Contributions Of the Human Medial Prefrontal Cortex To Associative Recognition

Memory: Evidence From Functional Neuroimaging

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology and Neuroscience in the Graduate School
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ABSTRACT

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Abstract

Neuroimaging studies of episodic memory, or memory of events from our personal past, have predominantly focused their attention on medial temporal lobe (MTL). There is growing acknowledgement however, from the cognitive neuroscience of memory literature, that regions outside the MTL can support episodic memory processes. The medial prefrontal cortex is one such region garnering increasing interest from researchers. Using behavioral and functional magnetic resonance imaging measures, over two studies, this thesis provides evidence of a mnemonic role of the medial PFC. In the first study, participants were scanned while judging the extent to which they agreed or disagreed with the sociopolitical views of unfamiliar individuals. Behavioral tests of associative recognition revealed that participants remembered with high confidence viewpoints previously linked with judgments of strong agreement/disagreement. Neurally, the medial PFC mediated the interaction between high-confidence associative recognition memory and beliefs associated with strong agree/disagree judgments. In an effort to generalize this finding to well-established associative information, in the second study, we investigated associative recognition memory for real-world concepts. Object-scene pairs congruent or incongruent with a preexisting schema were presented to participants in a cued-recall paradigm. Behavioral tests of conceptual and perceptual recognition revealed memory enhancements arising from strong resonance between presented pairs and preexisting schemas. Neurally, the
medial PFC tracked increases in visual recall of schema-congruent pairs whereas the MTL tracked increases in visual recall of schema-incongruent pairs. Additionally, ventral areas of the medial PFC tracked conceptual components of visual recall specifically for schema-congruent pairs. These findings are consistent with a recent theoretical proposal of medial PFC contributions to memory for schema-related content.

Collectively, these studies provide evidence of a role for the medial PFC in associative recognition memory persisting for associative information deployed in our daily social interactions and for those associations formed over multiple learning episodes. Additionally, this set of findings advance our understanding of the cognitive contributions of the medial PFC beyond its canonical role in processes underlying social cognition.
Dedication

A constant source of inspiration and strength in my life has been my parents for whom I dedicate this collection of work presented herein. They have provided me opportunities and life experiences they could only dream of while growing up in southern India. I thank them for instilling an appreciation for the importance of hard work and compassion. For all of this, I dedicate this to you Amma and Dad and express my deep appreciation for all you have done and continue to do for me.
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I want to express my deep gratitude to my advisor, Roberto Cabeza, for giving me an opportunity to pursue a doctoral degree in the brain sciences. Being in his laboratory the past several years has provided a suite of skills - the ability to approach a problem, understand its nuances, and identify potential solutions - which will help me in careers both in-and-outside the academic community. Additionally, I have had an opportunity to interact with some of the brightest minds from across the country and world. For all of this, I am grateful.

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Lastly, I want to thank my colleagues in the Cabeza laboratory with specific thanks to Erik Wing. Apart from our graduate school careers largely overlapping, he has been extremely helpful in sharing his wisdom and guidance with respect to research practices, various milestones of graduate school, and life in general.
General Introduction

Let us begin with a simple yet illustrative thought experiment. Suppose I administered a straw poll to cognitive neuroscientists investigating either episodic memory (group 1) or social cognition (group 2). For group 1 members, I ask them to list (in rank-order) the brain regions they thought crucial for episodic memory and for group 2 members; I ask them to do the same but for social cognition. Upon receiving the results, I then proceed to conduct a correlation analysis between these two lists. Obtaining a negative correlation between these two rank-ordered lists would be unsurprising to me. Explaining this negative correlation could be the wealth of studies on episodic memory reporting activity in the medial temporal lobe and the abundant studies of social cognition reporting activity in the medial prefrontal cortices among other regions (e.g., insula, temporoparietal junction). Inspection of reverse inference maps for the terms “social cognition” and “episodic memory” generated from an online meta-analysis tool (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) support this observation. Stark divisions in the brain based on functional contributions however are being disassembled with studies showing that medial temporal lobe sub-regions can support non-mnenomic functions including visual perception (Graham, Barense, & Lee, 2010; Lee, Barense, & Graham, 2005) and with studies showing that the temporoparietal junction is sensitive to goal-relevant states in attentional tasks (Mitchell, 2008). Another
area of the brain where functional divisions are being broken down is in the medial prefrontal cortex.

