MNI space. Blood-Oxygen-Level Dependent (BOLD) response were modelled with boxcar functions with the duration of stimulus presentations convolved with a canonical hemodynamic

function. Conditions modeled in general linear models (GLMs) differed among analyses and their details are covered in the corresponding result sections. Trials in which participants failed to make a response were modelled as a separate condition in all GLMs and were excluded from further analyses. All GLMs on the first level also included the top 6 aCompCor in white-matter and cerebrospinal fluid that explained the most variance as nuisance regressors. Linear contrasts of beta images generated from first level GLMs were taken to the second level for group-level statistical inferences. Our primary interest was in PrC, but we also conducted secondary analyses on other regions to determine the specificity of results we obtained in PrC. We focused on the hippocampus, entorhinal cortex, as well as anterior and posterior IT. Results in these regions were corrected for peak-level family-wise error within the group mask of each as mentioned before. We did not apply additional correction for multiple comparisons across these non-overlapping ROIs, given that regions other than PrC were not of primary interest. We also conducted exploratory whole-brain analyses with peak-level family-wise error correction.

3.2 Results

3.2.1 Behavioral results

In the test phase, participants' recent familiarity ratings correlated significantly with objective presentation frequencies, $t(29) = 12.70$, $p < .0001$ (mean Pearson's $R = 0.43$, $SD = 0.19$). In addition, their lifetime familiarity ratings were significantly correlated with the normative data both for the set of items presented during the test phase, $t(29) = 31.37$, $p < .0001$ (mean Pearson's $R = 0.54$, $SD = 0.09$) and those presented during the post-scan phase, $t(29) = 11.98$, $p < .0001$ (mean Pearson's $R = 0.44$, $SD = -.20$) (Figure 3.2A). These results demonstrate that overall participants were sensitive to familiarity signals on both time scales. The magnitude of the correlation coefficients were also similar to previous reports (Duke et al., 2017; Yang et al., 2019). The mean correlation between lifetime familiarity ratings and normative data was weaker, and the standard-deviation was larger in the post-scan than in the test-phase. This was in part driven by two participants having negative correlations in the post-scan phase. Notably, the same two participants showed positive correlations between their test-phase lifetime ratings and normative data with magnitudes comparable to other participants, suggesting that

they were not fully adhering to instructions in the post-scan phase. Given our interest in automatic familiarity signals, we retained their data and replaced only their post-scan lifetime familiarity ratings with normative ratings in later analyses.

When judging recent familiarity, participants tended to underestimate the presentation frequency significantly more for concepts with lower lifetime familiarity, $t(29) = 2.75$, $p = .005$ (Figure 3.2B). This pattern is consistent with the typical mirror effect, in that task-irrelevant lifetime familiarity biased judgement of recent familiarity. In the study phase, participants' response latencies decreased with increasing presentation frequency, $t(29) = -7.50$, $p < .0001$, and increasing degree of lifetime familiarity, $t(29) = -2.43$, $p = .022$ (Figure 3.2C). The reduction in response latencies with increasing presentation frequency is consistent with the well-established repetition priming effect, demonstrating an automatic increase in fluency due to recent exposure. Similarly, the reduction in response latencies with increasing lifetime familiarity can be considered as increased fluency due to lifetime exposure.

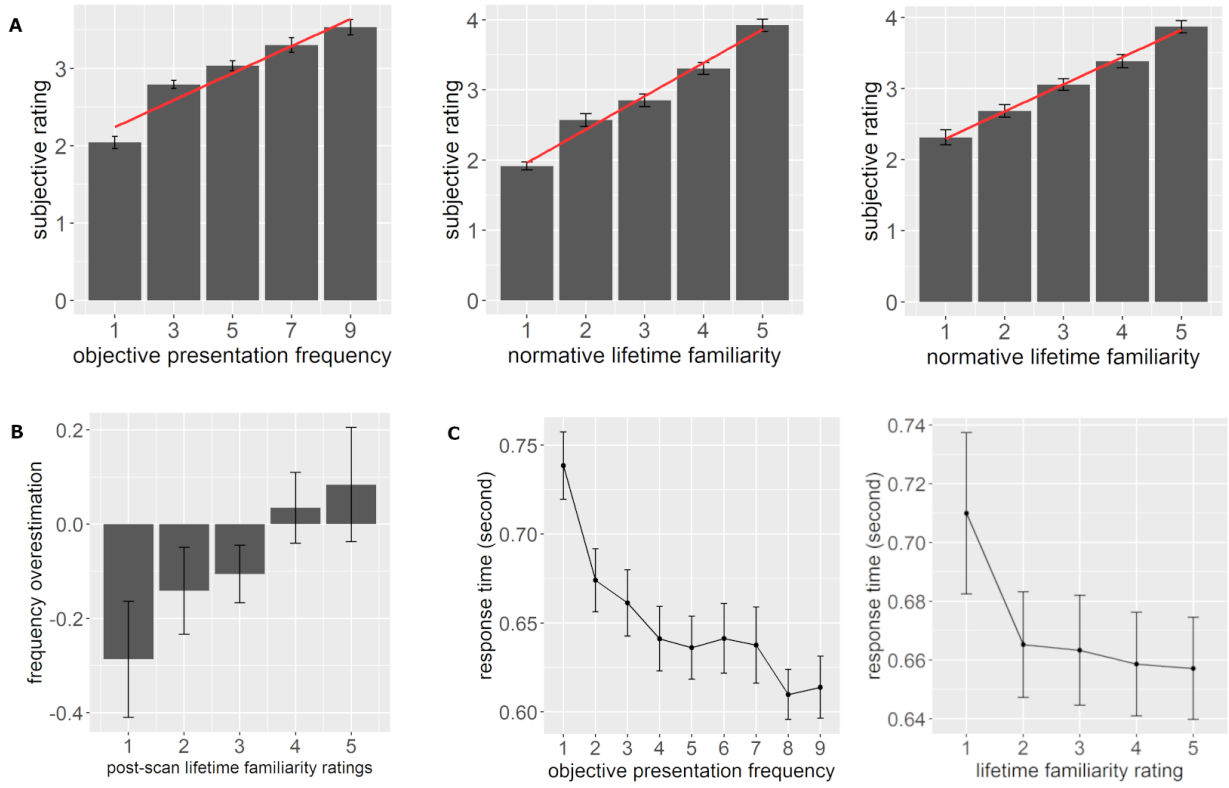

Figure 3.2: Behavioral results. A) Participants' judgements tracked objective presentation frequencies and normative lifetime familiarity in each corresponding task. Red lines represent linear regression fit. B) Participants' error in recent familiarity judgement was correlated with their judged lifetime familiarity. C) Participants' response latencies during animacy judgement reduced with increasing presentation frequency and lifetime familiarity. Error bars represent standard error of the mean.

3.2.2 fMRI results

3.2.2.1 Does PrC track task-relevant recent and lifetime familiarity?

First, we tested if PrC tracked cumulative recent or lifetime exposure when participants made judgements on those dimensions. We focused on the test-phase data and created a GLM with each level of ratings in each of the two tasks as separate conditions, resulting in 10 conditions. We generated a linear contrast testing decreasing activity with increasing degree of judged recent exposure, and a second contrast testing decreasing

activity with increasing degree of judged lifetime experience (contrast vector [2, 1, 0, -1, -2] from rating of 1 to 5). Then we conducted a conjunction analysis of the two contrasts against the global null hypothesis (Friston et al., 2005). A significant conjunction effect was found in the left PrC, $t(58) = 2.71$, $p = .023$ (FWE-corrected in PrC), peak MNI coordinates (-40, -20, -22) (Figure 3.3). Following prior work (Duke et al., 2017), we also tested a conjunction between increasing activity with increasing degree of judged lifetime familiarity and decreasing activity with increasing degree of judged recent exposure. This effect was not significant in the PrC when the default familywise error correction was applied (all $ps > .7$). With a much more lenient threshold (uncorrected $p < .05$), the previously reported effect (Duke et al., 2017) was significant in the left PrC $t(58) = 2.34$, $p = .01$ (uncorrected), peak MNI coordinates (-28, -22, -28).

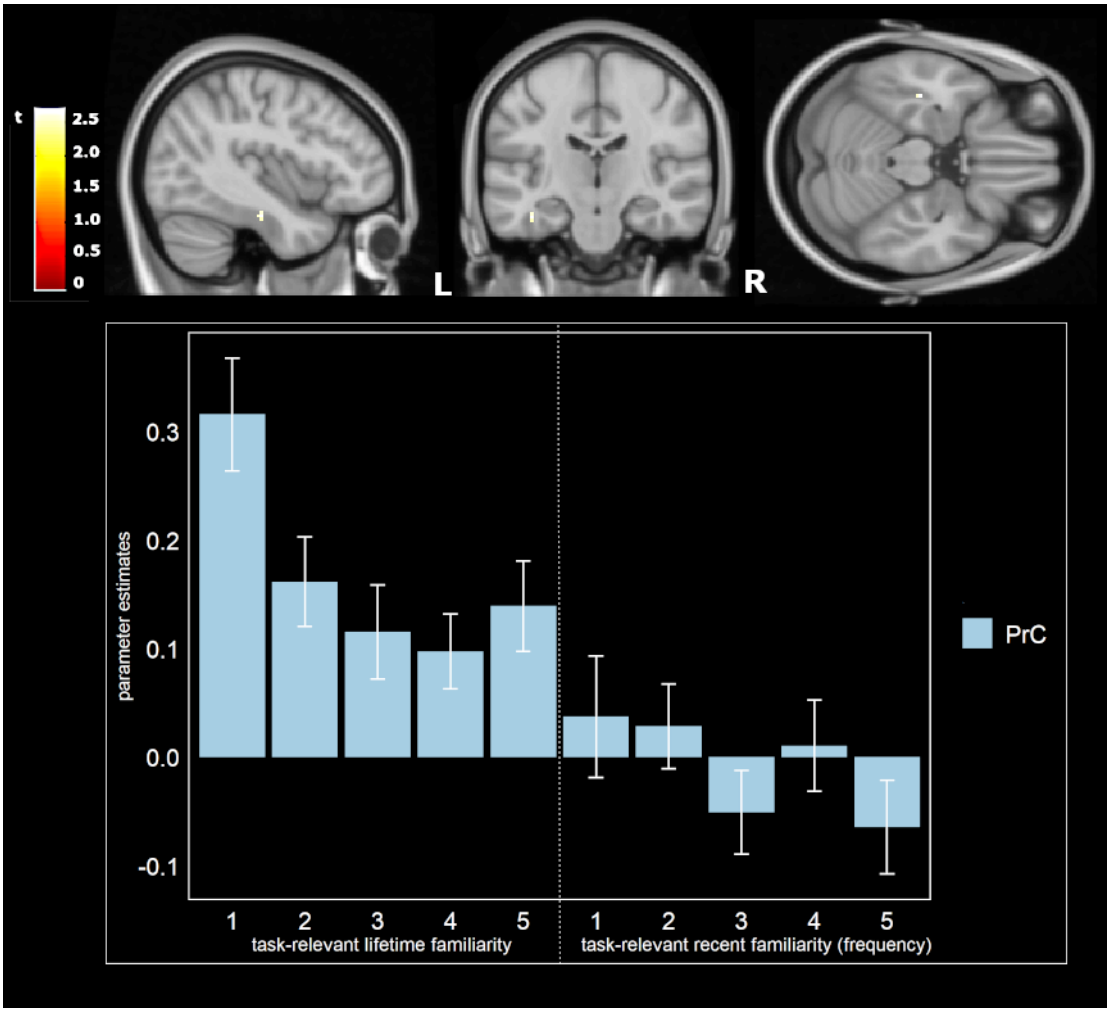

Figure 3.3: Task-relevant familiarity conjunction effect in left PrC during test-phase, the activation maps show only significant voxels within PrC after peak-level FWE-correction. Error bars represent standard error of the mean across participants.

3.2.2.2 Does PrC track recent familiarity when it is not relevant to the task at hand?

We tested if the PrC tracked degree of cumulative recent exposure when participants were not making memory judgements on that dimension. We created a GLM for the study-phase data, with each repetition modeled as a separate condition (i.e. 1st presentations to 9th presentations). A contrast was constructed to test if the activation during 1st presentations (90 trials) was greater than the average activation across the 7th,

8th, and 9th presentations (72 trials in total). This contrast reached significance in the left PrC, t (29) = 5.84, p = .002 (FWE-corrected in PrC), peak MNI coordinates (-36, -26, -22) (Figure 3.4).

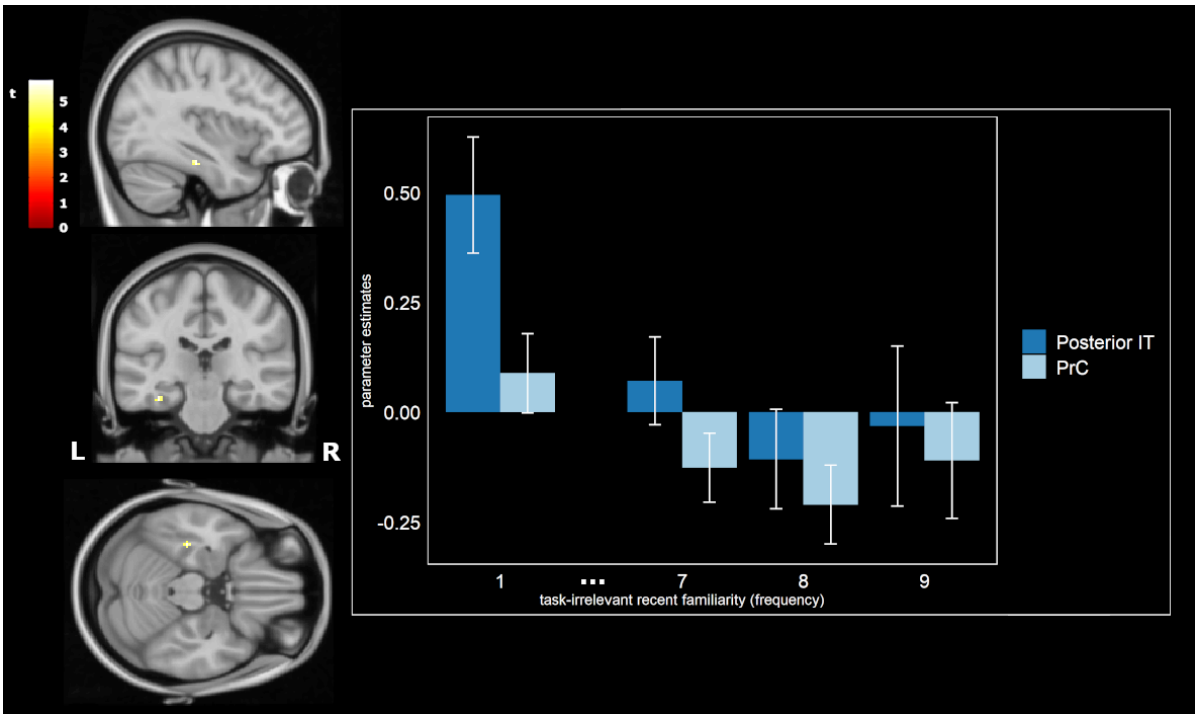

Figure 3.4: Task-irrelevant recent familiarity effect during study phase. Activation maps show only significant voxels within PrC after peak-level FWE-correction. Error bars represent standard error of the mean across participants.

3.2.2.3 Does PrC track lifetime familiarity when it is not relevant to the task at hand?

We conducted three analyses to test if the PrC automatically tracks cumulative lifetime familiarity. First, we tested if the PrC tracks lifetime familiarity when participants were making memory judgements on either timescale. Using data from the test phase, a GLM was constructed to model each level of lifetime familiarity ratings in both tasks as separate conditions. Lifetime familiarity ratings on stimuli used in the recent familiarity task came from the post-scan phase. We then generated two contrasts of decreasing activity with increasing degree of lifetime familiarity, one for each task (i.e. lifetime familiarity judgement and frequency judgement). A significant conjunction effect of the

two contrasts against the global null hypothesis was found in the left PrC, t (58) = 3.02, p = .005 (FWE-corrected in PrC), peak MNI coordinates (-40, -14, -26) (Figure 3.5). We note that this contrast was not independent from the conjunction analysis between judged degree of lifetime and recent familiarity since it used the same test-phase trials. Thus, we also conducted further analyses using independent data from the study phase.

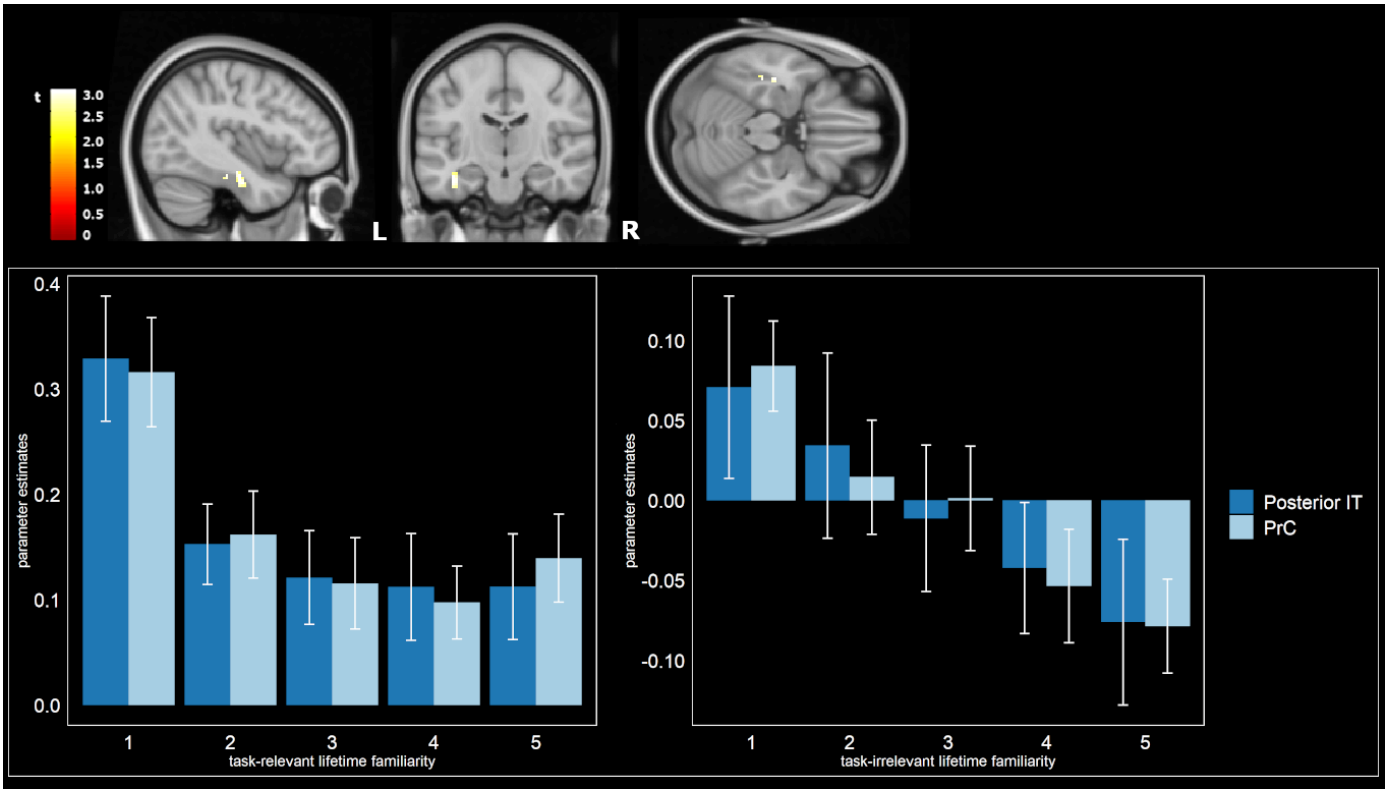

Figure 3.5: Lifetime familiarity conjunction effects during both lifetime (left) and recent (right) familiarity judgement, the activation maps show only significant voxels within PrC after peak-level FWE-correction. Error bars represent standard error of the mean across participants.