Although a traditional role of the medial prefrontal cortex has been in the service of processes underlying social cognition (Amodio & Frith, 2006), there is growing acknowledgement of its role in other domains, especially episodic memory (Euston, Gruber, & McNaughton, 2012; van Kesteren, Ruiter, Fernández, & Henson, 2012). Revising the title proposed by Amodio and Frith (Amodio & Frith, 2006) of the medial prefrontal cortex as “meeting of minds,” perhaps a new moniker could be the medial prefrontal cortex: ‘meeting of memory and social cognition’. A review of neuroimaging studies reporting medial prefrontal cortex activity in addition to two novel investigations described below further underscores a role for this region in potentially mediating the interactions between social cognition and memory.

Given the breadth, depth, and frequency of our social interactions can modulate our neural architecture (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; Sallet et al., 2011), it is important to understand the neural mechanisms supporting evaluation and later retention of these interactions. The studies described in this document add to the accumulating evidence highlighting a mnemonic role of the medial PFC.
1. The medial prefrontal cortex: Anatomy, connectivity, and function

Before proceeding to a review of the expansive cognitive contributions of the medial prefrontal cortex (hereafter referred to as medial PFC) as reported in the literature, in the sections that follow, I will briefly discuss the anatomy and connectivity of the medial PFC across three species: non-human primates, rodents, and humans. In doing so, I hope to lay the groundwork for the investigation of mnemonic role of the medial PFC and its potential usefulness in helping advance our understanding of the neural correlates of successful episodic memory. I note here that discussion of medial PFC connectivity with other neocortical regions is limited to the medial temporal lobe (hereafter referred to as MTL) given its relevance to the focus of the present research topic.

1.1 Non-human primates

1.1.1 Anatomy

The medial PFC is a component of a larger frontal cortical region often collectively referred to in the non-human primate literature as the orbital and medial prefrontal cortex (OMPFC). Histochemical studies have revealed that the medial PFC is composed of Brodmann areas (BAs) 10m, 24, 25, and 32. Moreover, BA 24 is divided into three sections: 24a, 24b, and 24c (Carmichael & Price, 1994; Vogt, Pandya, & Rosene, 1987). More recent investigations have also included BAs 9 and 14 as additional components of the medial PFC (Barbas, Ghashghaei, Dombrowski, & Rempel-Clower,
1999). I note that more anterior portions of the 10m region are thought to comprise the frontopolar cortex.

### 1.1.2 Connectivity

Consistent across numerous investigations examining OMPFC connectivity in the non-human primate brain is robust connectivity between OMPFC and medial temporal lobe regions. Retrograde tracing has identified an increase in the number of neurons labeled from the hippocampus in medial relative to orbital prefrontal cortical areas (Barbas & Blatt, 1995). Follow-up studies revealed that this pattern was specific to BAs 10 and 14 and that the medial PFC was the primary receiver of input from the MTL memory structures including the rhinal cortices (Barbas et al., 1999) and the hippocampus (Cavada, Compañy, Tejedor, Cruz-Rizzolo, & Reinoso-Suárez, 2000). Further corroborating medial PFC-MTL connectivity, using resting-state functional connectivity analysis in non-human primates, Vincent and colleagues (2007) report that in addition to a dorsal areas of the medial PFC being correlated with the posterior cingulated cortex, the temporoparietal and posterior parahippocampal cortices were also correlated with the seed region (Vincent et al., 2007). A similar pattern of connectivity findings has been reported in humans (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008).
1.2 Rodents