Using data from the animacy decision study phase, we tested if the PrC automatically tracks lifetime familiarity when participants were not making memory judgements on either timescale. A GLM was constructed to model each level of lifetime familiarity ratings as a separate condition. A contrast was generated to test for decreasing activity with increasing degree of lifetime experience. Again, we found a significant effect in the left PrC, t (29) = 6.06, p = .001 (FWE-corrected in PrC), peak MNI coordinates (-46, -20,

-28), demonstrating the presence of a lifetime familiarity signal that is independent of task demand (Figure 3.6, left).

Although participants' lifetime familiarity ratings were not significantly correlated with objective presentation frequency, it was still possible that small residual correlations contaminated the above effect. To fully rule out this possibility, we conducted another analysis, using data corresponding to only the first presentation of a word in the study phase. This allowed us to tightly control for any potential effect of different degrees of recent familiarity. We used the LSS-N approach (Abdulrahman & Henson, 2016). A separate GLM was constructed for each trial, with the first condition being the trial of interest, the second condition being all other trials that were presented for the same number of times as the trial of interest, and the remaining conditions being trials that were presented for different numbers of times. For example, if the trial of interest was the 3rd presentation of the word "apple", this trial was modelled as a single condition in the GLM. All other trials that were the 3rd presentations were modelled as another condition. The remaining conditions corresponded to trials of nth presentation with n being other than 3 (i.e. 1st, 2nd, 4th, 5th, 6th, 7th, 8th, and 9th). A contrast tested for decreasing activity with increasing degree of lifetime familiarity among first presentations ([2, 1, 0 ,-1 ,-2] across the 5 levels of lifetime familiarity), which was again significant in the left PrC, $t(29) = 5.16$, $p = .022$ (FWE-corrected in PrC), peak MNI coordinates (-34, -10, -36) (Figure 3.6, right).

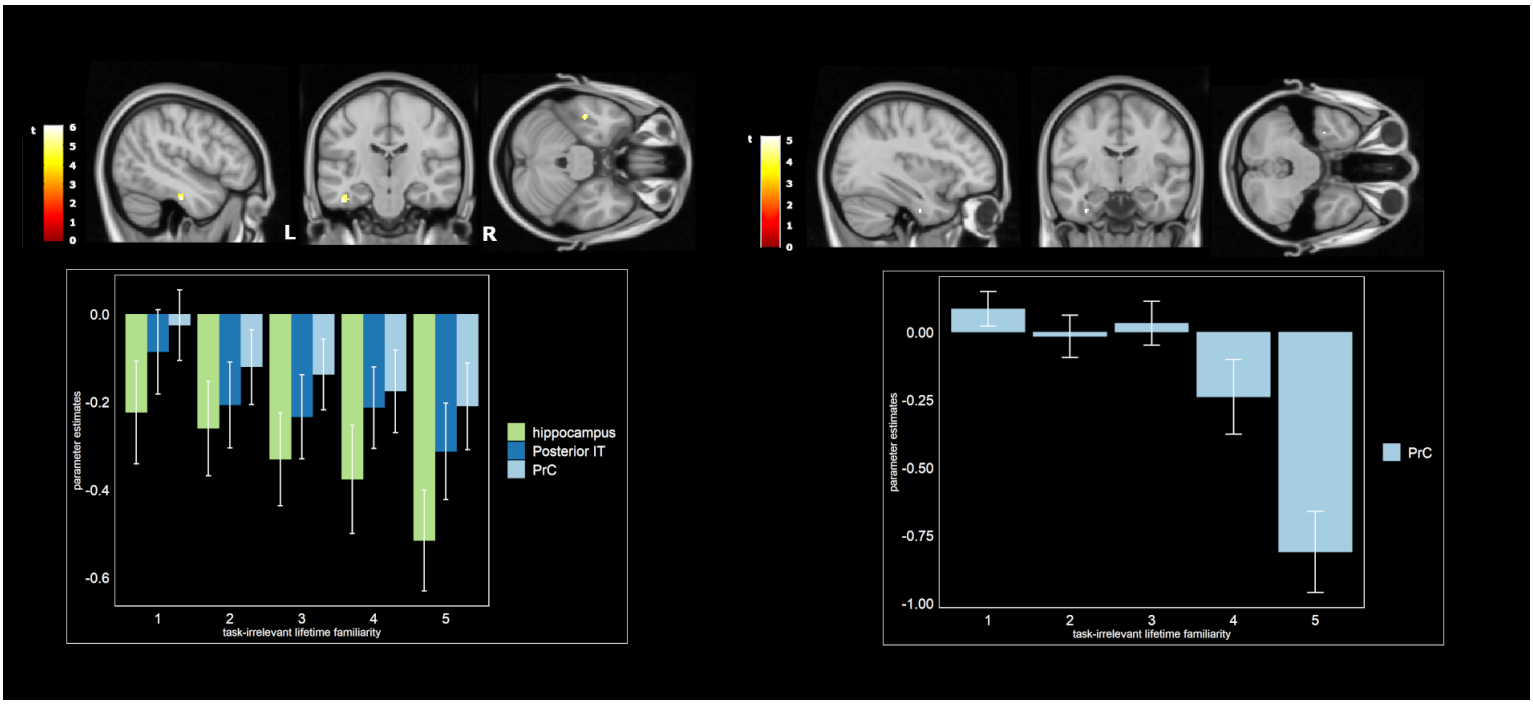

Figure 3.6: Task-irrelevant lifetime familiarity effects during animacy judgement with all trials (left) or only 1st presentations (right). Activation maps show only significant voxels within PrC after peak-level FWE-correction. Error bars represent standard error of the mean across participants.

3.2.2.4 Specificity of the PrC effects.

Outside of PrC, entorhinal cortex (ErC) and IT have also been reported to show familiarity effects, specifically in neurophysiological research (Fahy et al., 1993; Xiang & Brown, 1998). We thus conducted separate analyses in these regions, with IT being further divided into anterior and posterior portions (Kriegeskorte et al., 2008; Liu et al., 2013). We also explored potential familiarity effects in bilateral hippocampus given prior report of its involvement in tracking lifetime familiarity (Duke et al., 2017) and more broadly in recognition memory (Eichenbaum et al., 2007; Norman, 2010; Wais et al., 2006, 2010). We did not observe any significant effects in the anterior IT or ErC. In left posterior IT, task-irrelevant effects were observed for familiarity signals on both time scales (Figure 3.4, Figure 3.5, Figure 3.6, and Table 3.1), while left hippocampus selectively tracked lifetime familiarity during animacy judgement only (Figure 3.6 and Table 3.1). In addition to these region-based analyses, we conducted exploratory whole-

brain analyses as well. The main observation from the whole-brain analyses was a set of frontoparietal regions whose activity scaled with degree of task-relevant lifetime familiarity (Table 3.2). Critically, none of these analyses reveal a region other than PrC which consistently tracked familiarity signals across time scales and tasks.

Table 3.1. Significant results obtained in region-based analyses outside of PrC (FWE-corrected in each region at peak-level)

Analyses	**Regions**	**Statistics (peak-level)**	**p-values (FWE-corrected)**	**Peak MNI coordinates**	**Cluster size**
Conjunction analysis of decreasing signals with increasing task-relevant and -irrelevant lifetime familiarity in the test phase	*Left posterior IT*	*t (29) = 2.81*	*.022*	*-44, -30, -22*	1
Task-irrelevant recent familiarity effect in the study phase	*Left posterior IT (1)*	*t (29) = 5.25*	*.015*	*-50, -62, -18*	*2*
	Left posterior IT (2)	*t (29) =4.87*	*.034*	*-42, -64, -10*	*7*
Task-irrelevant lifetime familiarity effect in the study phase (all trials)	*Left posterior IT*	*t (29) = 5.00*	*.022*	*-48, -18, -26*	*3*
	Left hippocampus	*t (29) = 4.67*	*.008*	*-18, -16, -16*	*6*

Table 3.2: Exploratory whole-brain results (FWE-corrected at the peak-level).

Analyses	Regions	Statistics (peak-level)	p-values (FWE-corrected)	Peak MNI coordinates	Cluster size
Conjunction analysis of increasing signals with increasing task-relevant familiarity on both time scales	*Left superior medial frontal lobe*	*t (58) = 5.29*	*< .001*	*-2, 54, 6*	935
	Left precuneus	*t (58) = 3.94*	.003	*0, -66, 30*	29
	Retrosplenial cortex	*t (58) = 3.80*	.006	0, -42, 4	6
	Left anterior prefrontal cortex	*t (58) = 3.63*	.016	*-16, 72, 12*	2
Task-relevant lifetime familiarity effect	*Left angular gyrus*	*F (1, 58) = 72.85*	< .001	*-38, -80, 38*	207
	Left precuneus	*F (1, 58) = 60.88*	< .001	*-12, -58, 14*	236
	Left superior medial frontal lobe	*F (1, 58) = 51.55*	< .001	*-2, 60, 4*	79
	Right posterior cingulate	*F (1, 58) = 33.60*	.031	*10, -54, 12*	3

	Left superior frontal gyrus	*F (1, 58) = 32.27*	.045	*-22, 30, 42*	1
Task-relevant recent familiarity effect	*Left anterior cingulate (1)*	*F (1, 58) = 36.27*	.015	*-4, 44, 14*	5
	Left anterior cingulate (2)	*F (1, 58) = 36.24*	.015	*-2, 48, -2*	9
	Left superior medial frontal lobe	*F (1, 58) = 35.29*	.020	*-2, 54, 8*	17
Conjunction analysis of decreasing signals with increasing task-relevant and -irrelevant lifetime familiarity in the test phase	*Right middle cingulate*	*t (58) = 3.62*	.017	*20, 12, 34*	2
Task-irrelevant recent familiarity effect in the study phase (all trials)	*Left cerebellum*	*F (1, 29) = 47.89*	.031	*-38, -68, -22*	1

3.3 Discussion

We found that the left PrC tracked familiarity signals of recent and lifetime exposure when participants made memory judgements on the corresponding time scale. It also tracked lifetime familiarity when participants made memory judgement on recent changes of familiarity. Lastly, PrC simultaneously tracked familiarity signals on both time scales

even when no memory judgement was required. This pattern was also unique to PrC, as other regions did not consistently track familiarity signals across both time scales and tasks.

3.3.1 Familiarity on different time scales

In general, our results were consistent with Duke et al. (2017) to the extent that we found left PrC tracking both recent and lifetime familiarity when such signals were relevant to the task. However, it may appear puzzling that we found a consistent decrease in activation for increasing degree of familiarity across both time scales while Duke et al. used virtually the same paradigm but found an increase in activation with increasing degree of lifetime familiarity, and the often-reported decrease in activation with increasing degree of recent familiarity. Nevertheless, we note that such heterogeneity in the directions of BOLD signal change is prevalent among the few studies that report lifetime familiarity effects in PrC (Duke et al., 2017; Gimbel et al., 2017; Yassa & Stark, 2008). For example, Gimbel et al. (2017) used a modified Remember/Know (RK) paradigm with famous and non-famous faces in which participants made separate RK judgements with respect to recent study exposure and lifetime experience. When comparing Know with New responses, the direction of signal change in PrC differed between the two time scales (albeit the lifetime familiarity effect did not reach significance), but in an opposite direction to that reported in Duke et al. (2017). Mecklinger and Bader (2020) provided a potential explanation for this inconsistency. They postulated that non-famous faces, assumed to be completely novel, could be recognized based on their absolute level of familiarity rather than relative familiarity induced by recent study exposure, with the former dominating signals captured by lifetime familiarity judgement in the current study and in Duke et al. (2007). However, a more complex pattern of results was found in a study that used similar stimuli to Gimbel et al. (2017). Yassa and Stark (2008) used a continuous recognition paradigm that is similar to those used in the animal literature. Non-famous pictures, which presumably were novel at the exemplar level, were presented for different numbers of times, intermixed with famous pictures serving as references. Participants made a binary decision distinguishing repeated-non-famous and famous pictures from those that were

neither repeated nor famous. Activity in bilateral PrC tracked repetitions of the non-famous pictures reflecting a familiarity signal for recent exposure, as well as whether a picture was famous or not (reflecting lifetime familiarity). Critically, both increasing and decreasing activity were found in different regions of PrC for familiarity signals on both time scales. In contrast to the heterogeneous effects found in Yassa and Stark (2008), PrC familiarity effects in the current study were highly consistent in their directionality, similar to the dominant pattern of activity reduction found in fMRI studies of recent familiarity (Daselaar et al., 2006; Gonsalves et al., 2005; Henson et al., 2003, 2005; Montaldi et al., 2006; Weis et al., 2004). And such consistency was not limited to task-relevant conditions, but also generalized to conditions in which familiarity signals on either time scale was irrelevant to the task, hinting at a set of neural mechanisms that is common across time scales and task settings.

Parallel findings exist in non-human animal studies, neurons in PrC and neighbouring IT regions have been found to track prior exposure. The typical pattern is a reduced firing rate with increasing exposure (Brown & Banks, 2015; but see Hölscher et al., 2003). Critically, some of these neurons track history of prior exposure over weeks or months, while another partially overlapping population of neurons tracks history of recent exposure (Fahy et al., 1993; Xiang & Brown, 1998). Our results are largely consistent with this animal literature in that we found reduced (BOLD) activity in PrC in response to repeated recent exposure in an experimental setting and across a longer time scale outside of the experiment. Moreover, such effects occurred independently of task-relevance of the signal, indicating an automatic process. However, long-term familiarity effects in animal studies were constrained to repetitions in experimental settings, while lifetime familiarity probed in the current study involved much more diverse encoding contexts that occur across a much longer time scale. These differences along with the complex mapping between electrophysiological and hemodynamic responses (Henson & Rugg, 2003) caution against a direct comparison between the current study and non-human animal research.

3.3.2 Automaticity of PrC response to familiarity

The observation that PrC automatically tracks familiarity regardless of its task relevance is reminiscent of the neural priming effect, namely that repetition suppression is observed with shorter response latencies or increased accuracy that results from recent repetitions in indirect memory tasks (Dew & Cabeza, 2013; Henson et al., 2002; Heusser et al., 2013; J. L. Voss, Hauner, et al., 2009; W.-C. Wang et al., 2010, 2014). Indeed, along with the decreasing activity observed in left PrC with increasing repetition and degree of lifetime familiarity, we also observed significant reduction of response latency along both dimensions. Extant research linking PrC to implicit memory has focused mostly on recent repetition. Wang, Ranganath, and Yonelinas (2014) asked participants to make concrete/abstract judgements on a list of words in a study phase. These words were used as targets in a free-association task to measure implicit memory, and in a recognition memory task to measure explicit memory. PrC activity reduction was observed both for primed trials compared to unprimed trials in the free-association task, and for trials that participant confidently judged as old compared to those judged new in the recognition memory task. Similarly, Heusser, Awipi, and Davachi (2013) used a continuous priming paradigm in which participants made natural/manmade judgements on stimuli that were each presented twice through three possible modalities (i.e. as pictures, written words, or spoken words). The second presentation could either be within- or cross-modality, with all combinations forming 9 conditions in total. After the priming phase, they included a subsequent recognition task probing effects of explicit memory. They found that the magnitude of repetition suppression in the left PrC was positively correlated with differences in behavioral priming effects (i.e. reduction in response latencies) among the 9 conditions. However, a divergence between the current study and their findings is that they did not find a significant PrC repetition suppression effect when focusing on the within-modality condition of written words, which is most similar to the study phase in the current experiment. Furthermore, they did not find a significant PrC repetition suppression effect in conjunction analyses of all within-modality conditions or all cross-modality conditions. Despite this minor divergence, the repetition suppression effect observed in left PrC in the current study during animacy judgement is broadly consistent with extant literature on the involvement of PrC in implicit memory. Critically, we

additionally showed that the repetition suppression effect putatively linked to implicit memory was not restricted to recent exposure because left PrC showed similar task-irrelevant reduction in activity with increasing degree of lifetime familiarity accrued outside of the experimental setting. Moreover, just like in the case of recent familiarity, this repetition suppression effect was accompanied by a reduction in animacy decision latencies.

To this point, we have followed the line of reasoning in a vast literature on neural priming to argue that the repetition suppression effect in PrC observed during animacy judgement in the current study is consistent with an implicit memory interpretation by virtue of the task being indirect (i.e. requiring no intentional consideration of the memory signal). However, such an interpretation that hinges on the lack of intention directed at the memory signal has been criticized before (Henson & Rugg, 2003). A stricter definition of implicit memory effects requires demonstrating that participants lack conscious awareness of the memory signal (Henson & Rugg, 2003; Tulving & Schacter, 1990). One way to eliminate conscious prime processing is to present it briefly, about tens of milliseconds, followed by a mask. Studies employing such a masked-priming paradigm have also observed repetition suppression in PrC (Dew & Cabeza, 2013). Notably, priming effects observed with this paradigm tend to be short-lived compared to supraliminal paradigms (Henson, 2003), and are reminiscent of some inferior temporal (and potentially PrC) neurons reported to display short-lived memory effect that could be disrupted by just one intervening trial (Brown & Xiang, 1998). This suggests that priming effects observed in subliminal and supraliminal paradigms may depend on different mechanisms. To the extent that our focus was on a signal that can support long-term memory (e.g. familiarity), we focused on interpreting our results with reference to the broader literature concerning supraliminal priming effects.

Task-irrelevant lifetime familiarity effects were also observed in PrC during recent familiarity judgements. In this case the lifetime familiarity signal worked against participants' ability to make accurate judgement, as error magnitude of recent familiarity judgement was predicted by participants' lifetime familiarity ratings. Participants' inability to disregard the task-irrelevant lifetime familiarity signal in this case further

underlines the automaticity of familiarity signals. This pattern is consistent with the classic word-frequency mirror effect, in which high-frequency words, presumably having higher degree of lifetime familiarity, tend to be associated with higher false alarm rate in recognition paradigms (Coane et al., 2011; Glanzer & Adams, 1990; Mandler, 1980; Reder et al., 2000). Neuroimaging studies of word-frequency mirror effect are rare. de Zubicaray et al. (2005b) manipulated word frequency in a recognition paradigm. They found the behavioral mirror effect as high-frequency words resulting in more false alarm and less hit. However, fMRI effects of word frequency were observed only in left occipital, fusiform, and middle temporal regions, but not in PrC. This could be due to the differences in analysis strategy because they used a whole-brain approach (albeit with a liberal threshold), while the current study focused on PrC with small-volume corrections restricted to that region. Another possible reason for the divergent finding is that subjective lifetime familiarity ratings capture critical signals that PrC computes while normative word-frequency does not, given that we are not aware of any imaging studies reporting word-frequency effects in PrC while a small number of studies (Duke et al., 2017; Yassa & Stark, 2008), including the current one, did find PrC effects in various types of lifetime familiarity judgement. However, given that word-frequency and subjective ratings of lifetime familiarity tend to be positively correlated, further research is needed to tease apart their unique contribution to behavior and the associated neural correlates.

It is worth noting that the effect of task-irrelevant lifetime familiarity on memory judgements is not always detrimental. In other settings, task-irrelevant lifetime familiarity signals could play a faciliatory role. For example, in a recent study (Gurguryan et al., unpublished data), participants were given cue words representing concepts of varying degree of lifetime familiarity to retrieve an autobiographical memory. A high degree of lifetime familiarity with the cue concepts boosted participants' speed of access to an autobiographical memory. Regardless of the direction, the effect of a lifetime familiarity signal may be subtle yet pervasive whenever we make judgements about meaningful stimuli.

The fluency attribution theory (Jacoby et al., 1989) provides a framework to interpret both implicit and explicit memory (i.e. familiarity) effects observed in PrC (Dew & Cabeza, 2013). Fluency refers to increased ease of processing information, which can result from repeating a stimulus or a portion of its features. This framework also posits familiarity as an automatic process that relies on overlapping mechanisms supporting implicit memory. Our results suggest that fluency could arise not just on a short time scale but also through lifetime experience which was still being tracked by PrC even when the task focused on recent experience. This also indicates an attribution system located outside of PrC that selectively focuses on the aspect of the signal that is relevant to the task, as proposed by a recent model of recognition memory (Bastin et al., 2019). Given that fluency would increase monotonically with increasing exposure, the presence of this additional attribution system could also help to explain the non-monotonic response time observed in the test phase along the rating scale, in contrast to the relatively monotonic decrease of response time on the same set of stimuli in the indirect task which presumably does not engage the attribution system. What neural substrates generate such a response profile could be an interesting question to explore in future research.