1.2.1 Anatomy

In rodents, the prefrontal cortical region is divided into three divisions: a medial frontal region, a lateral frontal region, and a ventral frontal region. Within the medial frontal, there is a dorsal region (composed of precentral (PrC) and anterior cingulate (ACg) sub-regions) and a ventral region (composed of prelimbic (PrL), infralimbic (IL), and medial orbital cortices). The lateral frontal region is composed of a dorsal and ventral agranular insular region and a lateral orbital region. Lastly, the ventral frontal region is composed of ventral orbital and a ventral lateral orbital cortices (Dalley, Cardinal, & Robbins, 2004).

1.2.2 Connectivity

The connectivity profile for the rodent is quite similar to the one discussed for non-human primates. Ventral areas of the medial PFC (comprised of the IL and PrL) receives input from the MTL regions including the hippocampus and rhinal cortices. Additionally, projections from the amygdala and thalamus reach the IL and PrL sub-regions of the medial PFC (Heidbreder & Groenewegen, 2003; Hoover & Vertes, 2007).

1.3. Humans

1.3.1 Anatomy

The human medial PFC has a somewhat similar anatomical division as the divisions proposed for non-human primates. Specifically, the BAs corresponding to the
medial PFC is proposed to include areas 9, 10, 11, 14, 24, 25, and 32 (Amodio & Frith, 2006; Öngür, Ferry, & Price, 2003). Ongur and colleagues (2003) go on to suggest the following medial PFC divisions: 11m/11l for BA 11; 14c/14r for BA 14; 10m/10r/10p for BA 10; 32pl/32ac for BA 32; and finally 24a/24b for BA 24 (Öngür et al., 2003).

1.3.2 Connectivity

A preponderance of evidence exists that the medial PFC is a core component and functionally connected with the rest of the default mode network (Buckner, Andrews-Hanna, & Schacter, 2008). The term ‘default mode network’ denotes a set of brain regions including the medial PFC, posterior cingulate, precuneus, inferior parietal lobule, lateral temporal cortex and hippocampal formation. Activity in this set of regions reliably increases during passive baseline phases of functional neuroimaging paradigms and conversely decreases below baseline during task phases (for a more thorough discussion see Buckner et al., 2008). Functional connectivity analysis within the default mode network has revealed this is not a monolithic system but instead is comprised of two sub-networks: an MTL subsystem (including the hippocampus and ventral medial PFC) and a dorsal medial PFC including the lateral temporal cortex and temporoparietal junction (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). When examining structural connectivity via white matter fiber pathways between medial PFC sub-divisions and the MTL, one of the canonical white matter fiber systems, the uncinate fasciculus was identified as connecting medial and lateral prefrontal areas with anterior
temporal lobe regions (Catani & Thiebaut de Schotten, 2008; Schmahmann et al., 2007; Von Der Heide, Skipper, Klobusicky, & Olson, 2013).

### 1.3.3. Insights from a review of medial PFC anatomy and connectivity

Across species, there is strong correspondence in the proposed areas comprising the medial PFC. Relevant to subsequent sections, there is consistent anatomical, and functional connectivity evidence pointing to a robust bi-directional relationship between the medial PFC and MTL areas. I note here that across species, innate structural and functional connectivity suggest a dorsal/ventral division of the medial PFC. Indeed, meta-analyses and/or reviews in the domains of social cognition (Van Overwalle, 2009), self-referential processing (Northoff et al., 2006), autobiographical memory retrieval (Cabeza & St Jacques, 2007), and schema encoding and retrieval (Van Kesteren, Ruiter, Fernández, & Henson, 2012) suggest a functional dorsal/ventral divide. Later sections will discuss in detail the type of experimental paradigms and task conditions eliciting differential ventral and dorsal medial PFC activity. Additionally, I note here that in subsequent sections I will treat orbital areas of the medial PFC as belonging to the ventral medial PFC.

### 1.4 Cognitive contributions of the medial PFC: Evidence from the human neuroimaging literature

A majority of the existing human functional magnetic resonance imaging (hereafter referred to as fMRI) studies reporting medial PFC activity in experimental paradigms have supported the notion that the medial PFC plays a pivotal role in
affording us the ability to optimally understand, richly interact, and properly evaluate fellow members of our species. These essential human-specific processes are thought to serve as core components of the cognitive domain referred to as social cognition (Frith & Frith, 2007). In fact, the medial PFC’s role in social cognition is thought to arise before we reach adulthood (Grossmann, 2013). Buttressing this view of a canonical role of the medial PFC in social cognition, much discussion is provided for this interpretation in well-cited reviews (Amodio & Frith, 2006; Forbes & Grafman, 2010; Frith & Frith, 2007; Wood & Grafman, 2003) of medial PFC function.

Assuming an exclusively role of the medial PFC for social cognition, however, yields an incomplete treatment of its precise role in cognition given its engagement in cognitive tasks that impose minimal demands on social cognition. These include experimental paradigms related to self-referential processing, autobiographical memory retrieval, the processing and retention of schemas, and in episodic memory. In the following sections, I will briefly review relevant findings, theoretical proposals, and interpretations within each of these cognitive domains in the hopes of providing a more holistic picture as to the type of cognitive operations that reliably elicit medial PFC activity. Given the predominant view of the medial PFC as pivotal for social cognition, I begin there and proceed to its comparatively lesser known contributions to cognition.
1.4.1 Social cognition

While the domain of social cognition subsumes a variety of sub-domains and a spectrum of diverse experimental paradigms, I focus on a few sub-domains relevant to the present discussion and provide a brief overview of the reported medial PFC contributions for each sub-domain. The sub-domains discussed are as follows: social perception, mentalizing, affective perception and evaluation, judgment and decision-making and personal belief processing. In the following sections, I review relevant findings and paradigms in the order listed above. A substantive review, meta-analysis, or theoretical account of the findings in each sub-domain is cited in order to help readers identify resources to learn more about each domain.

1.4.1.1 Social perception

Much evidence exists highlighting a role of the medial PFC in supporting the perception and evaluation of static social stimuli (e.g. faces, scenes with persons) or stimuli replete with social interactions (e.g., movie clips). For example, Iacoboni and colleagues (2004) in an early study found increased activity in dorsal areas of the medial PFC for the passive viewing of movie clips depicting social interactions of multiple human agents as compared with a resting baseline task or even another experimental condition which contained fewer human agent interactions (Iacoboni et al., 2004). While one can assert that this is unsurprising given movie clips represent a stimulus class that is dynamic, engaging, and well endowed with social content, this finding extends to
relatively impoverished stimulus classes including faces. Studies comparing judgments that emphasize the social dimensions (e.g. attractiveness, preference, or approachability) of facial stimuli as opposed to demographic (e.g. age or gender) dimensions have found increased medial PFC engagement during social evaluative conditions (Chen, Welsh, Liberzon, & Taylor, 2010; Hall et al., 2010; Winston, O’Doherty, Kilner, Perrett, & Dolan, 2007). In fact, a meta-analysis conducted of neuroimaging studies wherein participants evaluated face stimuli along the dimensions of either trustworthiness or attractiveness identified a positive relationship between medial PFC activity and trustworthiness judgments. This finding led the authors to posit a role of the medial PFC in positive emotional evaluations of social stimuli (Mende-Siedlecki, Said, & Todorov, 2013).