3.3.3 Task-relevant memory effects at the whole-brain level

Although we focused on PrC, we also conducted exploratory whole-brain analyses (Table 3.2). We found a set of a frontoparietal regions that selectively tracked task-relevant memory signals. These regions overlap with those that have been reported to track recent task-relevant memory signals in recognition memory studies (Cabeza et al., 2011; D. I. Donaldson et al., 2009; Frithsen & Miller, 2014; Hutchinson et al., 2009; Johnson et al., 2013; Vilberg & Rugg, 2008a), and may contain the sources of the task-dependent ERP effects as reported in our previous work (Yang et al., 2019). In particular, the ventral posterior parietal cortex (vPPC) has been shown to be sensitive to the task relevance of mnemonic status. By manipulating the task-relevance of such information, Elman and Shimamura (2011) showed that vPPC tracked task-relevant mnemonic status about recent exposure during recognition judgement, while remained agnostic in an implicit task (i.e. color judgement). Although we did not observe a vPPC effect sensitive to mnemonic

status of recent exposure, we did observe a similar effect for task-relevant lifetime experience. This is paralleled by findings from a recent study on memory judgement based on life experience. Brown et al. (2018) collected pictures captured over a few weeks by wearable cameras from participants who lived on campus. These pictures were used in a modified RK paradigm in which participants were asked to distinguish between events from their own lives and those from others' lives, probing autobiographical memory. Activity in the left angular gyrus and precuneus were found to scale continuously from remember responses to correct rejections. The authors interpreted this effect as reflecting an evidence-accumulation process underlying explicit memory judgement, which has previously been associated with intra-parietal sulcus (Gonzalez et al., 2015a; Sestieri et al., 2017; Wagner et al., 2005). Although we did not directly probe autobiographical memory, it is reasonable to assume that lifetime familiarity judgements engage common processes underlying some form of autobiographical judgement, such as personal semantics (Renoult et al., 2016). Furthermore, the parietal effect that we observed may reflect mnemonic accumulation along that dimension. Notably, no region other than PrC showed a consistent familiarity effect across both time scales and irrespective of task relevance. Our findings thus suggest a specific role of PrC in tracking familiarity of word concepts in general.

3.3.4 Limitations and future directions

Although PrC has typically been linked to familiarity rather than recollection, it is interesting to consider whether the PrC effect we observed could reflect recollective processes. For the frequency task, it has been suggested that familiarity is the primary source supporting this type of judgement (Hintzman & Curran, 1994). We included only old items in the frequency task to maximize the need to rely on a graded familiarity signal arising from degree of recent exposure. Nonetheless, Hintzman (2004) did propose a recollective process that could contribute to frequency judgements. In his framework, later presentations of the same stimuli "remind" participants of previous presentations, which are encoded together with the current presentation in a recursive process. The depth of recursive reminding forms the bases for judging frequency. However, Hintzman's framework was developed to account for the distinct behavioral effect when

comparing the first presentations of an old stimulus with those that are novel. Since we did not include any novel stimuli in our frequency task, it seems unlikely that qualitatively different processes were engaged. Moreover, a recursive reminding mechanism differs from the typical episodic recollective process, which is tied to a specific time and space. The extent to which a graded and temporally nonspecific recollective process like recursive reminding engages the same neural substrates as episodic recollection is an open question.

It has been suggested that lifetime familiarity judgements are more likely to engage recollective processes (Cabeza et al., 2004). However, a recent study has found the opposite pattern. That is, participants were more likely to rely on recollection in their judgements about recent laboratory exposure (Chen et al., 2017). Moreover, using the same paradigm as in the current study, we have shown in a previous study (Bowles et al., 2016b) that a patient (HC) with hippocampal damage and documented impairments in recollection (Kwan et al., 2010; Rosenbaum et al., 2011) performed lifetime familiarity judgements normally. In contrast, patient NB, who suffered a focal anterior temporal-lobe lesion that includes left perirhinal cortex but spares the hippocampus, showed a deficit in making recent and lifetime familiarity judgements but normal recollection performance. This double dissociation revealed that recollective processes, even if they occur spontaneously, are not the main contributor to either type of memory judgement made in the current study. In addition, spontaneous recollection may be more likely to occur when the task does not require participants to focus on other aspects of memory. This could explain why our current results showed only a hippocampal effect of lifetime familiarity during the animacy judgement which did not demand careful consideration of graded memory signals across a particular time scale. Thus, although we could not completely rule out the contribution of recollective processes in either of our tasks, we interpreted our PrC results as reflecting primarily familiarity.

An interesting question to consider is whether these familiarity signals are best considered as segments of the same continuous dimension or whether they form separate and orthogonal dimensions. Behaviorally, since people generally do not confuse familiarity judgements on different time scales, it seems that the latter is true. However,

this could also mean that some additional mechanisms (e.g. attribution) selectively focus our attention on segments of a common familiarity axis based on task goals. This would be consistent with the classic dual-process model of recognition memory that postulates a familiarity as a one dimensional continuous signal (Jacoby et al., 1989; Yonelinas, 2002; but see Coane et al., 2011). The precise dimensionality of the neural representation of familiarity signals likely depends on the spatial scale of inquiry. We showed that at a regional level, a common neural substrate tracked familiarity across time scales and task goals. However, different neuron populations may underly such effects at a spatial scale not resolvable with fMRI, as suggested by animal electrophysiological work (Fahy et al., 1993; Xiang & Brown, 1998). In addition, a seemingly multidimensional neural code, as indexed by separable populations showing different types of familiarity effects, could still represent a unidimensional signal (Chaudhuri et al., 2019). Future research would benefit from a careful characterization of the extent of representational overlap of familiarity signals on different time scales and task goals, in PrC and beyond.

3.4 Conclusion

To conclude, the current study identified PrC as a region of convergence across a wide range of familiarity effects. These effects could be categorized along two dimensions. Time scale and task-relevance were tracked consistently only by PrC, reinforcing the notion of familiarity as an automatic signal. Given existing, albeit of different volume, literatures on the effects of priming, mirror, and familiarity judgements on both recent and lifetime exposures in PrC, these findings may not be surprising. However, our novel contribution is that we investigated these two dimensions in a single experiment with closely matched task structure and stimulus characteristics. The current study also added to the emerging neuroimaging literature of lifetime familiarity in that it is the first to identify task-irrelevant lifetime familiarity effects in PrC, accompanied with a behavioral mirror effect.

Chapter 4

4 « A decision hierarchy of familiarity judgement »

4.1.1 Familiarity in MTL and beyond

Recognition memory, the ability to track prior occurrences, is a key component of human cognition. Memory can be supported by familiarity and/or recollection, with the former being a continuous and automatic signal devoid of contextual information, whereas the latter is a threshold process that includes contextual information (Yonelinas, 2002; Yonelinas & Jacoby, 1995). A large portion of studies in the field of recognition memory has focused on the medial temporal lobe, featuring perirhinal cortex (PrC) as a key region for familiarity processes (Daselaar et al., 2006; Eichenbaum et al., 2007; Henson et al., 2003; Montaldi et al., 2006). However, several frontoparietal regions have also been observed to be sensitive to familiarity in neuroimaging studies, that is, they produce a graded increase or decrease in activity with varying levels of familiarity or memory strength (Gilmore et al., 2015; Horn et al., 2016; Maril et al., 2003; Montaldi et al., 2006; Scalici et al., 2017). In Chapter 3, we showed that BOLD activity in the left PrC automatically tracks familiarity of concrete concepts that is accrued through recent and lifetime exposure regardless of whether such signals are relevant to the task at hand. Although the focus of that study was on PrC and its surrounding MTL regions, we also identified several frontoparietal regions which mostly showed decision-dependent activity such that their activity differentiated degrees of familiarity only when the familiarity signal was relevant to the task. In the current study, we aimed to use decision making models to quantify the contributions of these regions (i.e. PrC and frontoparietal) to decision-making processes during familiarity judgements.

Cowell et al. (2019) proposed a general framework to understand memory, in which the authors argued for a decomposition of processes into representations and operations. The primary example is recollection, which is a cognitive process that can be decomposed into a representation (multidimensional associations) and its operation, specifically pattern completion. However, in this framework, familiarity is somewhat of a singularity because it is considered as a unidimensional strength signal. Cowell et al. commented

that in this case the process (familiarity) is reducible to an operation, which is the computation of a strength signal. Note that a unidimensional strength signal may result from a computation over multidimensional memory traces (Hintzman, 1984). The singularity arises because an ensuing judgement and phenomenological experience references only a unidimensional signal. From this perspective, the multidimensional trace based on which the unidimensional strength is calculated may be considered "pre-familiarity". However, to make a familiarity-based judgement, the unidimensional strength signal, which can be considered as the representation of familiarity processes, can be subjected to further operations, such as decision processes that combine it with, or modify it based on, task goals.

4.1.2 A decision hierarchy of memory judgement

A useful way to characterize these operations is by placing them on a decision hierarchy. Siegel et al. (2011) described perceptual decision-making in a three-stage schematic. It starts with evidence encoding, followed by evidence-action mapping, and then action planning. It seems rather straightforward to transfer this schematic to memory-based decisions such as those based on familiarity, with a small change to only the first stage, where the evidence does not directly come from sensation but is retrieved from memory (D. I. Donaldson et al., 2009; Ratcliff, 1978). Neural substrates of distinct stages have been reported in animal electrophysiology studies on perceptual decision-making. For example, it is possible to distinguish regions coding for evidence from those coding for the decision variable (DV), with the former representing domain-specific and momentary information while the latter represents a time-integral of the evidence and other task-relevant information such as prior beliefs and subjective values (Gold & Shadlen, 2007). Although with fMRI we may not have the spatiotemporal resolution allowing us to map brain activity to specific stages, we can still infer the relative positions of different brain regions along the decision hierarchy by gauging the relative predictive power of their activity on behavioral measurements of decision-making (e.g. accuracy and response time). Moreover, the superior coverage afforded by fMRI is an advantage for scaling up the investigation to cover more regions.

One promising method to compare neural correlates based on a decision hierarchy is by using the neurally-informed drift-diffusion model (DDM) (Mack & Preston, 2016; O'Connell et al., 2018; Wiecki et al., 2013). With this approach, trial-by-trial variability of the DDM parameters can be linked to trial-by-trial variability in the neural data. After DDM fitting with behavioral data, metrics of goodness-of-fit for such a neurally informed model can be compared with other models without the link to neural data, or with models that link to neural data from different brain regions, for example, in the case of fMRI. Based on model comparisons, a decision hierarchy can be inferred. The assumption of this approach is that a region more directly involved in the decision-making processes produces a superior model fit. In other words, if a region is more directly involved in producing the memory decision, trial-by-trial fluctuation of activity in that region would explain additional variance in the behavioral data in terms of choice and response time through a generative model like the DDM. This method has been successfully applied to investigate questions about recollection and cortical reinstatement by Mack and Preston (2016). Participants were first exposed to pictures of famous faces or places. They then learned to associate pictures of objects with famous faces or places. And finally in a delayed match-to-memory task (DMTM), they were presented with the object pictures and asked to retrieve the associated face or place during a delay and compare their retrieved picture with a test probe to produce a match/mismatch response. A metric of trial-level reinstatement was calculated as a correlation between voxel patterns during the pre-exposure phase and that of the delay period in the DMTM task, separately for faces/places and match/mismatch. This metric, calculated separately by region, was then included in the DDM as a regressor to explain trial-by-trial variation of model parameters. A model with hippocampal reinstatement metric of places in match trials and a model with PrC reinstatement metric of face trials outperformed the baseline behavioral models. On the other hand, models with a reinstatement metric from the occipitotemporal cortex did not outperform the baseline model, suggesting that reinstatement effects in this region do not directly contribute to the memory decisions as compared to MTL regions.

4.1.3 The present study

Instead of focusing on recollection and cortical reinstatement of multidimensional representations as in Mack and Preston (2016), we attempted to infer a decision-hierarchy of memory judgement based on recent familiarity, assumed to be a unidimensional strength signal, with a similar model-comparison approach. We analyzed an existing multi-echo fMRI dataset collected in Chapter 3. Participants made frequency judgements on words referring to concrete concepts such as shirt and monkey that had been recently presented in a study phase (recent familiarity), and lifetime familiarity judgements on concepts that had not been presented in the study. In the present research, we restricted our analyses to recent familiarity (frequency) judgement data for two reasons. First, it has been shown that this task mainly taps into familiarity process (Anderson et al., 2021; Bowles et al., 2010; Duke et al., 2017; Hintzman, 2001). Second, it can be binarized based on trial-level accuracy, which is required for model fitting (A. Voss et al., 2013). In previous analyses of the fMRI data, we identified a set of frontoparietal regions, mostly on the medial aspect, that tracked recent and lifetime familiarity signals when they were relevant to the task, consistent with previous reports of the broad involvement of these regions in memory tasks (D. I. Donaldson et al., 2009; Euston et al., 2012; Hebscher et al., 2020; Minxha et al., 2020; Richter et al., 2016; Simons & Spiers, 2003; Wagner et al., 2005; Ye et al., 2018). Furthermore, we found that BOLD activity in PrC, a region linked to both familiarity-based recognition and priming (Daselaar et al., 2006; Eichenbaum et al., 2007; Henson et al., 2003; Heusser et al., 2013; Montaldi et al., 2006; J. L. Voss, Hauner, et al., 2009; W. Wang & Yonelinas, 2012), tracked recent and lifetime familiarity irrespective of their relevance to the task at hand.

Several studies have suggested that further operations on MTL memory signals occur in frontoparietal regions (Bastin et al., 2019; D. I. Donaldson et al., 2009; Gluth et al., 2015; Minxha et al., 2020). Theories on what functions these operations serve in memory decisions can be distinguished by their relative positions on a decision hierarchy. Broadly speaking, they can be classified into two views. The first view is that these regions are responsible for the experiential aspects of memory such as metamemory (Baird et al., 2013; Ye et al., 2018) or vividness (Richter et al., 2016). To the extent that metamemory

or metacognition in general can be considered a post-decision process (Yeung & Summerfield, 2012) and dissociable from the primary decisions (Fleming & Dolan, 2012), this view suggests that signals in these regions are less predictive of memory judgement performance than are MTL regions. The second view posits that frontoparietal regions are responsible for decision-making operations that produce the ensuing behavioral report (D. I. Donaldson et al., 2009; Euston et al., 2012; Wagner et al., 2005). This view suggests that signals in these regions better predict performance on memory judgments than do MTL regions.

The main advantage of applying neurally-informed DDM to familiarity judgement can be seen by considering one particular theory of the latter camp, the mnemonic accumulator hypothesis (Wagner et al., 2005), which proposes that subregions in the posterior parietal cortex accumulates noisy memory information to produce the explicit judgement. In other words, activity in these regions indices a mnemonic DV. In human fMRI studies, support for the mnemonic accumulator hypothesis often take the form of graded changes in BOLD activity (T. I. Brown et al., 2018b; Hutchinson et al., 2009; Sestieri et al., 2014). However, the same pattern has been used to index familiarity per se (Daselaar et al., 2006; Horn et al., 2016; Yassa & Stark, 2008). The lack of specific links between graded changes in BOLD activity and different cognitive processes involved speaks to the singularity of familiarity judgement alluded by Cowell et al.(2019). By taking into consideration accuracy and response time, neurally-informed DDM offers additional constraints to tease apart in a single experiment not only which regions track familiarity, but also how they do so differently in terms of their involvement in decision making. As such, this approach offers a more complete understanding on the neural mechanisms that support familiarity judgement.

Based on our previous findings and the literature on the link between PrC and familiarity, we predicted that trial-by-trial BOLD activity in PrC would contribute to the decision-making processes during judgement of recent familiarity, resulting in a superior fit of the DDM compared to the baseline model without neural information. The contribution of frontoparietal regions were evaluated relative to PrC. If frontoparietal trial-by-trial BOLD activity holds more predictive power than that of PrC resulting in a better DDM fit, then a

decision-making account is favored. Otherwise, if models fit with their activity were inferior to PrC, then an experiential account was favored.

4.2 Methods

This Chapter is based on the same dataset as Chapter 3. Specifically, the participants (section 4.2.1), the materials (section 4.2.2), the procedure (section 4.2.3), and imaging acquisition and preprocessing steps (section 4.2.4) are largely repeated from Chapter 3.

4.2.1 Participants

Thirty-one right-handed participants (24 females), aged between 18 and 40 years old (mean age = 27) were recruited from Western campus community through OurBrainsCAN and were compensated for CAD $20 per hour. In order to participate, they needed to meet the following criteria: speak fluent English, grew up in North America, and reported no history of psychological or neurological disorder. One participant was excluded from all analyses due to excessive motion during the scanning session. All procedures were approved by Western University Health Sciences research ethics board.

4.2.2 Materials

Stimuli were words representing 180 concrete English concepts selected from a database based on Canadian norms (McRae et al., 2005). These words were selected to cover a wide range of lifetime familiarity based on the normative data (Mean = 5.9, Rang = 7.2 on a 9-point scale). They were divided into 10 sets of 18 words, matched on mean and average of feature-overlap with respect to the entire database, normative lifetime familiarity, log word frequency, number of letters, and number of syllables. This was done using the “Match” software which sampled from the initial sets of stimuli (10 in our case) to create another sets of stimuli (10 in our case) with matched dimensions in terms of mean, median, standard deviation (van Casteren & Davis, 2007). The match among the output sets was confirmed with a MANOVA in R (Pillai’s trace = 0.17, F (45, 850) = 0.68, p = .94). 5 sets of the stimuli were chosen to be used in the study phase and for

judgement of recent familiarity, while the other 5 sets were used for judgement of lifetime familiarity. This assignment was counterbalanced across participants.

4.2.3 Procedure

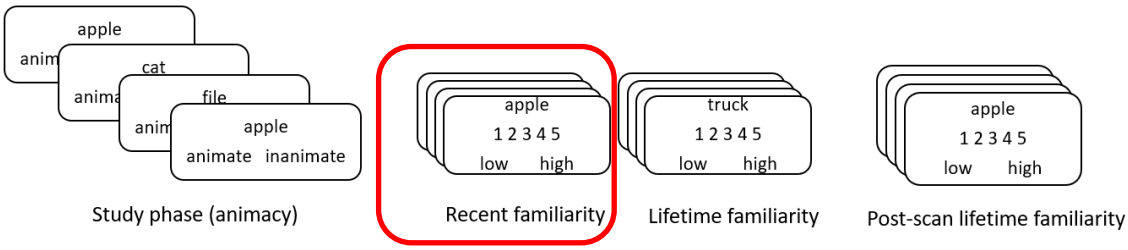

Figure 4.1: Behavioral paradigm. The current study focused on data acquired during the recent-familiarity task.

The experiment consisted of 3 phases with the first 2 phases carried out inside the scanner (Figure 4.1). For the 2 scanned phases, stimuli were presented on a projector screen inside the scanner. For the last phase outside of the scanner, stimuli were presented on a laptop. The analyses in the current study focused on the recent familiarity task.

Participants started with a study phase, in which they incidentally encoded 5 sets of stimuli (i.e. 90 unique concepts in total) while making animacy judgement. Critically, stimuli from each of the 5 sets were presented once, three times, five times, seven times, and nine times, respectively, resulting in a total of 450 trials. Each trial began with a fixation cross, whose duration was jittered across trials with a minimal duration of 1 second, maximal duration of 4 seconds, and a mean duration of 1.5 seconds. Following the fixation cross, a stimulus appeared on the screen for 1.5 seconds. Participants were asked to judge whether the word represented an animal or not by pressing their left or right index finger on two MR-compatible button boxes. The finger assignment was counterbalanced across participants. Responses made within the 1.5 seconds of stimulus presentation and during the fixation screen following the presentation of the stimulus were registered. The presentation order was pseudorandomized with the constraint that

the same stimulus could not reappear within 3 trials. Participants were told to disregard the repetitions and make their judgement as usual.