Complementing the above findings, in a series of tightly controlled investigations, Mitchell and colleagues have advanced our understanding of the conditions under which medial PFC is preferentially engaged. In showing increased medial PFC recruitment when forming impressions of persons as opposed to non-human species (Mitchell, Macrae, & Banaji, 2005) or when judging the appropriateness of trait descriptors for persons compared with objects (Mitchell, Heatherton, & Macrae, 2002), these studies have elucidated a role in medial PFC in supporting appraisal of the social dimensions of everyday stimuli. In sum, the medial PFC exhibits particular sensitivity to information related to our everyday social interactions.
1.4.1.2 Mentalizing

Understanding the beliefs and desires of other members of our species and in-turn their relationship to our own beliefs and desires is vital for one’s survival and optimal function in a complex living environment. This ability to acknowledge another’s beliefs and desires is referred to in the literature as mentalizing or exhibiting theory of mind (ToM) abilities (Gallagher & Frith, 2003). Human neuroimaging studies examining the neural correlates of this ToM ability have consistently reported a network of regions including the medial PFC as supporting the ability to infer the mental states of other members (Fletcher et al., 1995; Goel, Grafman, Sadato, & Hallet, 1995; Isoda & Noritake, 2013). A majority of these studies have isolated neural activity specific to mentalizing by presenting short verbal stories (Fletcher et al., 1995), cartoons (Gallagher et al., 2000), or video clips (Kuilen, Bogler, Swerts, & Haynes, 2014) and requiring participants to assess the actions and motivations of the agents in the presented scenario. Recent findings have extended the role of the medial PFC to supporting the ability to infer the state of entire groups of people (Contreras, Schirmer, Banaji, & Mitchell, 2013). While robust evidence is suggestive of a critical role the medial PFC plays in mentalizing abilities, some have theorized that another region of the default mode network, the temporoparietal junction, is the sole region responsible for endowing humans with the ability to mentalize (Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Saxe & Wexler, 2005). Whether this is indeed the case, however, is beyond the scope of the present discussion but is an area of intense
debate. I close by noting that a prominent review of mentalizing (Gallagher & Frith, 2003) suggests the possibility that in order to accurately predict the actions and motivations of others, humans may possibly rely on well-established templates for human behavior (i.e. scripts) based on previous experiences. The acknowledged role of memory in buttressing processes underlying social cognition will be important as it relates to subsequent discussion of the medial PFC in supporting memory for schema-related information. When examining Figure 2A in a meta-analysis of social cognition (Van Overwalle, 2009) we find the areas of activity within the medial PFC engaged during tasks of theory of mind beliefs. Visual inspection reveals that the majority of the activations reside in dorsal areas of the medial PFC. In short, the medial PFC through possible a schema-like mechanism is critical in the evaluation of other intentions, beliefs, and motives and thus plays a vital role in our ability to assess the internal states of others.

1.4.1.3 Affective perception and evaluation

Across non-human primate, rodent, and human species, the medial PFC exhibits strong anatomical and functional connectivity with limbic regions associated with emotional processing (see section I). In light of this, hypothesizing a role of the medial PFC in supporting perception and evaluation of emotional stimuli is reasonable. Human neuroimaging evidence supports this hypothesis. In an early study examining neural activity for evaluation of pleasant, neutral, and unpleasant emotional pictures, activity
in the medial PFC was recruited specifically for evaluation of pleasant pictures (Lane et al., 1997). A specific positive-valence role of the medial PFC was also found in another study finding increasing activity in ventral areas of the medial PFC for positive evaluations of faces (Hackjin Kim, Somerville, Johnstone, Alexander, & Whalen, 2003). Meta-analyses (Phan, Wager, Taylor, & Liberzon, 2002; Van Overwalle, 2009) however have revealed that the medial PFC is one of the most commonly reported regions in emotional perception and contributes to all emotion types regardless of valence. This is also supported by imaging findings showing the medial PFC is engaged for both emotional faces and pictures regardless of emotion type (Britton, Taylor, Sudheimer, & Liberzon, 2006). Supporting this, inspection of emotion-related activity in the medial PFC as revealed by a meta-analysis on social cognition (Van Overwalle, 2009). Figure 2C in that meta-analysis reveals that both positive and negative emotions elicit activity spanning the entire dorsal/ventral divide of the medial PFC.