After participants were familiarized with use of button boxes in a practice session, they were given verbal and written instructions about the test phase. This phase consisted of two tasks in alternating blocks of 5 trials. One task involved judgement of recent familiarity, in which participants were presented with stimuli that they had seen in the study phase and were asked to judge relatively how frequently they had saw each of them on a 5-point Likert scale with 5 being most frequent. The other task involved judgement of lifetime familiarity, in which participants were presented with stimuli that they had not seen in the study phase (i.e. the other 5 sets of stimuli, see Materials) and were asked to judge how familiar they were with the thing that the word represents based on their lifetime experience, again on a 5-point Likert scale with 5 being most familiar. The lifetime familiarity task was not included in analyses of the current study due to difficulty of defining trial-level accuracy for that task. Before the tasks switch, a prompt was shown on the screen to let participants know what the next block would be. Participants indicated their ratings using the key mapping they had learnt in the practice phase. Regardless of the task, each trial started with a fixation cross of jittered length, with a minimal duration of 2.5 seconds, maximal duration of 10 seconds, and a mean duration of 4 seconds, followed by 2.5 seconds of stimulus presentation. Responses made during the presentation of the stimuli and the fixation cross following that were registered. Participants were told to rely on their intuition and refrain from spending too much time on each trial when making the judgement.

After the scanning session, participants were asked to judgement of lifetime familiarity on stimuli used in the study phase and during recent familiarity judgement. This task was also not analyzed in the current study due to difficulty of defining trial-level accuracy.

4.2.4 Imaging acquisition and preprocessing

The scanning was carried out with a Siemens Prisma 3 Tesla scanner. We acquired T1-weighted (MPRAGE, 208 slices; TR 2400 ms; TE 2.28 ms; flip angle 8 degrees; FOV 256*256 mm; 0.8 mm isotropic voxels) and T2-weighted (SPC, 208 slices; TR 3200 ms;

TE 564 ms; FOV 256*256 mm; 0.8 mm isotropic voxels) anatomical scans for each participant. Functional runs were acquired with echo-planar imaging (EPI) protocol, with 2 mm isotropic voxels covering the whole brain. Slices were oriented perpendicular to the hippocampal long axis. Multiband factor of 2 and GRAPPA factor of 3 were used. The TR was 2.5 seconds. To reduce susceptibility artifact in the PrC region, we acquired our functional data with 3 echoes at 12.00 ms, 29.94 ms, and 47.88 ms (Kundu et al., 2017), which were later combined into one image at the preprocessing stage. We also acquired fieldmaps for denoising purposes at the end of the scanning session. In this study we focus on the test phase, which was divided into 4 runs of about 5 minutes each, with short breaks in-between.

Imaging data were preprocessed with fMRIPrep 1.5.4 (Esteban et al., 2019). A detailed description autogenerated by fMRIPrep is included in the Appendix B. The T1-weighted (T1w) image was corrected for intensity non-uniformity, skull-stripped, and normalized to FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model (MNI152NLin6Asym). Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast in FSL. Whole-brain masks in this MNI space from all participants were added together to form a group-level explicit mask used in the first-level general linear model.

For each functional run, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Susceptibility distortion was corrected using a fieldmap. The functional scan was then co-registered to the T1w with 6 degrees of freedom. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering. Slice-time correction was performed using AFNI. The BOLD time-series were then resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions (preprocessed BOLD). A T2* map was estimated from the preprocessed BOLD by fitting to a monoexponential signal decay model with log-linear regression. For each voxel, the maximal number of echoes with reliable signal in that voxel were used to fit the model.

The calculated T2* map was then used to optimally combine preprocessed BOLD across echoes. The optimally combined time series was carried forward as the preprocessed BOLD. The BOLD time-series were resampled into MNI152NLin6Asym. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA) was performed on the preprocessed BOLD in the MNI space after removal of non-steady state volumes and spatial smoothing with an isotropic, Gaussian kernel of 6mm FWHM (full-width half-maximum). Corresponding "non-aggressively" denoised runs were produced after such smoothing. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor,Behzadi et al., 2007). Anatomical components (acompcor) were calculated separately within the WM and CSF masks. All analyses used the non-aggressively denoised data in the MNI space.

4.2.5 ROI definition

We defined four ROIs (Figure 4.2) prior to the feature/voxel selection stage. PrC and hippocampus were defined anatomically using Automatic Segmentation of Hippocampal Subfields (ASHS) (Yushkevich et al., 2015) in each participant's native T1w and T2w space. These masks were individually transformed to MNINLin6Asym space with ANTS, using each participant's registration file between their native space and the MNI space produced by fMRIPrep 1.5.4 (for details, see fMRIPrep documentation). Then a group level PrC mask was defined by including voxels that overlapped among 75% of the participants. The hippocampal group mask was defined similarly, with the additional procedure of excluding any overlapping voxels with the PrC group mask.

Frontal and parietal ROIs were defined in a data-driven manner. We first constructed a general linear model (GLM) in SPM12 with each response option in each of the two memory tasks coded as conditions (10 in total). Trials in which participants failed to make a response were modelled as an additional condition. Each trial was modelled as a boxcar with duration equal to the stimulus presentation time (i.e. 2.5 seconds) and convolved with the canonical hemodynamic function. 6 aCompCor for WM and CSF were included as nuisance regressors. We did not include motion regressors to prevent reintroducing motion artifact into the data after ICA-based denoising during the preprocessing stage. First-level t-contrasts of increasing BOLD activity with increasing

degree of judged recent familiarity (contrast weights [-2, -1, 0, 1, 2] through ratings 1-5) were computed within each participant. These contrasts were tested on the second level with a one-sample t-test. We used a liberal peak-level threshold of $p < .01$ uncorrected and a cluster-level threshold of $p < .05$ corrected for family-wise error across the whole-brain. Two clusters located on the medial aspects of frontal (mPFC) and parietal (mPPC) regions showed significant effects under these thresholds. They remained as the only two significant clusters when we changed the peak-level threshold from $p < .01$ uncorrected to $p < .001$ uncorrected, in which case only the extent of the two clusters changed. We thus used the more liberal peak-level threshold of $p < .01$ uncorrected to sample voxels broadly before feature-selection.

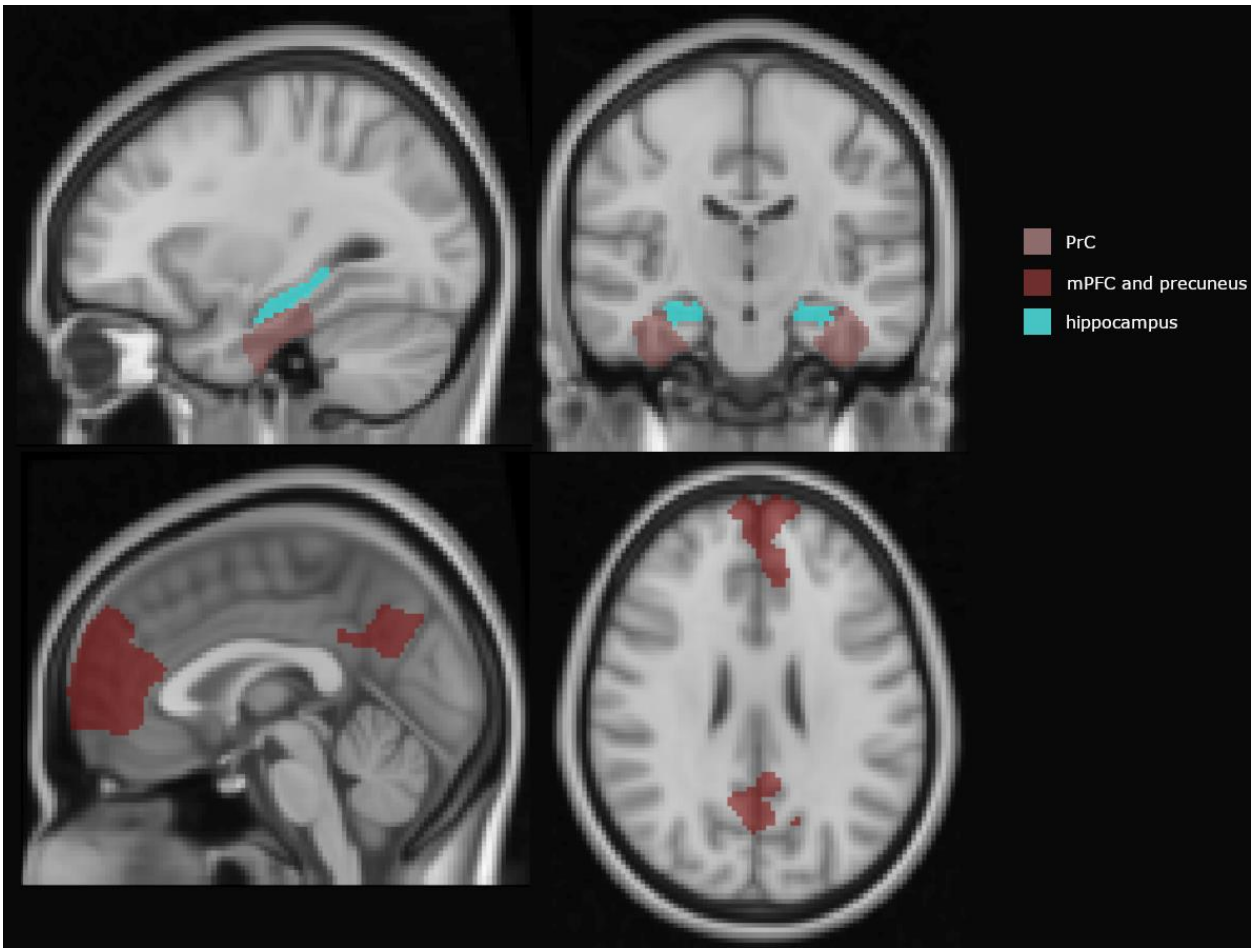

Figure 4.2: Group-level ROIs for feature-selection in the MNI space.

4.2.6 Single-trial fMRI signal extraction

We used LSS-N (Abdulrahman & Henson, 2016) to estimate trial-level BOLD activity. For each run of each participant in the test phase, activation on each trial was estimated with its own GLM. The design matrix of the GLMs contained at most 12 conditions. The exact number depended on the presence or absence of conditions in a given run. The first condition was the trial of interest, modelled as a single boxcar with duration equal to the presentation time (i.e. 2.5 seconds). The second condition consisted of all other trials on which the participant gave the same response (e.g., a recent familiarity rating of 4). The third to eleventh conditions corresponded to trials on which the participant gave other responses (e.g. recent familiarity 3, lifetime familiarity 5, etc.). Finally, we included a condition indicating trials on which the participant failed to respond. Aside from design columns of experimental conditions, we also included 6 aCompCor for WM and CSF as nuisance regressors. Only the beta estimates of the trials of interest in the recent-familiarity task were subjected to further analyses. This procedure thus yielded a beta estimate for each voxel on each recent-familiarity trial of each run for each participant.

4.2.7 Feature/voxel selection

To reduce computational cost and to avoid washing out memory signals with noise, we performed voxel selection in each ROI prior to averaging across voxels. For each voxel, a regression model was constructed with single-trial beta estimates as the independent variable, and a participant's recent familiarity ratings as the dependent variable. We fit this model to each voxel within each ROI, then extracted the top 5% of voxels in each ROI based on magnitude of the regression slope. We looked for a negative slope for PrC and a positive slope for mPPC and mPFC given the different directions of familiarity effects observed in these regions. Hippocampus served as a control region since we did not expect to find familiarity signals in this region. Both positive and negative slopes were used separately to select voxels in the hippocampus. We chose to select voxels based on regression slope rather than a goodness-of-fit measurement (e.g. t-statistics) because we were interested in linking the trial-by-trial fluctuation of the BOLD activity to DDM parameters. A goodness-of-fit measurement normalizes against such fluctuation and biases towards voxels showing little trial-by-trial variance. Trial-level activity of the

selected voxels were then averaged within each ROI to form a ROI-activity vector. Since the primary goal of the study was to compare neurally informed models across regions, to account for different signal-to-noise ratios, we z-scored this vector across trials within each ROI for each participant.

4.2.8 Hierarchical drift-diffusion model fitting

We used HDDM (0.9.2) (Wiecki et al., 2013) to fit the hierarchical drift-diffusion model (DDM). This approach has two main advantages. First, it reduced the number of trials required to obtain stable parameter estimates, which made it more applicable to neuroimaging studies. Second, it allows for a relatively straightforward way to link a trial-level covariate, in our case single-trial BOLD activity, with trial-level DDM parameters.

Since the judgement in this dataset was not binary, we first binarized participants' responses by defining a trial-level accuracy measurement (A. Voss et al., 2013). We rank ordered the 5 levels of objective presentation frequency, which gave the objective presentation frequency the same range as participants' subjective ratings of recent familiarity. Then in the recent familiarity task, a trial was defined as correct if a participant's rating (five-point scale) matched the rank of the objective presentation frequency. We used a posterior-predictive test to check if the models were of sufficient complexity to capture key characteristics of the data after the binarization procedure. After a model had converged, we used its parameters to generate simulated choice and RT data. Five hundred data points were simulated for each parameter set, which took into consideration the hierarchical nature of the dataset (i.e. participant and trial levels). If the observed data, in terms of accuracy and RT quantiles, fell into the 95% credible interval of the simulated data, the model was considered of sufficient complexity to provide a good fit.

We fit several models with the binarized behavioral data. A baseline model was constructed with three DDM parameters, drift-rate (v), decision-threshold (a), and non-decision time (t) using behavioral data only. All three parameters were allowed to freely vary according to the five levels of objective presentation frequencies (conditions) in a

within-participant manner, with the presentation frequency of 1 acting as the intercept condition. In HDDM formula, this corresponded to ["a ~ C(stim,Treatment(1))","v ~ C(stim,Treatment(1))","t ~ C(stim,Treatment(1))"]. Then for the neurally informed models, we added single-trial BOLD activity as a factor associated with trial-by-trial variation of each parameter. This was done separately for each of the three DDM parameters and for each of the four ROIs, resulting in 15 neurally-informed DDMs in total (three for each ROI except for the hippocampal control region which had six models due to the bidirectional voxel-selection step). For example, a model that included the effect of PrC activity on drift-rate (v) would be: ["a ~ C(stim,Treatment(1))","v ~ **PrC_z** + C(stim,Treatment(1))","t ~ C(stim,Treatment(1))"]. In addition to the hippocampus, we included a set of lower-level control models. These models included random vectors instead of actual BOLD activity linked to each of the DDM parameters. These models were expected to not outperform the baseline model. Although the hippocampal control model might outperform the baseline model, it should not outperform other neurally informed models since we did not expect this region to play a primary role in a familiarity-based task (Bowles et al., 2010; Köhler & Martin, 2020). All models were fit with three MCMC chains of length 30000 each, with 10000 burn-in samples discarded. A model was considered converged if its Gelman-Rubin statistics were smaller than 1.1 for all parameters when evaluated across the three chains.

After confirming a model had properly converged and was of sufficient complexity, we proceeded to compare models within each ROI to find the best performing one based on their deviance information criterion (DIC). We then compared the winning model of each region to the baseline model and to winning models of other regions to infer a decision hierarchy.

4.3 Results

4.3.1 Behavioral results

With the rather strict accuracy-coding scheme, participants still performed above chance across all levels of objective presentation frequency (Figure 4.3 left), suggesting that they were sensitive to our experimental manipulation and properly engaged in the task. The

raw RT distribution generally showed an invert-U shape across the 5 degrees of judged recent familiarity, although there were some heterogeneities across objective presentation frequency levels (Figure 4.3, lower right). This was more apparent when comparing RT under the accuracy-coding scheme (Figure 4.3, upper right), even though participants' RT on accurate trials was reliably lower compared to inaccurate trials when collapsed across levels of objective presentation frequency, t (29) = -4.09, p = .0002. For this reason, we treated levels of presentation frequency as different within-participant conditions and allowed all HDDM parameters to vary freely across them in all of our models.

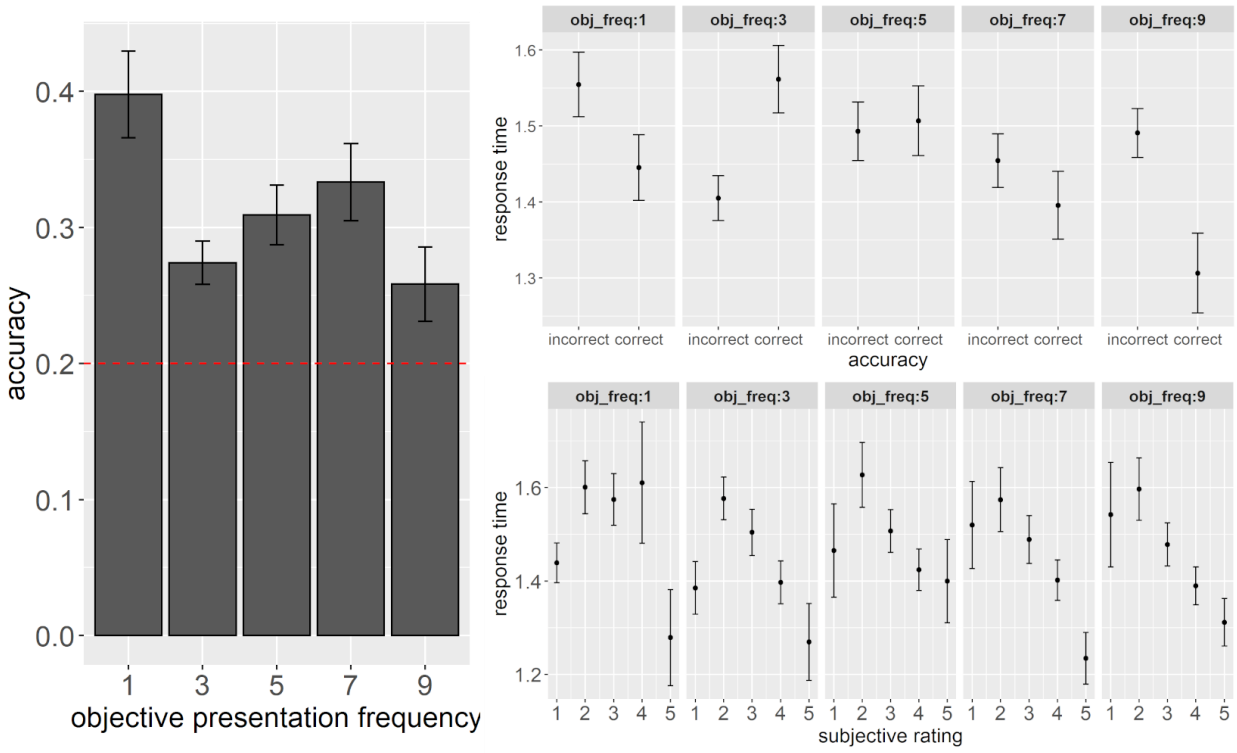

Figure 4.3: Descriptive statistics of behavioral results during recent familiarity judgement. Left: mean accuracy for each level of objective presentation frequency. The red dashed line represents chance-level performance (out of five options). Upper right: mean response time as a function of accuracy and objective presentation frequency. Lower right: mean response time as a function of subjective rating of recent familiarity (before binarization with accuracy) and objective presentation frequency. Error bars represent standard error of the mean across participants.

4.3.2 HDDM model comparison

All DDMs converged after 30000 samples. In addition, all models passed the posterior-predictive test, indicating sufficient model complexity. We thus proceed to compare the various models within and across regions.

The baseline model had a DIC value of 5723, which was outperformed by at least one neurally informed model from each ROI. Within each ROI, the model with the decision-threshold (a) that varied by single-trial BOLD activity provided the best fit, with the exception of the hippocampal control model with voxels selected for a positive slope (i.e. increasing activity with increasing degree of judged recent familiarity). Critically, none of the random control models outperformed the baseline model and none of the hippocampal models outperformed winning models in other regions. Finally, when comparing winning models among the remaining 3 ROIs, the model containing mPFC activity provided the best fit, followed by the PrC model, and the mPPC model (Table 4.1).

Table 4.1: DIC values of DDMs, winning models in each ROI were made bold.

Model	**DIC**		
Baseline models	5723		
PrC models	v ~ roi_z	a ~ roi_z	t ~ roi_z
	5725	**5669**	5673
mPPC models	v ~ roi_z	a ~ roi_z	t ~ roi_z
	5725	**5694**	5713
mPFC models	v ~ roi_z	a ~ roi_z	t ~ roi_z
	5725	**5662**	5698
	v ~ roi_z	a ~ roi_z	t ~ roi_z

Hippocampal control model (select voxels with positive slope)	5725	5706	**5701**
Hippocampal control model (select voxels with negative slope)	v ~ roi_z	a ~ roi_z	t ~ roi_z
	5725	**5711**	5712
random control model	v ~ rand_z	a ~ rand_z	t ~ rand_z
	5725	5726	5725

4.3.3 Group-level posterior analyses of HDDM parameters

Since the parameters were estimated in a Bayesian framework, we can directly calculate the proportion of the posterior density that was greater or less than 0, similar to a one-sample t-test. We used "P" to denote these test statistics to distinguish them from the frequentist "p" and used the same .05 cutoff as a criterion of significance. We calculated the proportion of posterior density that is greater than 0, and reported the smaller value between the returned P and 1-P, which provided two-tailed statistical tests. These tests were conducted on the regression slopes of the winning models in PrC, mPPC, and mPFC. Significance in these tests indicates a trial-by-trial link of BOLD activity in respective regions with the DDM parameter on top of what can be explained by presentation frequency. For all three regions, the posterior density was significantly different from 0, all Ps < .0001. The regression slope was positive in PrC and negative in the other two regions (Figure 4.4: Posterior density of the regression slopes between decision-threshold and single-trial BOLD activity, plotted for the winning model in each ROI.). In terms of absolute magnitude, regression slopes did not differ between regions, PrC with mPPC, P = .67; PrC with mPFC, P = .29; and mPPC with mPFC, P = .16.

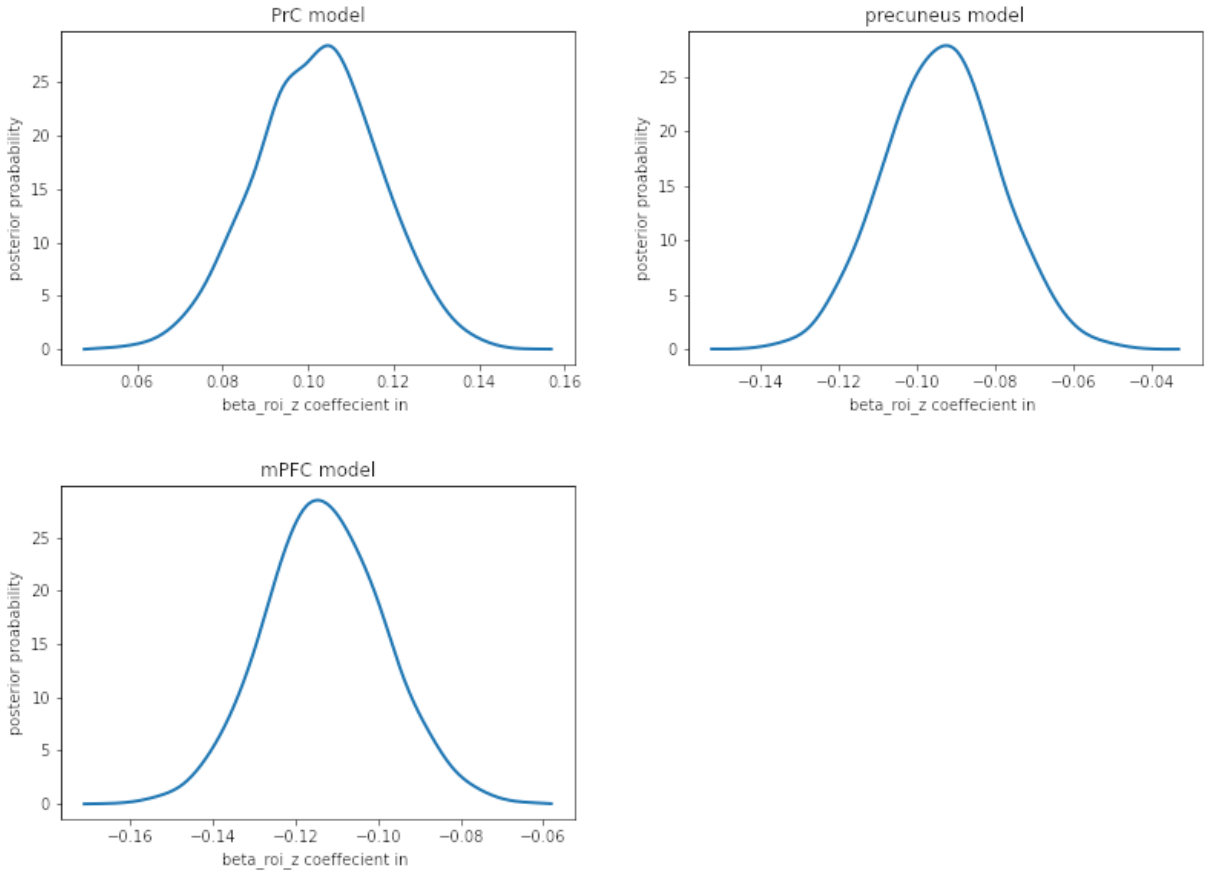

Figure 4.4: Posterior density of the regression slopes between decision-threshold and single-trial BOLD activity, plotted for the winning model in each ROI.

4.4 Discussion

We found that a decision hierarchy existed for recent familiarity judgments by comparing drift-diffusion models informed by trial-by-trial variations of BOLD activity in multiple brain regions. PrC activity contributed to the memory decision by virtue of providing a superior fit to behavioral data when such activity was incorporated in the model. Moreover, mPFC activity was more strongly related to the memory decision than were PrC signals, whereas familiarity signals in mPPC had a relatively weaker link to decision making. This pattern of results is consistent with the interpretation that familiarity information coded in PrC is further processed to suit the task goal in mPFC, with mPPC potentially responsible for processes more auxiliary to the primary memory decisions.

In electrophysiological studies of perceptual decision making, it is possible to distinguish evidence from the decision variable, with the former representing fleeting signals that change from moment to moment and the latter representing the integration of evidence and other information such as prior beliefs and value over time (Gold & Shadlen, 2007). It is tempting to generalize this distinction to the relationship between PrC and frontal/parietal regions, with PrC representing evidence while frontal or parietal regions represent the decision variable that accumulates evidence over time, as hinted in the original conceptualization of the mnemonic accumulator hypothesis (Wagner et al., 2005). In the current study, with the exception of the hippocampal control region, the best fitting models in all regions were linked to the decision threshold, which can be thought as reflecting modulation of the decision variable. However, with fMRI we often lack the spatial and more importantly the temporal resolution to make a clear distinction between evidence (**v**) and the decision variable (**a**) due to the temporally integrative effects of BOLD response (but see Tremel & Wheeler, 2015). A separate issue unrelated to technical limitations is that neural substrates involved in decision-making may not form strictly discrete stages (O'Connell et al., 2018) to be uniquely mapped onto terminologies such as "evidence" or "decision variable". Given these considerations, we refrained from interpreting the link between specific parameters of the DDM and BOLD data. We instead focused on the quantitative comparison of the overall model performance.

Familiarity can be thought as an automatic process (Jacoby et al., 1989; Yonelinas & Jacoby, 2012). As such, it is not restricted to explicit recognition but is also present during indirect memory tasks. Consistent with this view, PrC activity has been shown to track familiarity independently from intention of retrieval, for example, in repetition priming paradigms (Dew & Cabeza, 2013; Heusser et al., 2013; J. L. Voss, Hauner, et al., 2009). Similarly, in previous analyses of the fMRI dataset used in the current study, we also found that PrC activity automatically tracked not only recent but also lifetime familiarity. Such automaticity suggests that other systems are involved to interpret or process the familiarity signal to suit various task goals, which have been collectively termed "attribution system". Although this framework was initially developed based on behavioral data alone (Jacoby et al., 1989), it has been recently incorporated into a neural cognitive model by Bastin et al. (2019), with the attribution system mapped onto

frontoparietal regions. However, the functions served by the attribution system are diverse. Importantly, some of the functions can be distinguished in terms of their stage of involvement in the decision-making process. One function of the attribution system is to inform decisions with memory signals, potentially by further processing the memory signal in combination with task goals and prior beliefs. This type of operation implies that signals represented in the attribution system, or subcomponents of it, are more predictive of the decision outcome than the memory signal in its raw form. On the other hand, the attribution system could also inform experiential aspects of the memory decision, such as vividness of recollection or metamemory judgements such as confidence ratings. This type of operation instead implies that signals represented in the attribution system are dissociable from the outcome of the primary decision.

One account that linked the attribution system closely to decision-making processes is the mnemonic accumulator hypothesis. This has been proposed as a function of the PPC, and was inspired by perceptual decision-making literature on the lateral intraparietal sulcus (Wagner et al., 2005). It postulates that PPC, in particular the lateral aspect, accumulates task-relevant mnemonic evidence putatively coded in MTL. Once the accumulation reaches a threshold, a decision is made. While intuitively appealing, evidence supporting this view is not particularly strong. In part, it stems from the difficulty to study such a hypothesis that demands high spatial and temporal resolution with human neuroimaging techniques. Consequently, evidence in favor of a mnemonic accumulator interpretation generally takes a rather nonspecific form of graded BOLD activity across degrees of memory strength (T. I. Brown et al., 2018b; Hutchinson et al., 2009; Sestieri et al., 2014). However, this pattern alone can and has been interpreted as familiarity (Daselaar et al., 2006; Horn et al., 2016; Yassa & Stark, 2008). To complicate things further, the graded activity may not be monotonic with respect to memory strength. When confidence and memory strength were dissociated, different regions (Sestieri et al., 2014) or neurons (Rutishauser et al., 2018a) in the PPC may track either, appearing to form symmetric and asymmetric accumulators, respectively. In the current study, we instead focus on another key characteristic of a mnemonic accumulator, namely its close involvement in the decision-making process. Note that the mPPC ROI in the current study were defined by the presence of a grade familiarity effect to begin with. However, we found that trial-by-

trial activity in this region did not predict memory decisions, in terms of RT and accuracy, better than that of the PrC, as demonstrated by an inferior DDM fit (Table 4.1). We note that similar findings, without the use of neurally-informed DDMs have also suggested that graded memory signals in mPPC may not be directly involved in decision making. In Guerin and Miller (2011), participants studied pictures of faces that were presented for different numbers of times. These stimuli were later paired according to their presentation frequencies to form three categories: pairs in which both faces had high presentation-frequency (h-h), pairs in which one of the faces had high frequency while the other had low frequency (h-l), and pairs in which both were of low frequency (l-l). Participants were asked to select the face in a pair with higher presentation frequency during a test phase. The authors generated two fMRI contrasts dissociating the amount of information retrieved and the accumulated evidence in favor of a decision. A contrast of the amount of retrieved information could be formed by comparing h-h pairs with l-l pairs, assuming pairs with overall higher presentation frequency during study corresponded to more information being retrieved at test. A contrast of decision-evidence was formed by comparing l-h pairs with the average of l-l and h-h pairs, assuming the evidence informing the decision was the difference in the amount of information retrieved between the two faces in each pair. The decision-evidence contrast did not reveal any stable effects, although an anterior cingulate cluster that did not survive the statistical threshold was found to track response uncertainty (i.e. more activated for l-l and h-h as compared to l-h). On the other hand, the contrast of amount of information retrieved revealed a number of parietal regions, on both the lateral and the medial aspects. Since the absolute amount of information retrieved for pairs of faces was irrelevant to the task, this pattern of results suggested that memory effects observed in parietal regions were not directly tied to making the memory decisions.

What could the mPPC signal be? One possibility is that it is related to metamemory, which is also a function postulated for the attribution system (Bastin et al., 2019). Metamemory can be viewed as a post-decision process (Yeung & Summerfield, 2012). It is widely accepted that metamemory accuracy can be dissociated from performance on the primary task (Fleming & Dolan, 2012). And sequential sampling models, of which DDM is a subclass, have been developed to explain the dissociation by considering

metacognitive judgement as either relying on a separate evidence-accumulation process or occurring after the threshold of the primary decision has been reached (Del Cul et al., 2009; Pleskac & Busemeyer, 2010). Ye et al. (2018) provided strong evidence supporting such a dissociation in humans. They causally manipulated mPPC (precuneus) activity through transcranial magnetic stimulation (TMS). Participants performed two-alternative-forced-choice tasks that either required a memory judgement or a perceptual one. TMS on the precuneus site selectively diminished participants' ability to make accurate metamemory judgement while leaving primary task performance unchanged. Although without a causal manipulation, our findings are consistent with the metamemory interpretation of mPPC functions given the inferior performance of the mPPC model in explaining task performance compared to the other two regions.

Similarly, mPFC has also been implicated in metamemory (Baird et al., 2013; Bastin et al., 2019; Fleck et al., 2006; Modirrousta & Fellows, 2008; Morales et al., 2018). Here the same vein of reasoning suggests that its role in the current study was unlikely to involve metamemory, given the superior ability of trial-by-trial activity in mPFC to predict task performance compared to PrC activity. However, other subregions within mPFC or more broadly PFC could be involved in metamemory, which we aim to explore in future research (see below). Our results are consistent with a more general role of mPFC in combining context with memory signal to select appropriate actions (Euston et al., 2012), although a nuance of our findings is that our task probed recent memory. Euston et al. (2012) posited that for recent memory, hippocampus is responsible for storing the associations between context, events, and responses while mPFC represents them separately. Only for remote memory, mPFC takes over the role of hippocampus to represent and store associations. This suggests that for recent memory, hippocampal representations are more conjunctive and do not generalize well across task goals as compared to mPFC representations. Decisions could be made based on the conjunctive representation to include all relevant information. However, a different pattern has been found in a recent study by Minxha et al. (2020). They recorded electrophysiological activity in mPFC and hippocampus while human participants were making binary mnemonic or visual categorization judgement on images either with button press or saccade. Critically, the memory judgement was based on recent exposures. They found

that the representation of memory strength was dependent on the task goal (memory or categorization) in mPFC but not in hippocampus. Moreover, participants' choices with either modality could be more reliably decoded from mPFC neuronal activity compared to hippocampal activity. Consistent with their findings, we found that trial-by-trial activity in the mPFC predicted task performance better than that of the MTL region (i.e. hippocampus and PrC) during a memory decisions of recent exposure. Whether mPFC regions are differentially involved in making decisions about remote memory remains an open question. This could in principle be studied with the same dataset used in the current study since our paradigm also included lifetime familiarity task which was closely matched to judgement of recent familiarity in terms of structure and stimuli characteristics. Given that judgement of lifetime familiarity would rely on memory information more remote than those involved in judgement of recent familiarity, this presents a unique opportunity to compare the relative position of mPFC on the decision-hierarchy when the memory decisions are on different time scales in a relatively well-controlled manner. However, some technical difficulties need to be overcome first (see below).

Another question is whether the decision hierarchy in other types of memory judgement also maps onto the same set of regions. In the framework laid out by Bastin et al. (2019), the attribution system is common to familiarity and recollection. Although different tasks or content would likely involve different subregions in frontal and parietal cortices (Tosoni et al., 2008; Vilberg & Rugg, 2008b), on a larger spatial scale, a common mnemonic decision hierarchy including PFC, PPC, and MTL seems plausible. The mPPC region in the current study mainly occupied the precuneus according to the Automated anatomical labelling atlas (version 3, Rolls et al., 2020). Together with mPFC, it is considered as a subnetwork of the default model network (Ritchey & Cooper, 2020; Yeo et al., 2011). Although familiarity effects have been commonly observed in these regions (Duke et al., 2017; Gilmore et al., 2015, 2019; Horn et al., 2016; Montaldi et al., 2006; Scalici et al., 2017; Vilberg & Rugg, 2008b), some researchers have grouped mPFC and mPPC into a "posterior medial" (PM) network and linked it to processes more related to recollection (Ritchey & Cooper, 2020). Despite the difficulty in determining the precise boundaries with nearby networks involved more in familiarity in mPPC (Buckner &

DiNicola, 2019; Bzdok et al., 2015; Gilmore et al., 2015), the link between mPPC and recollective processes does provide a possible explanation that the reason why the mPPC model performed less well than the other models in the current study is the primary reliance on familiarity in the task we employed. This also suggests that the relative position of mPPC on the decision hierarchy may change when a recollection-based memory decision is required. Future studies could investigate this possibility by including a task that can be used to separate recollection versus familiarity-based memory decisions, such as with a remember/know paradigm (Yonelinas & Jacoby, 1995).

One of the main limitations of the current study was the binarization procedure needed to fit the data with DDM. Although it has been suggested that such binarization could be a valid way of dealing with tasks involving more than two options (A. Voss et al., 2013), this was suboptimal since it complicated the interpretation of individual model fit. A better alternative would be to use sequential sampling models that can naturally accommodate more than two response options, for example, with race models or competing accumulators (Ratcliff & Starns, 2013; Rowe et al., 2010). A technical difficulty with such models is that the likelihood function is often unknown, which prevent them to be incorporated in a Bayesian framework. A newer version of HDDM has included a method to approximate the likelihood using simulated data using artificial neural networks, termed likelihood approximation network (LAN, Fengler et al., 2021). However, at the time of writing this paper, a LAN that can accommodate tasks with 5 response options had not been implemented. Another benefit aside from not requiring binarization, is that multi-alternative models can be fit with data lacking trial-level accuracy measurement. For example, lifetime familiarity judgement, whose accuracy cannot be evaluated objectively at the single-trial level (Duke et al., 2017). Since lifetime and recent familiarity can be dissociated both in behavior and in neural correlates, it is interesting to ask whether a similar decision hierarchy exists for this kind of judgement. Because the dataset used in the current study included lifetime familiarity judgements, we hope to return to this question in the future once the necessary software has been developed.

Another limitation was the feature/voxel selection step. This was implemented mainly to reduce the possibility that average over many voxels in a large region may wash out the trial-by-trial variability critical for our analyses and to reduce computation time. Ideally, one would remain agnostic to any effect that may be present in a GLM-style analyses and direct compare the neurally-informed DDMs in a purely data-driven manner, for example, with each voxel's trial-by-trial activity. This would generate a whole-brain decision map for the particular type of task considered. Provided that the task is sufficiently general, such a map would be highly valuable in answering both inter- and intra-network questions of decision-making. The main difficulty though, is the sequential nature of posterior sampling process, which is time consuming and cannot be parallelized within each chain. Since each model would need to be fit with at least 2 chains to assess convergence, even if we project the fMRI data onto a lower resolution space (e.g. fsaverage5 with 10,000 vertices per hemisphere), a mass-univariate whole-brain neurally-informed DDM fit will require a significant amount of time and computational resources. For a rough estimate, with the settings used in the current study, it will take 18750 hours when parallelized across 64 CPUs. The time needed would be further multiplied by the desire to include features other than univariate fMRI activity (e.g. searchlight pattern similarity measurement of different sizes). But including other representational format in the model comparison approach is essential to provide a "fair competition" among regions since the scale and topology of the representational content can very well differ among them. Due to the significant cost of this approach, it would be best to apply it on high-quality open datasets with a prototypical task so that later studies can build up on the results to test new hypotheses.

4.5 Conclusion

By comparing neurally-informed DDMs that incorporated trial-by-trial activity in different brain regions, to our best knowledge, the current study is the first to reveal a decision-hierarchy for judgements of recent familiarity. Specifically, mPFC activity was found to be most strongly involved in decision-making processes, followed by PrC activity, and then by mPPC activity. This pattern suggests that, at least for recent familiarity judgement, mPPC is unlikely to act as a mnemonic accumulator. Rather, its

activity may reflect experiential aspects of memory decision such as metamemory. On the other hand, mPFC activity may reflect goal-action mapping or decision-making more generally.

Chapter 5

5 « General Discussion »

The main goal of the current thesis is to provide a more comprehensive picture of the neural mechanisms underlying how people judge familiarity. Between the two processes proposed to support recognition memory (Mandler, 1980; Yonelinas, 2002), familiarity, being a relatively automatic and fast-acting process (Jacoby et al., 1989), is perhaps the most basic form of recognition memory. However, compared to recollection, it is also less well specified (Mandler, 2008). Research on recognition memory has largely constrained the inquiry to familiarity induced by recent exposure in laboratory settings, while the term "familiarity" when used to describe real-life experience often spans a considerably longer period of time and involves multiple diverse episodes. Behaviorally, it has been shown that people can provide reliable estimates of this form of lifetime familiarity (McRae et al., 2005; Moreno-Martínez et al., 2014a; Schröder et al., 2012b), and that lifetime familiarity of meaningful stimuli can affect judgements of recent exposure (Coane et al., 2011; Reder et al., 2000). Recent neuroimaging and patient studies have also provided initial demonstrations of common neural substrates associated with both recent and lifetime familiarity (Bowles et al., 2016a; Duke et al., 2017). The current thesis built upon this research and explored whether ERP and fMRI correlates of recent familiarity also track lifetime familiarity. Informed by the fluency-attribution theory (Bastin et al., 2019; Jacoby et al., 1989) and decision-making literature (Gold & Shadlen, 2007; Ratcliff, 1978; Ratcliff, Sederberg, et al., 2016), I also explored whether these neural correlates can be distinguished based on their degree of involvement in familiarity-based judgements under different task goals. To these ends, I conducted an ERP study and an fMRI study with closely matched stimulus characteristics and task structures, which allowed me to probe for neural responses to different degree of recent and lifetime familiarity in both task-relevant and -irrelevant conditions. In addition, I used the recently developed approach of neurally-informed DDM to conduct a modeling study that incorporated the fMRI data to reveal a decision hierarchy among brain regions during recent familiarity judgements. Overall, this research contributed to our knowledge

about familiarity judgement on different time scales by establishing automaticity of familiarity signals and the use of such signals in decision processes at the neural level.