Paralleling findings of the medial PFC in affective perception and evaluation is mounting evidence that the medial PFC supports processing of stimuli depicting moral actions or violations (for a review: Greene & Haidt, 2002; Moll, Zahn, Oliveira-souza, Krueger, & Grafman, 2005). Given that participants normatively rate moral violations as more emotionally arousing then non-moral, social violations (e.g. “You see a woman drinking her entire cup of coffee using a stirring spoon”) (Clifford, Iyengar, Cabeza, & Sinnott-Armstrong, 2015) and that emotion-sensitive regions support evaluation of
specific forms of moral violations (Lewis, Kanai, Bates, & Rees, 2012), it is reasonable to conclude that medial PFC activity for moral violations reflects processing of the affective and social aspects of the violation. Potentially speaking to this is evidence of a domain-general contribution of the medial PFC for evaluating moral content. Studies report medial PFC engagement in moral evaluation when stimuli are presented in pictorial (Harenski & Hamann, 2006; Moll, de Oliveira-Souza, Eslinger, et al., 2002), verbal (Heekeren et al., 2005; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002), or auditory (Moll, Eslinger, & Oliveira-souza, 2001) stimulus modalities. Collectively, these results are suggestive of its robust engagement in appraisal of moral actions. More recently, fMRI studies (Parkinson et al., 2011; Robertson et al., 2007) interrogating the neural correlates of the moral foundations theory (Graham et al., 2013; Haidt, 2013) report that the dorsal area of the medial PFC as the sole region supporting evaluation of a diverse set of moral violations falling into the categories of harm, dishonesty, and disgust (Parkinson et al., 2011). Figure 2A from a meta-analysis of social cognition (Van Overwalle, 2009) presents the activation corresponding to evaluation of moral content in more dorsal areas of the medial PFC. In short, the medial PFC is an important region in the perception of evaluation of affective-laden stimuli. Though its valence-specific contributions are still unresolved, there is agreement that it is a region that contributes to emotional processes.
1.4.1.4 Judgment and decision making

The somatic marker hypothesis (Bechara, Damasio, Damasio, & Anderson, 1994; Bechara, Damasio, & Damasio, 2000; Bechara & Damasio, 2005; Damasio, 1996) has served as an influential theoretical proposal suggesting a role of the medial PFC in decision making. Briefly, with specific regard to ventral areas of the medial PFC, the somatic marker hypothesis proposes that the medial PFC serves as a mediator between the outcomes of past decisions and the emotional state previously associated with those decisions. Consequently, for future decisions, the medial PFC affords the individual the ability to act upon the past reward history and associated somatic state to dictate the best option to take (Bechara et al., 2000; Damasio, 1996). Much of the evidence in support of this seminal proposal has come from patients with lesions focal to ventral areas of the medial PFC and more recently in fMRI studies. The task typically administered in these neuropsychological studies involves having a participant make selections from four card decks. Critically, two of the decks are advantageous in the long-term, with a net positive outcome, and two of the decks are disadvantageous in the long-term, with a net negative outcome. A robust finding is that patients with medial PFC continuously choose from disadvantageous decks and this is thought to occur given an inability to associate rewards with the emotional states experienced after a loss (Bechara et al., 1994; Bechara, Damasio, Damasio, & Lee, 1999).
In more recent fMRI studies of decision-making, the medial PFC has been linked to tracking the perceived reward value of stimuli (for a review: O’Doherty, 2004). Specifically, medial PFC activity has been found to correlate with payoff magnitude in a study wherein participants explored which slot out of four yielded the maximal dollar amounts (Daw, O’Doherty, Dayan, Dolan, & Seymour, 2006) and increases in medial PFC activity have been reported during the anticipation of high monetary benefits (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005). Remarkably, in one study measuring participant-specific discounting functions, medial PFC activity was found to increase with reward value and decrease as a function of increasing delay period (Kable & Glimcher, 2007). In the context of the medial PFC contribution to social cognition, a study by Hare and colleagues (2010) found via a parametric analysis that medial PFC activity was modulated by the extent to which participants were willing to donate to a charity (Hare, Camerer, Knoepfle, O’Doherty, & Rangel, 2010). Figure 2C from a meta-analysis of social cognition (Van Overwalle, 2009) contains the distribution of foci found for studies evaluating reward learning and reporting activity within the medial PFC. As expected, the majority of the foci related to reward learning are found in the ventral and orbital areas of the medial PFC. In short, ventral areas of the medial PFC are predominantly involved in judgment and decision making processes and is thought to encode the associated value assigned to stimuli as they are encountered.
1.4.1.5 Personal belief processing