In Chapter 2, I investigated whether the LPC, a commonly observed ERP correlate of recognition memory that has been recently linked to decision-making processes, flexibly tracked both recent and lifetime familiarity in a decision-dependent manner. That is, I tested whether it selectively tracks the type of familiarity signal that is relevant to the task at hand. For comparison, I conducted similar analyses on ERPs in an earlier time window corresponding to the FN400 and N400, which have primarily been linked to familiarity in previous studies (Rugg & Curran, 2007). The LPC was more positive for stimuli judged to have a higher degree of familiarity. Critically, this was true for both recent and lifetime familiarity, and a formal comparison of scalp topographies between the two types of judgements showed that they both had a similar centroposterior distribution. Moreover, the LPC showed a decision-dependent effect in that it was not present when the familiarity signals were irrelevant to the task. When comparing words presented many times versus those presented a few times during an animacy judgement task, a task-irrelevant recent familiarity effect in the LPC time window was observed. However, this effect had a markedly different scalp distribution. Similarly, different degree of lifetime familiarity in task-irrelevant conditions (i.e. animacy or recent familiarity judgement) did not elicit an LPC effect. In addition, to explore where the decision-dependent LPC effect originated, I conducted a source localization analysis using data from during that time window, which showed a similar modulation of task-relevance on current density estimates in the left ventral lateral parietal region. However, given that the study did not include participant-specific anatomical scans or photogrammetry information (information about relative positions between individual electrodes and anatomical fiducials), conclusions from the source localization analysis are limited. Results in the earlier time window were more complex. ERP recorded on centroposterior electrodes, potentially representing a N400 effect, appeared to track degrees of familiarity across timescale regardless of task-relevance. When participants judged recent familiarity, a topographically distinct effect appeared to extend somewhat anteriorly and tracked the degree of recent familiarity, potentially representing an FN400. Consistent with the fluency-attribution framework, these findings indicate that neural mechanisms underlying

automatic processes of familiarity signals on both time scales are engaged earlier than that of decision-related processes. However, for recent familiarity, another earlier decision-related component is also present, which matches the behavioral findings in Coane et al. (2011) suggesting fast-acting mechanisms underlying the computation of recent (relative) familiarity.

A previous neuroimaging study showed that PrC was involved in tracking both recent and lifetime familiarity (Duke et al., 2017). However, one limitation of that study was that it only focused on task-relevant conditions. Chapter 3 aimed to address this limitation and to extend the ERP findings in Chapter 2 with a focus on the role of specific brain regions in the MTL. A region in the left PrC showed decreasing activity with increasing degree of judged recent and lifetime familiarity, as revealed by a conjunction analysis. Left PrC was also sensitive to task-irrelevant recent familiarity as demonstrated by a repetition suppression effect during animacy judgement in the study phase. Critically, when task-irrelevant familiarity was probed in animacy and recent familiarity judgement by recoding the trials based on participants' lifetime familiarity rating of those stimuli collected after the scanning session, PrC also tracked task-irrelevant lifetime familiarity in both conditions. To my best knowledge, this is the first report of a task-irrelevant lifetime familiarity effect in PrC. This pattern was also specific to PrC and was not found in surrounding MTL and IT regions. Lastly, at the whole-brain level, activity in a set of frontoparietal regions, including the medial frontal region, precuneus, and angular gyrus, were modulated by familiarity only in task-relevant conditions. Consistent with the fluency-attribution framework, these findings suggest that familiarity effects in PrC reflect fluency signals similar to the N400 effect found in Chapter 1, while activity in frontoparietal regions are tied to the attribution system.

Chapter 4 addressed how activity across brain regions contributes to judgement of familiarity using a model-comparison approach. I focused on the judgement of recent familiarity and binarized participants' responses by accuracy. This allowed me to fit the data with a drift-diffusion model (DDM) and differentiate the contribution of neural activity in different regions to the familiarity judgements within a single experimental condition. Using a hierarchical Bayesian approach, trial-by-trial variations of the DDM

parameters that represented different components of the decision-making processes were linked to trial-by-trial activity change in regions showing familiarity effects in the previous chapter, including PrC, medial prefrontal (mPFC), and medial parietal cortex (mPPC). This approach produced a set of neurally-informed DDMs, whose goodness-of-fit measurements were used to quantify the involvement of each region in decision-making processes during judgement of recent familiarity. Compared to the baseline model without neural information, incorporating trial-by-trial fMRI activity produced better fitting models for all three regions. Furthermore, when comparing across regions, the model with mPFC activity produced the best fitting model, followed by the PrC model, and then the mPPC model. These results represent the first evidence of a decision hierarchy among brain regions implicated in familiarity judgements and suggest that the attribution system (Bastin et al., 2019) can be further decomposed into subcomponents based on their degree of involvement in decision processes.

5.1 Relation to the fluency-attribution theory

The most relevant theoretical framework for the current research is the fluency-attribution theory initially developed by Jacoby and colleagues (Jacoby et al., 1989) and more recently elaborated in the IM model by Bastin et al. (2019). Fluency is thought to be an automatic signal arising from general processing of the stimuli and thus its neural correlates should be present even when an explicit judgement of prior occurrences is not required. In contrast, the attribution system is goal-directed and is involved in decision making and in generating explicit judgements as well as the conscious experience of memory retrieval.

Before discussing neural data, I would like to point out that the involvement of an attribution system during familiarity judgements can be inferred from the behavioral data alone. Fluency is often operationalized as reduced response time (Whittlesea & Williams, 1998). A monotonic decrease in RT can then be viewed as a monotonic increase in fluency, such as the pattern observed during animacy judgements with an increasing number of presentations or increasing degree of lifetime familiarity (see Figure 3.2). However, during recent or lifetime familiarity judgements, RT plotted as a function of participants' ratings showed an inverted-U shape (see Figure 4.3 for recent familiarity

judgements). A similar non-monotonic shape has been reported in studies of recognition memory involving confidence ratings (Daselaar et al., 2006). Given that participants' recent and lifetime familiarity ratings were positively correlated with the objective presentation frequency and normative lifetime familiarity, respectively, if fluency was the only process involved, then RT during familiarity judgements should be monotonic with respect to participants' ratings. The inverted-U shape thus indicates the involvement of other processes in generating the familiarity judgement. Perhaps the most straightforward explanation of this pattern involves including a decision-making process, which is a component of the attribution system as suggested by Bastin et al. (2019). The decision-making process can be modeled as accumulating evidence over time until it crosses a decision boundary (O'Connell et al., 2018). In a recently developed variant of this type of models, Ratcliff and Starns (2013) showed that the shape of the RT distribution followed the shape of decision boundaries across levels of confidence. Alternatively, the nonmonotonic shape of the RT across levels of confidence can be explained by recollection. A particularly relevant version of the dual-process model was proposed by Atkinson and Juola (1973). As discussed in Chapter 1, this model assumes that recollection (i.e. an extended search process) is engaged only when the familiarity signal is not diagnostic to the memory judgement. Whether the familiarity signal is diagnostic or not depends on whether it falls below a low threshold corresponding to a "new" response with high confidence, or above a high threshold corresponding to an "old" response with high confidence, assuming confidence ratings are approximations of the memory strength. Interpreted within this framework, recognition judgements with intermediate confidence are made slower because additional search (i.e. recollection) is involved. However, this is at odds with other dual-process models and neuroimaging findings. For example, in the model proposed by Yonelinas (1994), recollection is thought to produce highly confident recognition only. Consistent with this view, neuroimaging studies have also found hippocampal activity tends to be associated with the highest level of recognition confidence while PrC activity shows a more graded pattern (Daselaar et al., 2006; Montaldi et al., 2006). Hence, a decision-making process, as a part of the attribution system, provides a better account of the RT effect observed in the current study. The current thesis provided novel insights on potential neural mechanisms

underlying the changes in the shape of the RT between task-relevant and task-irrelevant conditions by showing that a set of ERP and fMRI correlates were also modulated by task-relevance.

As a side note, the reader may have noticed that in previous chapters, I generally used the term “familiarity” rather than “fluency” to describe the hypothetical mnemonic signal or the observed neural correlates. The reason behind this choice is that the term “familiarity” entails fewer assumptions about RT. Given the inverted-U shape of RT observed in the test phase and the fact that task-irrelevant effects in the test phase were computed as linear contrasts of participants’ ratings, familiarity is the more accurate term. On the other hand, for task-irrelevant contrasts conducted during animacy judgements, the more appropriate terminology may be fluency since RT in this task decreased monotonically with repetitions (i.e. increased familiarity/memory strength) and it presumably did not involve the mnemonic attribution system.

5.1.1 Neural correlates of task-irrelevant familiarity

In Chapter 3, PrC BOLD activity was found to track both recent and lifetime familiarity regardless of task-relevance. This is consistent with previous research that linked PrC activity reduction in repetition priming paradigms (Heusser et al., 2013; J. L. Voss, Lucas, et al., 2009) and familiarity during explicit recognition of recent exposure (Daselaar et al., 2006; Eichenbaum et al., 2007; Montaldi et al., 2006). The former can be understood as an effect of task-irrelevant recent familiarity, and the latter an effect of task-relevant recent familiarity. A well-known behavioral phenomenon of the interaction between the two types of familiarity is the word-frequency mirror effect, in which high-frequency words, presumably having higher degree of lifetime familiarity, result in a higher proportion of false alarms in a recognition memory paradigm, indicating a heightened level of recent familiarity. Given that both familiarity signals have been found in PrC, it is expected that neural correlates of word-frequency mirror effects should also be observable in this region. At a minimum, such neural correlates could take the form of a task-irrelevant lifetime familiarity or word frequency effect during judgement of recent familiarity. However, the few studies that have attempted to localize the neural correlates of word-frequency mirror effect in humans failed to reveal any PrC effect (de Zubicaray

et al., 2005a, 2005b). Chapter 3 represents the first report of a task-irrelevant lifetime familiarity effect in PrC, accompanied with a behavioral effect similar to the word-frequency mirror effect, namely increased frequency overestimation for stimuli given high lifetime familiarity ratings. This pattern is also consistent with findings from electrophysiological studies in non-human animals that firing rates of PrC neurons track familiarity signals on multiple time scales, which also appear to be insensitive to task-relevance (Fahy et al., 1993; Xiang & Brown, 1998). In terms of the time course of this automatic familiarity signal, in Chapter 2 I found an early ERP effect with a posterior scalp distribution resembling an N400, which tracked both recent and lifetime familiarity regardless of task-relevance. Interestingly, this ERP component has been linked to repetition priming (Kutas & Federmeier, 2011; Rugg, 1985) and recognition memory (J. L. Voss & Federmeier, 2011a). In addition, it is sensitive to task-irrelevant word frequency (Bridger et al., 2014; Rugg, 1990). Hence, both PrC BOLD activity and a posterior ERP in the 300-500 ms post-stimulus window indexed the automatic aspect of familiarity judgement, irrespective of time scale. This correspondence between neural correlates across two modalities in the same experimental paradigm is a novel contribution to our understanding on the automatic components of familiarity.

5.1.2 Neural correlates of the attribution system

One of the main characteristics of the attribution system is that it is goal-directed. Thus, sensitivity to the manipulation of task-relevance is a necessary condition for neural correlates involved in attribution. In Chapter 2, the FN400 effect and the LPC effect met this criterion, as did the frontoparietal regions showing task-relevant effects in Chapter 3.

A recent review by Mecklinger and Bader (2020), which contained a detailed treatment of the FN400, explicitly linked this component to the attribution system. They interpreted the FN400 as attribution of unexpected fluency to prior occurrences. This specific type of attribution process is also thought to be closely related to the computation of recent (relative) familiarity (Coane et al., 2011). Although the paradigm employed in the current thesis did not involve any manipulation on the expectation of fluency, the FN400 effect observed in Chapter 2 is largely consistent this view in that it tracked only task-relevant recent familiarity. In an attempt to link this ERP component to brain regions, Mecklinger

and Bader suggested that the FN400 may have a generator located in the lateral prefrontal cortex (PFC). This was based on a previous report that this region was more activated during familiarity-based as compared to recollection-based recognition (Dobbins et al., 2003; Henson et al., 1999) and the observation that FN400 amplitude modulated lateral PFC activity during simultaneous recording (Hoppstädter et al., 2015). Interestingly, in Chapter 3, medial rather than lateral frontal activity tracked task-relevant recent familiarity. This discrepancy could perhaps be explained by differences between the recent familiarity task used in the current thesis, which included only studied items and required participants to make grade judgements, and the old/new recognition task typically employed in recognition studies. However, it is worth noting that the K > R contrast in Henson et al. (1999) used to extract the lateral PFC effect also revealed medial PFC effect. In addition, a K > N contrast, which could also be interpreted as indexing recent familiarity, revealed both lateral and medial PFC effects. Thus, it seems that task-relevant recent familiarity effects in the frontal regions are not restricted to the lateral aspects, which is in line with evidence from other behavioral task implicating medial PFC in decision-related processes (Euston et al., 2012).

Based on their common link to recent familiarity (Curran, 2000; Daselaar et al., 2006; Montaldi et al., 2006; Rugg & Curran, 2007; Woodruff et al., 2006), Hoppstädter et al. (2015) attempted to directly link PrC BOLD activity with FN400 amplitude in a simultaneous EEG-fMRI study. Although the study replicated the FN400 and the LPC old/new effect when analyzing the EEG data in isolation and revealed a set of medial frontoparietal effect similar to those observed in the current thesis, a link between the FN400 amplitude and PrC BOLD activity was not observed. One explanation for this negative finding could be the severe signal dropout commonly observed in the PrC region, and simultaneous EEG-fMRI recording might have further constrained the signal quality. Aside from this potential technical issue, the lack of correspondence between FN400 and PrC BOLD activity could also reflect a genuine functional difference between the two neural correlates. In the current thesis, the parallel effects between the N400, which was topographically distinct from the FN400, and PrC BOLD activity lend some support for this interpretation. These results suggest that the FN400 and PrC BOLD activity index qualitatively different processes, with the former potentially linked to an

attribution system for recent familiarity located in frontal regions. It is worth noting that, as pointed out by Mecklinger and Bader, the FN400 effect observed in the current thesis did not extend as frontally as in other reports (e.g. Woodruff et al., 2006). Due to the difficulty in assessing topographical differences across studies and the fact that the behavioral paradigm used here involved frequency judgement instead of the more commonly used old/new judgement, caution is warranted when interpreting the effect as a canonical FN400.

One extension made in the model by Bastin et al. (2019) regarding the attribution system is that it is common to both familiarity and recollection. Together with previous research, the results on the LPC effect in Chapter 2 and the frontoparietal BOLD activity in Chapter 3 speak to such generality, as both types of neural correlates were found to be sensitive to task-relevance, and have both been linked not only to familiarity (Brezis et al., 2016; Horn et al., 2016; J. L. Voss, Lucas, et al., 2009) but also recollection (Curran, 2000; D. I. Donaldson & Rugg, 1998; Ritchey & Cooper, 2020; Wilding & Rugg, 1996; Woodruff et al., 2006). The current thesis demonstrated for the first time that they tracked familiarity signals of different time scales, providing further evidence for a general mnemonic-attribution system. However, the attribution system as conceptualized by Bastin et al. is an umbrella term that captures a host of cognitive processes. A number of subcomponents of the attribution system can be distinguished based on their involvement in decision-making processes during the memory judgement. Below I draw on past research and findings in the current thesis to discuss potential neural correlates for these subcomponents.

5.1.2.1 Experiential aspects of memory attribution

One function assumed to be supported by some subcomponents of the attribution system is the subjective experience of memory. Both frontal and parietal regions have been linked to this aspect, such as vividness or metacognitive experiences. For example, Baird et al. (2013) showed that interindividual differences of metacognitive accuracy in a recognition memory task was correlated with resting-state functional connectivity between a seed region in the anterior medial prefrontal cortex and intraparietal sulcus and precuneus. Interestingly, BOLD activity in the precuneus, which formed part of the

mPPC ROI in Chapter 4, has also been linked to the experience of vividness during a recollective task (Richter et al., 2016). Moreover, in a recent TMS study, direct manipulation of precuneus activity affected participant metacognitive judgement in a memory task while leaving the memory judgement itself and performance on a perceptual task unaffected (Ye et al., 2018). Although the current paradigm was not designed to provide a clear dissociation between cognitive and metacognitive processes, the finding that the neurally-informed DDM with mPPC activity outperformed the baseline model indicated that mPPC was involved in decision making during familiarity judgements. In addition, since the model with PrC activity provided a better fit, it appears that the signal coded by the mPPC was not as relevant to the decision as that of PrC. As metacognitive processes are thought to depend only partially on the information used to make a first-order (cognitive) judgement (Fleming & Dolan, 2012; Yeung & Summerfield, 2012), this pattern is consistent with a metacognitive interpretation of mPPC function during familiarity judgements.

Metacognition is commonly measured with confidence ratings, which in recognition memory studies has also been taken as an approximation of familiarity or memory strength (Hintzman, 2004). A subtle distinction can be found in the behavioral paradigms between the two fields. Whereas metacognitive confidence is typically measured with a two-step procedure in which the confidence rating is given after an initial first-order judgement, mnemonic confidence often involves a single rating capturing both an "old/new" and a confidence judgement. This subtle point aside, we can assume that an explicit confidence judgement necessarily involves some form of metacognitive processes. From this prospective, the LPC effect in Brezis et al. (2016) reviewed earlier could also be interpreted as reflecting metacognition or metamemory more specifically. In each trial, participants provided an "old/new" judgement concurrently with a confidence rating. For stimuli judged to be old, a following RK judgement was used to separate recollection from familiarity-based recognition. They first replicated the canonical LPC effect thought to reflect recollection by showing that a parietally centered ERP in the 500 ms to 1000 ms time window was more positive to R than to K responses. Critically, when they compared ERPs between trials associated with high versus low confidence ratings while controlling for the RK effect through a sampling procedure, an

effect similar to the LPC was observed, namely that high confidence trials were associated with more positive ERPs concentrated on parietal electrodes. However, when they pitted the RK status against confidence by comparing high-confidence K responses with low-confidence R responses, the LPC effect was not as prominent. Thus, the LPC effect likely reflects a mixture of processes, with one of them being metacognition. The LPC effect selective to task-relevant familiarity found in Chapter 2 is also consistent with this interpretation. However, based on the sensitivity of task-relevance alone, a metacognitive interpretation cannot be distinguished from a decision-making interpretation (see below), although its parietal distribution and the related mPPC finding in Chapter 4 provide some hint that a metacognitive interpretation may be more likely.

5.1.2.2 Decision-making aspects of memory attribution

Another function served by subcomponents of the attribution system is to make decisions based on the memory signals provided by the core system, which largely consists of MTL regions (Bastin et al., 2019). One influential model regarding this aspect of attribution is the mnemonic accumulator hypothesis (Wagner et al., 2005). This view was inspired by the well-established role of intraparietal sulcus in perceptual decision-making (Gold & Shadlen, 2007; Shadlen & Newsome, 2001). Hence, it is mainly a model for parietal regions, in particular the lateral parietal regions. Due to the limited spatiotemporal resolutions of noninvasive neuroimaging techniques, evidence in favor of this interpretation in humans usually takes the form of demonstrating activity modulation by subjective rather than objective memory status (Wheeler & Buckner, 2003), or a graded activity change across different levels of memory strength (T. I. Brown et al., 2018b; D. I. Donaldson et al., 2009; Sestieri et al., 2014). Another characteristic of a potential neural correlate of mnemonic accumulator is that its activity should be more predictive of behavioral measurements of the decision than that of the upstream processes. This was demonstrated in Chapter 4 by the superior model fit as a result of incorporating mPFC activity as compared to PrC activity. Nevertheless, it is worth noting that although this pattern is consistent with a mnemonic accumulator, other decision-related processes linked to this region may produce similar patterns, such as memory-choice mapping (Euston et al., 2012; Minxha et al., 2020), uncertainty (Fleck et al., 2006), and

performance monitoring (D. I. Donaldson et al., 2009). Distinguishing these theories requires further research.