The attitudes and beliefs we subscribe to (e.g. ‘Climate change is a real, measurable phenomenon’) comprise a core component of what makes us unique individuals. According to a recent theoretical framework, Connors & Halligan (2015) proposed that the role of beliefs in everyday life can be categorized in four ways: As listed on pg. 3 of the review, (1) “beliefs provide a consistent and coherent representation of a subject’s world”, (2) “beliefs provide an explanatory framework for interpreting the world and processing incoming information”, (3) “beliefs serve important social functions” (Connors & Halligan, 2015, pg. 3). I note that the authors mention four functions of beliefs but have reported three of the functions here as I deemed them relevant to the present and subsequent discussions. Interestingly, much of the framework’s assumptions of the role of beliefs in our everyday lives overlap squarely with our discussion in previous sections of the social cognitive processes that engage the medial PFC. Specifically, the proposed functions align well with the medial PFC’s role in script knowledge, mentalizing, and judgment and decision making. As such, a pivotal role of the medial PFC in supporting belief formation and evaluation is certainly reasonable to assume.

Though fMRI evidence of the neural correlates of attitude and belief processing is scant, what evidence does exist largely supports a key role for the medial PFC. fMRI studies of beliefs have instructed participants to rate the veracity of belief statements
from various categories. Harris and colleagues found that in a belief (when participants believed the presented statement) > disbelief (when participants disbelieved the presented statement) contrast, activity was elicited from a ventral area of the medial PFC, while the reverse contrast (disbelief > belief) yielded activity from areas related to conflict and emotion (Harris, Sheth, & Cohen, 2008). In a follow-up study on the neural correlates of religious and non-religious beliefs among religious and non-religious groups, a ventral area of the medial PFC was found when comparing instances where participants thought a belief was true as opposed to false (i.e. true > false). Interestingly, there were no differences found in this region between religious and non-religious groups and between religious and non-religious statements (Harris et al., 2009). A role for the medial PFC in belief processing also extends to content more political in nature. Activity in ventral areas of the medial PFC has been reported to increase as a function of subjective ratings of how individualistic a political belief may be (Zamboni et al., 2009) and also increases as a function of subjective ratings of how important an sociopolitical issue is to that individual (Falk, Spunt, & Lieberman, 2012). Though not a perfect match to the discussion of belief processing in the brain, Figure 2D as found in a meta-analysis of social cognition (Van Overwalle, 2009) presents a distribution of foci, in the dorsal medial PFC, associated with self-reference and social scripts. In short, a role of the medial PFC in the encoding and processing of belief-information is possible given its
role in understanding the mental state of other beliefs (i.e. mentalizing), its role in script formation and as we will see in the next section, its role in self-referential processing.

1.4.2 Self-referential processing

1.4.2.1 Self-versus-other referential processing

On a daily basis, we undertake actions - from the clothes we purchase to the issues we advocate for - that inherently demand evaluating our internal desires and thoughts against information from the external environment. In fact, this ongoing comparison enables us to understand what makes each of us a unique member of society. In the literature, this internal evaluation of external stimuli and the processes that underlie this comparison has been referred to as self-referential processing (Rogers, Kuiper, & Kirker, 1977; Symons & Johnson, 1997) or the processing of information in relation to one’s self. Interestingly, given the extent to which we undertake such processing on a daily basis, some have speculated that each individual as a schema or concept of oneself that guides our subsequent decision making and actions (Markus, 1977; Rogers et al., 1977).