Another question regarding neural correlates of mnemonic accumulator is how tightly it is coupled with the motor response. The seminal finding that inspired the mnemonic accumulator hypothesis, namely lateral intraparietal neurons showing an accumulator-like response profile in perceptual decision-making tasks in monkeys, could be considered as more related to action planning (O'Connell et al., 2018). On the other hand, a recently identified ERP component in humans has been shown to reflect a more abstract form of evidence accumulation (O'Connell et al., 2012). This centroparietal positivity (CPP) was sensitive to task-relevant perceptual evidence (i.e. coherent motion of dots) regardless of whether the appropriate behavioral output mapping was known ahead of time by the participants (Twomey et al., 2016). Critically, when the ERPs were time-locked to stimulus onsets, the time window of this component overlapped with that of the LPC effect observed in the current thesis (though with an earlier onset). Although their task and the corresponding profile of response time differed significantly from the current research, the presence of the CPP is consistent with the interpretation that parietal ERPs in the LPC time window contain decision-related signals, which could represent processes occurring after evidence encoding but before the formulation of action plans. Assuming neural activity in mPPC partially contributed to the LPC effect, the finding in Chapter 4 that the DDM with mPPC activity performed worse than the DDM with mPFC activity seem to be consistent with the idea that mPPC activity represents an intermediate stage of decision making. However, given that the mPPC model was also outperformed by the PrC model, which presumably represented "raw" familiarity signals, from a fluency-attribution point of view, it suggests that the mPPC activity may not be directly involved in generating the explicit memory judgement and instead reflect auxiliary processes that nonetheless depend on partial information supporting the explicit judgement, such as metacognition. Ultimately, these possibilities will need to be investigated in future research, perhaps with simultaneous EEG-fMRI recordings together with source localization analyses.

5.2 Familiarity of other time scales and heterogeneity of PrC lifetime familiarity effect

It is worth noting that familiarity signals operating on other time scales may also exist, and the current thesis only addressed two somewhat extreme examples (recent and lifetime) along a continuum. One paradigm that can be considered as an intermediate case in terms of time scale is the controlled autobiographical retrieval task (Cabeza et al., 2004). This procedure taps memories that often span an extended period of time (e.g. weeks) and involve multiple episodes, yet is confined within a segment of the participants' entire lifetime experience. In this paradigm, a group of participants wear cameras that take pictures as they go through their lives in a common environment, for example, a university campus. Later, a recognition judgement requiring them to distinguish between pictures taken by themselves and those taken by other participants provides a controlled way of assessing autobiographical memory (T. I. Brown et al., 2018b; Cabeza et al., 2004). Brown et al. (2018) combined this paradigm with a modified RK procedure, in which a recognition decision was classified into several categories: Recollection (R) if they participants could recollect specific episodic details regarding the experience captured by the photos, Familiar (F) if the experience seemed familiar without recovering episodic details, "Unsure" and "Not yours" which corresponded to a Guess and New judgement. They also included a "Know but not familiar (K)" category to capture recognition based solely on semantic information. A linear contrast of increasing activity across different levels of memory strength (i.e. correct-rejections (CR), K, F, and R) returned significant results in several frontoparietal regions, including angular gyrus, precuneus and medial PFC, similar to the set of regions found to track task-relevant lifetime familiarity in Chapter 3. This pattern suggests that these regions may be involved in tracking graded memory strength regardless of the time scale on which the memory was formed or probed.

Interestingly, Brown et al. (2018) also found an effect in PrC, whose activity increased with respect to memory strength. In contrast, analyses in Chapter 3 revealed decreasing activity with increasing levels of both recent and lifetime familiarity in PrC. What is even more puzzling is that Duke et al. (2017) also observed PrC BOLD activity increases with

judged degree of lifetime familiarity, using a behavioral paradigm very similar to the current one. However, as discussed in Chapter 3, only a small number of fMRI studies have employed judgements of lifetime familiarity (Duke et al., 2017; Gimbel et al., 2017; Yassa & Stark, 2008), and the directions of signal change with respect to lifetime familiarity in these studies were highly varied. Notably, in electrophysiological studies with non-human animals, both an increase and a decrease in firing rate related to long-term familiarity have also been reported in PrC neurons (Fahy et al., 1993; Hölscher et al., 2003; Xiang & Brown, 1998), although in this case reduction in activity (i.e. firing rate) seems to be more prevalent. Miller and Desimone (1994) found separate groups of neurons in IT that responded to repetition in a delayed-match-to-sample task with either increased or decreased firing rate. Moreover, neurons showing repetition suppression were not sensitive to task-relevance as repetitions of non-match (i.e. task-irrelevant) stimuli happening in-between the initial presentation of a target stimulus and its repetition also induced a repetition suppression effect. On the other hand, for neurons showing repetition enhancement, the effect was only present for task-relevant stimuli, with intervening repetitions of non-match stimuli producing the same level of activity as their first presentations. Although these neurons were recorded in IT, given that this region has often been studied together with PrC in monkeys and that repetition effects were commonly observed in both regions (M. W. Brown & Banks, 2015), it is possible that such coupling between task-relevance and the direction of repetition effect also exists in PrC. This provides one explanation of the increase in PrC activity with respect to lifetime familiarity observed in Duke et al. (2017), since it was analyzed only in the task-relevant condition. More research is needed to determine whether the direction of signal changes in PrC as measured with fMRI holds any functional significance.

5.3 Relationship to the representational hierarchical model of PrC functions

Although Chapter 3 focused on the mnemonic aspect of PrC, it is worth pointing out that current results were not incompatible with the representational view which suggests that PrC plays a broader role in cognition. The model holds that PrC is not only involved in memory but also in perception by combining conceptual and perceptual features to form

conjunctive representations of objects (Bussey & Saksida, 2007; Cowell, 2012; C. B. Martin et al., 2018). In fact, the automaticity of PrC familiarity signals suggests that the mnemonic signal may be a byproduct of the representational content in PrC. As Cowell et al. (2006) demonstrated in a modeling study, by having a representational code that is more conjunctive than earlier regions, PrC activity is more robust against interference. This was simply due to the fact that if intervening stimuli consist of random features, it is less likely for them to have exactly the same feature composition of the remembered items, despite that a subset of their features may overlap. Thus, the mnemonic function of PrC can be largely explained by its representational content. However, at a finer spatial scale, neurons specialized in memory or perception may be distinguishable. For example, Rutishauser et al. (2015) showed that minimally overlapping neuronal populations in human hippocampus were selective to either the old/new status of or the category of visual stimuli. To the extent that hippocampus can be thought as a downstream layer on the representational hierarchy (Bussey & Saksida, 2007), it is possible that the same pattern may hold in PrC. Functional characterization at this spatial scale is beyond the reach of noninvasive neuroimaging techniques on which the current thesis focused.

Another idea born out of the representational hierarchy framework is the distinction between representation and operation (Cowell et al., 2019). The primary example put forward by Cowell et al. (2019) was recollection, which is a cognitive process that can be decomposed into its representation, multidimensional/associative patterns, and its operation, pattern completion. For familiarity though, the distinction between process, representation, and operation is less clear, in part due to its being considered as a unidimensional signal which does not leave much room for a representational interpretation. It may be helpful to further decompose operation into mnemonic-specific operations and attribution-related operations. For example, whereas pattern completion and global matching (Hintzman, 1984) could be considered as mnemonic-specific operations that return a multidimensional pattern and a unidimensional strength (i.e. “intensity” of the match), respectively. Decision-making mechanisms such as evidence accumulation could be considered as an attribution-related operation that takes the output of the mnemonic-specific operation and modifies them to suit task goals. This view is also consistent with the general spirit of Wixted and Mickes' (2010) dual-process model

in which recollection and familiarity signals come from separate distributions. During a memory decision, these distributions can either be considered separately, as in RK paradigms, or summed together as in old/new recognition paradigms. Regarding representations of familiarity, from the perspective of a representational hierarchy, familiarity signals at different levels of feature conjunction could be considered as having different representations as proposed by Bastin et al. (2019). The current research suggests that familiarity on multiple time scales may also be considered as having separate representations. Thus, the representational aspect of familiarity may be more diverse than previously thought. Furthermore, some neural correlates that I identified were selective to task relevance but not to the time scale of the familiarity signals, which may be considered as indexing operations that act on arbitrary familiarity representations according to task goals.

5.4 « Limitations and future directions»

One limitation of the lifetime familiarity task used in the current thesis is that it is a relatively open-ended judgement. Another way to put it is that the decision on lifetime familiarity may depend on a variety of evidence. Because few studies have seriously considered lifetime familiarity judgements, there is little established theoretical background. However, limited empirical evidence does suggest the potential involvement of both episodic and semantic processes. For example, Duke et al. (2017) reported that participants' lifetime familiarity ratings were positively correlated with the perceived ease of recollecting an episode containing the corresponding concepts, and the amount of semantic knowledge of those concepts. In an unpublished dataset, I also found a similar pattern, with the amount of semantic knowledge and the ease of episodic recollection each having independent contribution to the perceived lifetime familiarity. Moreover, in that study, a "frequency of exposure" rating was also included, which showed additional contribution to lifetime familiarity ratings over and above the effects of episodic ease and semantic knowledge. Studies with NB have demonstrated that recollection, at least as conceptualized in dual-process models of recognition memory, was unlikely to be essential for lifetime familiarity judgement, since estimations of NB's recollective ability was normal in a wide variety of recognition memory paradigms (Köhler & Martin, 2020).

Thus, the positive correlation between the ease of recollection and the lifetime familiarity ratings may be conceptualized as “non-critical” or task-irrelevant recollection. Notably, this type of recollection has been shown to be behaviorally similar to familiarity in process-dissociation paradigms, in terms of being relative fast and automatic (Yonelinas & Jacoby, 1996), though whether the neural correlates of non-critical recollection differ from familiarity or “critical” recollection remains unknown. The aspect of semantic knowledge is also of importance when comparing lifetime and recent familiarity, since mere repetitions in a laboratory setting would not be accompanied by a gain of knowledge, while cumulative exposure in real life often would. Consequently, any neural correlates found to differentiate the two types of familiarity could reflect a difference in semantic knowledge (e.g. Angular Gyrus BOLD activity for lifetime familiarity in Chapter 3). A potentially fruitful approach for future studies on lifetime familiarity is to conduct item-centric analyses. Such analyses could help discern concepts whose lifetime familiarity are more strongly related to episodic processes versus those that are more strongly related to semantic processes, both behaviorally and in terms of neural correlates.

On a related note, it would be interesting to test whether neural correlates of lifetime familiarity also form a similar decision hierarchy. Chapter 4 focused only on judgements of recent familiarity due to the need to binarize the behavioral data to accommodate DDM, which was impossible for lifetime familiarity judgement because there is no known ground truth that would allow verification of trial-level accuracy. As mentioned earlier, this could be accommodated in a newer version of the HDDM (Fengler et al., 2021), which introduced race models that can be fit with data from tasks with more than two response options and do not require trial-level accuracy measurements. This can also be applied to the recent familiarity judgement in the current thesis, which would help validate the findings in Chapter 4 by model participants’ graded judgements directly without binarization. However, as of now, it only supports tasks with up to four response options and the performance of the software does seem to deteriorate when the number of response options increases. Hence, further development and validation of this software is needed before it can be utilized for these purposes. Finally, another aspect of the neurally-informed DDM that can be improved is its scale. In Chapter 4, the ROI-

definition and feature-selection steps were used to select voxels whose activity were modulated by judged degree of recent familiarity. A more powerful approach is to forgo these selection steps and instead generate a whole-brain “decision map” by fitting neurally-informed DDMs to each voxel or slightly down-sampled unit space to alleviate the computational cost. This data-driven approach could reveal, in a much more detailed manner, not only what regions form a network for a specific type of decision (memory or otherwise), but also how regions within the network contribute differently to such decisions.

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6

Appendices

Appendix A (Chapter 2): Local peak amplitudes and two-step PCA.

We first measured local peak amplitude of the ERPs using ERPLAB within the two time windows typically examined for the LPC and FN400/N400. Specifically, the LPC peak was sought as a positive local peak within the window of 500 to 800 ms. And the FN400/N400 peak was sought as a negative local peak within the window of 300 to 500 ms.

Secondly, we also performed two-step PCA (temporal then spatial) on the ERP data following the guidelines in Dien (2012) using the ERP PCA toolkit (Dien, 2010). The data were down-sampled to 128 Hz due to RAM limitations. The number of factors retained was determined through a parallel test. Factors representing the two ERP of interest were chosen through visual inspection guided by previous literature. The LPC was defined as a positive peak with a parietally-centered topography within the time window of 400 to 800 ms. The FN400/N400 was defined as a negative peak with a (frontal) parietal distribution within the time window of 300 to 500 ms. The LPC time window was relaxed to allow overlapping with the FN400/N400 time window in PCA analyses as the procedure is designed to separate temporally overlapping components. Factors were then fed to the autoPCA process to extract peak channel and peak value. These values for selected factors that represent either LPC or FN400/N400 served as inputs to a robust ANOVA for inferential statistics.

Below we present a table showing the outcomes of these analyses in comparison with our preferred, previously reported methods (mean amplitude with a priori selected time window, local peak amplitude with a priori selected time window, and PCA), along with a figure illustrating the Principal Components linked to the ERP effect we reported in the manuscript. The same ANOVA models were used across mean amplitude and local peak measurements. For the PCA-based analyses, we also report the peak latency and the peak electrode as produced by the autoPCA process. To aid this comparison, we present them in the order as they appear(-ed) in the manuscript with corresponding current page

numbers. Please note that there a few empty cells for PCA based analyses as they could not be computed and would be largely redundant after the spatial PCA step.

Table A1: Statistical results across three different measurement types on key contrasts.

	Mean amplitude (as reported in previous versions)	Local peak	PCA
1. ANOVA on the LPC amplitude in the test phase (p. 6)	anteriority x response: $F(1, 46) = 18.96$, $p < .001$, $\hat{\eta}_G^2 = .005$	anteriority x response: $F(1, 46) = 21.86$, $p < .001$, $\hat{\eta}_G^2 = .007$	531 ms to 539 ms, on electrode PO3, main effect of response, $T_{WJt}/c\ (1.0, 42.0) = 20.59$, $p < .0001$ (figure S1a)
2. Post-hoc t-tests on 1. Response effect in each level of anteriority (p. 6)	Centroposterior: $t(46) = 1.96$, $p = .028$, $d = 0.29$ Anterior: $t(46) = -1.19$, $p = .88$, $d = -0.17$	Centroposterior: $t(46) = 1.40$, $p = .085$, $d = 0.20$ Anterior: $t(46) = -1.72$, $p = .95$, $d = -0.25$	
3. LPC topographical comparison between the two tasks in the test phase (p. 7)	No effect involving the task factor returned significance, all $ps > .15$	No effect involving the task factor returned significance, all $ps > .20$	

4. Study phase frequency effect in the LPC time window (p . 7)	anteriority × laterality × presentation frequency interaction; F (1, 47) = 6.82, p = .012, $\hat{\eta}_G^2$ < .001	anteriority × laterality × presentation frequency interaction; F (1, 47) = 1.65, p = .20, $\hat{\eta}_G^2$ < .001 However, there is a marginally significant main effect of frequency, F (1, 47) = 3.98, p = .052, $\hat{\eta}_G^2$ = .017	594 ms to 602 ms, on electrode Cz, significant presentation frequency effect, T_{WJt}/c (1.0,43.0) = 4.96, p = .031.(figure S1b)
5. Topographical comparison between the study and the test phase frequency effect in the LPC window (p. 7)	anteriority × phase: F (1, 42) = 10.18, p = .003, $\hat{\eta}_G^2$ = .04	anteriority × phase: F (1, 42) = 7.76, p = .008, $\hat{\eta}_G^2$ = .024	
6. Comparing LPC lifetime exposure effect between the two tasks in the test phase (p. 8)	anteriority × lifetime exposure × task: F (1, 46) = 4.76, p = .034, $\hat{\eta}_G^2$ = .001	anteriority × lifetime exposure × task: F (1, 46) = 4.98, p = .031, $\hat{\eta}_G^2$ = .002	484 ms to 492ms, on electrode PO3, significant task × lifetime exposure: T_{WJt}/c (1.0,42.0) = 5.12, p = .027. (figure S1c)

7. Post-hoc ANOVA on 6. LPC lifetime exposure effect in each task (p. 8)	During lifetime exposure judgement: anteriority × lifetime exposure: $F(1, 46) = 15.37$, $p < .001$, $\hat{\eta}_G^2 = .008$ During recent exposure judgement: no effect involving the factor "lifetime exposure" was significant, all $ps > .1$	During lifetime exposure judgement: anteriority × lifetime exposure: $F(1, 46) = 10.90$, $p = .002$, $\hat{\eta}_G^2 = .008$ During recent exposure judgement: no effect involving the factor "lifetime exposure" was significant, all $ps > .1$	During lifetime exposure judgement, significant lifetime exposure effect: $T_{WJt}/c (1.0,42.0) = 17.11$, $p < 0.001$. (figure S1c) During recent exposure judgement, nonsignificant lifetime exposure effect: $T_{WJt}/c (1.0,42.0) = 0.40$, $p = .53$. (figure S1c)
8. Lifetime exposure effect in the study phase in the LPC time window (p. 8)	marginally significant main effect of lifetime exposure in the LPC time window, $F(1, 42) = 3.94$, $p = .054$, $\hat{\eta}_G^2 = .007$	Significant main effect of lifetime exposure in the LPC time window, $F(1, 42) = 7.00$, $p = .011$, $\hat{\eta}_G^2 = .014$	484 ms to 492 ms, on electrode Cz, significant lifetime exposure effect, $T_{WJt}/c (1.0,43.0) = 8.30$, $p = .0054$. (figure S1d) 656 ms to 664 ms, on electrode

			POz, significant lifetime exposure effect, T_{WJt}/c (1.0,43.0) = 8.01, p = .0063. (figure S1e) Note that in both principle components, stimuli with low degree of lifetime exposure evoked more positive amplitude, which is consistent with the ERP results.
9. Topographical comparison between the study and the test phase lifetime exposure effect in the LPC window (p. 8)	anteriority × laterality × phase: F (1, 42) = 7.86, p = .008, $\hat{\eta}_G^2$ = .007	Nonsignificant anteriority × laterality × phase: F (1, 42) = 2.73, p = .11, $\hat{\eta}_G^2$ = .002 However, there is a significant anteriority x phase interaction: F (1, 42) = 10.68, p = .002, $\hat{\eta}_G^2$ = .028	

10. ANOVA on the (F)N400 amplitude in the test phase (p. 10)	Marginally significant anteriority × response interaction: F (1,46) = 4.04, p = .050, $\hat{\eta}_G^2$ < .001 Significant 4-way interaction of anteriority × laterality × task × response: F (1, 46) = 7.08, p = .011, $\hat{\eta}_G^2$ < .001	Nonsignificant anteriority × response interaction: F (1,46) = 2.88, p = .097, $\hat{\eta}_G^2$ < .001 Significant 4-way interaction of anteriority × laterality × task × response: F (1, 46) = 10.11, p = .003, $\hat{\eta}_G^2$ < .001	453 ms to 460 ms, on electrode Fp1, significant task × response: T_{WJt}/c (1.0,42.0) = 10.74, p = .002. Post hoc test showed that high lifetime responses elicited more positive voltage: T_{WJt}/c (1.0,42.0) = 7.98, p = .008. (figure S1f)
11. (F)N400 topographical comparison between the two tasks in the test phase (p. 10)	anteriority × laterality × task, F (1, 46) = 5.73, p = .021, $\hat{\eta}_G^2$ = .003	Nonsignificant anteriority × laterality × task, F (1, 46) = 1.88, p = .18, $\hat{\eta}_G^2$ = .002 However, there is a marginally significant interaction of laterality x task: F (1, 46) = 3.80, p = .057, $\hat{\eta}_G^2$ = .005	

12. Study phase frequency effect in the (F)N400 time window (p. 10)	anteriority × presentation frequency interaction, F (1, 47) = 4.45, p = .040, $\hat{\eta}_G^2$ = .001	Nonsignificant anteriority × presentation frequency interaction, F (1, 47) = 2.87, p = .097, $\hat{\eta}_G^2$ = .001	No factor resembling an (F)N400 was identified.
13. Topographical comparison between the study and the test phase frequency effect in the (F)N400 window (p. 10)	anteriority × laterality × phase, F (1, 42) = 8.23, p = .006, $\hat{\eta}_G^2$ = .005	Nonsignificant, all ps > .13	
14. Comparing (F)N400 lifetime exposure effect between the two tasks in the test phase (p. 11)	no significant interactions involving lifetime exposure × task, all ps > .08	Significant lifetime exposure x task interaction, F (1, 46) = 5.96, p = .019, $\hat{\eta}_G^2$ = .009 Post-hoc t-tests showed that the effect of lifetime exposure was numerically more consistent with the polarity of the (F)N400 in the lifetime exposure task, t (46) = 1.60, p = .058, d = 0.23	No factor resembling an (F)N400 was identified.

15. Lifetime exposure effect in the study phase in the (F)N400 time window (p. 11)	anteriority × laterality × normative lifetime exposure, F (1, 42) = 6.61, p = .014, $\hat{\eta}_G^2$ < .001	anteriority × laterality × normative lifetime exposure, F (1, 42) = 5.46, p = .024, $\hat{\eta}_G^2$ < .001	No factor resembling an (F)N400 was identified.
16. Topographical comparison between the study and the test phase lifetime exposure effect in the (F)N400 window (p. 11)	No significant interaction involving the factor "experimental phase", all ps > .3	No significant interaction involving the factor "experimental phase", all ps > .5	

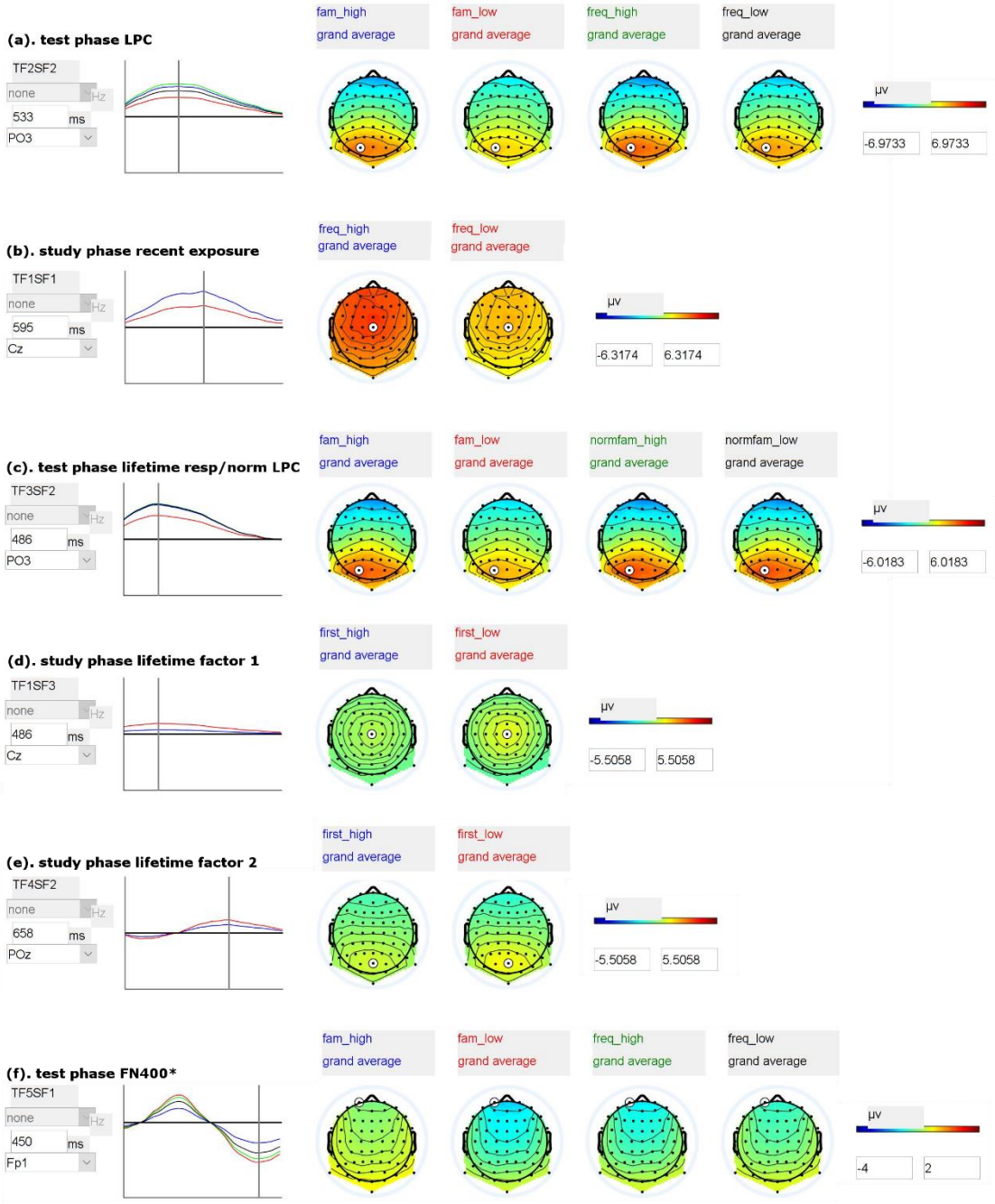

Figure A1: (a)-(e) components with a positive peak in LPC time window, (f) a component with a negative peak in FN400/N400 time window. Principle components largely replicated the effects acquired in analyses using mean ERP amplitude. The

figure shows peak latencies and electrodes detected through the autoPCA process, along with the waveform of the principal components and corresponding topographies in each condition. Please refer to Table A1 for more contrast details for each subpanel.

Appendix B (Chapter 3 and 4): Details of fMRIPrep preprocessing and relevant references

Anatomical data preprocessing

The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al. 2010), distributed with ANTs 2.2.0 (Avants et al. 2008, RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 5.0.9, RRID:SCR_002823, Zhang, Brady, and Smith 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 6.0.1, RRID:SCR_001847, Dale, Fischl, and Sereno 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438, Klein et al. 2017). Volume-based spatial normalization to two standard spaces (MNI152NLin2009cAsym, MNI152NLin6Asym) was performed through nonlinear registration with antsRegistration (ANTs 2.2.0), using brain-extracted versions of both T1w reference and the T1w template. The following templates were selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c [Fonov et al. (2009), RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym], FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model [Evans et al. (2012), RRID:SCR_002823; TemplateFlow ID: MNI152NLin6Asym].

Functional data preprocessing

For each of the 10 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. A B0-nonuniformity map (or fieldmap) was estimated based on a phase-difference map calculated with a dual-echo GRE (gradient-recall echo) sequence, processed with a custom workflow of

SDCFlows inspired by the epidewarp.fsl script and further improvements in HCP Pipelines (Glasser et al. 2013). The fieldmap was then co-registered to the target EPI (echo-planar imaging) reference run and converted to a displacements field map (amenable to registration tools such as ANTs) with FSL's fugue and other SDCflows tools. Based on the estimated susceptibility distortion, a corrected EPI (echo-planar imaging) reference was calculated for a more accurate co-registration with the anatomical reference. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration (Greve and Fischl 2009). Co-registration was configured with six degrees of freedom. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9, Jenkinson et al. 2002). BOLD runs were slice-time corrected using 3dTshift from AFNI 20160207 (Cox and Hyde 1997, RRID:SCR_005927). The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. A T2* map was estimated from the preprocessed BOLD by fitting to a monoexponential signal decay model with log-linear regression. For each voxel, the maximal number of echoes with reliable signal in that voxel were used to fit the model. The calculated T2* map was then used to optimally combine preprocessed BOLD across echoes following the method described in (Posse et al. 1999). The optimally combined time series was carried forward as the preprocessed BOLD. The BOLD time-series were resampled into several standard spaces, correspondingly generating the following spatially-normalized, preprocessed BOLD runs: MNI152NLin2009cAsym, MNI152NLin6Asym. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA, Pruim et al. 2015) was performed on the preprocessed BOLD on MNI space time-series after removal of non-steady state volumes and spatial smoothing with an isotropic, Gaussian kernel of 6mm FWHM (full-width half-maximum). Corresponding "non-aggresively" denoised runs

were produced after such smoothing. Additionally, the “aggressive” noise-regressors were collected and placed in the corresponding confounds file. The BOLD time-series, were resampled to surfaces on the following spaces: fsaverage5. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al. 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al., 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 5% variable voxels within a mask covering the subcortical regions. This subcortical mask is obtained by heavily eroding the brain mask, which ensures it does not include cortical GM regions. For aCompCor, components are calculated within the intersection of the aforementioned mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run (using the inverse BOLD-to-T1w transformation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components’ time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al. 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using

antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos 1964). Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer).

Many internal operations of fMRIPrep use Nilearn 0.6.0 (Abraham et al. 2014, RRID:SCR_001362), mostly within the functional processing workflow. For more details of the pipeline, see the section corresponding to workflows in fMRIPrep's documentation.

The above boilerplate text was automatically generated by fMRIPrep with the express intention that users should copy and paste this text into their manuscripts *unchanged*. It is released under the CC0 license.

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Appendix C (Chapter 4): posterior analyses of the baseline model

We also compared the posterior estimates of the baseline model parameters across different presentation frequencies to explore potential patterns in the frequency judgement across different objective presentation frequencies (Figure C2). Note that due to the within-subject coding of the frequency factor, a presentation frequency of 1 was modelled as the intercept, with all other conditions (i.e. presentation frequencies) modelled relative to it. This means that the interpretation of the statistics would differ between the intercept and other conditions. Specifically, for the intercept condition, a significant difference from 0 means that the particular parameter in that condition was significantly different from 0. For other conditions, a significant difference from 0 means that the particular parameter in those conditions were significantly different from the intercept condition.

For the intercept condition (i.e. presentation frequency of 1), all three parameters differed significantly from 0 (all Ps < .0001), with decision threshold (**a**) and non-decision time (**t**) being positive while drift-rate (**v**) being negative. The negative **v** resulted from the accuracy being less than 50% in this condition. For the condition with presentation frequency of 3, **a** was marginally smaller compared to the intercept condition, P = .050, and **v** was significantly smaller compared to the intercept condition, P < .0001. For the condition with presentation frequency of 5, only **v** was significantly different from (i.e. smaller than) the intercept condition, P = .001. For the condition with presentation frequency of 7, **a** was significantly smaller than that the intercept condition, P = .029, and **v** was significantly smaller compared to the intercept condition, P = .022. For the condition with presentation frequency of 9, only **v** was significantly different from (i.e. smaller than) the intercept condition, P < .0001. **t** did not differ from the intercept condition in any other conditions, all Ps > .17.

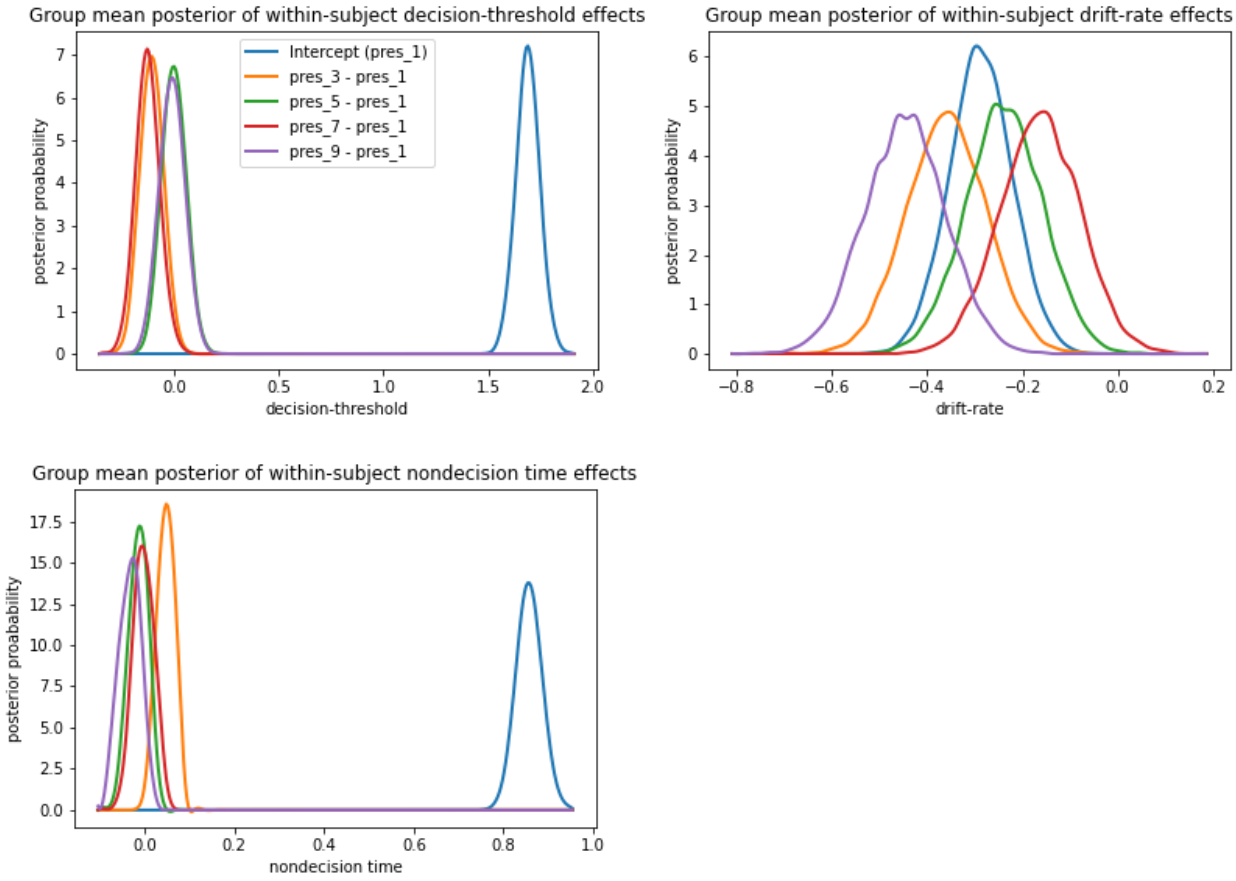

Figure C2. Posterior distribution of baseline model parameters for each level of objective presentation frequency. Conditions were coded relative to presentation frequency of 1, which served as the intercept.

Curriculum Vitae

Haopei Yang

Education

PhD candidate *(Neurosciene)* **2017-present**

Western University, London, Ontario

Thesis title: Roles of the perirhinal cortex and the posterior parietal cortex in memory decisions

Supervisors: Dr. Stefan Köhler

Master of Science *(Neuroscience)* **2015-2017**

Western University, London, Ontario

Thesis title: Mechanisms involved in the assessment of long-term cumulative familiarity of object concepts: An ERP study

Supervisor: Dr. Stefan Köhler

Bachelor of Science (*Honors Specialization in Psychology*) **2012-2014**

University of Prince Edward Island, Charlottetown, Prince Edward Island

Thesis title: Neural correlates of perceived consonant and dissonant dyad chords in human brain

Supervisor: Dr. Thomy Nilsson

Bachelor of Engineering (*Major in Digital Media Arts*) **2007-2011**

North China University of Technology, Beijing, China

Publications

Yang, H. & Köhler, S. (2019). Global matching and fluency attribution in familiarity assessment. *Behavioral and Brain Sciences, 42.* https://doi.org/10.1017/S0140525X19001912

Yang, H., Laforge, G., Stojanoski, B., Nichols, E. S., McRae, K., & Köhler, S. (2019). Late positive complex in event-related potentials tracks memory signals when they are decision relevant. *Scientific Reports, 9(1), 9469.* https://doi.org/10.1038/s41598-019-45880-y

Gurguryan, L., Yang, H., Köhler, S., & Sheldon, S. (submitted). Lifetime familiarity influences cued autobiographical memory retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*

Anderson, N., Baena, A., Yang, H., & Köhler, S. (2021). Deficits in Recent but not Lifetime Familiarity in Amnestic Mild Cognitive Impairment. *Neuropsychologia*

Brooks, G., Yang, H., Köhler, S. (2021). Feeling-of-knowing experiences breed curiosity. *Memory*

Ongoing projects

Yang, H. & Köhler, S. (in preparation). Perirhinal cortex tracks recent and lifetime experience with object concepts regardless of decision relevance

Wu, A.*, Yang, H.*, Chatterton, M., & Köhler, S. (in preparation). Visceral feedback in memory judgement

Yang, H., Köhler, S., & Mur, M. (in preparation). Recognition memory signal as an emergent property of hierarchical networks

Yang, H., Gurguryan, L., Sheldon, S., & Köhler, S. (in preparation). lifetime familiarity: semantic, episodic, and more.

Technical abilities

Experience in programming with

- MATLAB
- R
- Python
- Bash (Linux cluster)

Experienced in collecting, preprocessing, and analyzing data from

- EEG
- fMRI
- Eye-tracking and pupillometry
- ECG

Additional Research Experience

Research assistant **2014**

Advancing Interdisciplinary Research in Singing, University of Prince Edward Island

- Providing technical support of NeuroScan SynAmp2 and STIM2 system

Awards and Recognition

Western Graduate Research Scholarship Awards **2021 Fall**

Western University, London, Ontario

$4,400

Western Graduate Research Scholarship Awards **2020-2021**

Western University, London, Ontario

$13,000

Western Graduate Research Scholarship Awards **2019-2020**

Western University, London, Ontario

$13,000

Western Graduate Research Scholarship Awards **2018-2019**

Western University, London, Ontario

$13,000

Neuroscience Travel Awards **2018**

Western University, London, Ontario

$500

Western Graduate Research Scholarship Awards **2017-2018**

Western University, London, Ontario

$13,000

Conference presentations

Yang, H., Mur, M., & Köhler, S. (2021, February) *Recognition memory signal as an emergent property of hierarchical networks.* Presented at the 2021 Neuroscience Research Day at Western University, London, Ontario, Canada

Yang, H., McRae, K., & Köhler, S. (2018, March) *Late positive event-related potential tracks outcomes of cumulative memory judgements.* Data blitz presented at the spring 2018 meeting of the Toronto Area Memory Group, Toronto, Ontario, Canada

Poster presentations

Yang, H. & Köhler, S. (2021, November) *Perirhinal cortex automatically tracks recent and lifetime experience with objects regardless of decision relevance.* To be presented at the 2021 meeting of the Society for Neuroscience

Yang, H., Laforge, G., Stojanoski, B., Nichols, E., McRae, Ken., & Köhler, S. (2019, February) *Late positive complex in event-related potentials tracks memory signals when they are decision relevant.* Poster presented at the 48th Annual Conference of the Lake Ontario Visionary Establishment, Niagara Falls, Canada

Yang, H., McRae, K., & Köhler, S. (2018, March) *Late positive event-related potential tracks perceived degree of recent as well as cumulative lifetime experience in memory judgments.* Poster presented at the 25th Annual Meeting of the Cognitive Neuroscience Society, Boston, MA, United States of America

Yang, H., McRae, K., & Köhler, S. (2017, February) *LPC tracks recent as well as cumulative lifetime experiences with object concepts.* Poster presented at the 46th Annual Conference of the Lake Ontario Visionary Establishment, Niagara Falls, Canada.

Teaching Experience

Introduction to Statistics Using R (Graduate level) **2020**

- Graded coding assignments and final projects

Human Memory Teaching assistant **2018 & 2020**

- Graded student assignments, presentations, and exams
- Designed course structure
- Held office hours

Bilingualism Teaching assistant **2019**

- Graded student assignments, presentations, and exams
- Held office hours

Research in Cognitive Psychology **2018**

- Graded assignments, presentations, and exams
- Taught various research techniques during weekly lab sessions

Introduction to Psychology Teaching assistant **2015-2017**

- Graded student assignments
- Provided chapter reviews
- Held office hours