Abundant neuroimaging evidence supports a crucial role of the medial PFC in self-referential processing (Northoff & Bermpohl, 2004; Northoff et al., 2006). Specifically, evidence exists that self-referential as opposed to perceptual (e.g. indoor/outdoor judgments) (Gusnard, Akbudak, Shulman, & Raichle, 2001; Jenkins & Mitchell, 2011), semantic (e.g. meaning judgments) (e.g. Zysset, Huber, Ferstl, & von
Cramon, 2002), or even third-party stimulus evaluations (D’Argembeau, 2007) elicits activity in the medial PFC. In identifying the brain regions supporting self-referential processing, some fMRI investigations have presented personality trait-adjectives (e.g. ‘jealous’) and instructed participants to judge whether traits accurately described either themselves (i.e. ‘self’ condition) or another individual (i.e. ‘other’ condition). Consistent across these studies is the finding of greater medial PFC activity for the ‘self’ condition regardless if the ‘other’ condition is a familiar person (e.g. a US president) (Kelley et al., 2002), a close individual (Heatherton et al., 2006), or a fictional character (Pfeifer, Lieberman, & Dapretto, 2007). Furthermore, even when emotional valence of the trait-adjective is taken into consideration (Fossati et al., 2003; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006) the medial PFC supports both positive and negative trait adjectives evaluations.

The medial PFC however, does not uniformly contribute to self-referential processing. Accumulating evidence suggests that whereas ventral regions of the medial PFC support self-referential processing of stimuli perceived as similar to one’s self (e.g. shared socio-political beliefs), dorsal regions of the medial PFC support self-referential processing of stimuli perceived dissimilar to one’s self (Jenkins, Macrae, & Mitchell, 2008; Mitchell, Banaji, & Macrae, 2005; Mitchell, Macrae, & Banaji, 2006). This pattern of findings also is also found in the autobiographical memory literature, which I will discuss in subsequent sections. Figure 4 of a meta-analysis of self-referential processing
(Northoff et al., 2006), represents a potential division of the self-referential processing neural system with ventral medial PFC areas marked in red and dorsal medial PFC areas marked in green. Figure 2A from the same meta-analysis presents a distribution of foci from a meta-analysis of self vs. other-referential processing as it pertains to multiple cognitive (e.g. memory) and stimulus (e.g. verbal) categories. In short, the medial PFC contributes to information processing as it relates to the self and some have suggested a division of the medial PFC based on its evaluation of self and non-self attributes.

1.4.2.2 Self-referential enhancement effects on memory

Early findings from the cognitive psychology literature suggested that self-referential encoding of material was a far superior (as indexed by incidental recall) form of information encoding as compared to more traditionally instructed forms of encoding including semantic or perceptual encoding (Rogers et al., 1977; Symons & Johnson, 1997). Of interest to future discussion, Rogers and colleagues (1977) even posit that a potential reason for a self-specific superior mnemonic advantage could be “that the self is a well-structured and powerful schema” (Rogers et al., 1977, pg. 686). The neural correlates underlying this enhancement effect on memory termed the self-referential effect (SRE) (Symons & Johnson, 1997) has been addressed in a number of investigations.

In an fMRI investigation interrogating the brain regions supporting memory for personality-trait adjectives previously encoded in relation to the self, medial PFC activity was found to contribute to subsequently remembered relative to activity for
subsequently forgotten trait-adjectives (Macrae, Moran, Heatherton, Banfield, & Kelley, 2004). Buttressing this finding, preliminary lesion evidence, ultimate useful demonstration of structure-function relationships, have found that patients with lesions to the medial PFC show markedly lower SRE effects when compared to normal controls or patient groups with lesions to temporal and occipital regions (Philippi, Duff, Denburg, Tranel, & Rudrauf, 2012). This pattern of findings also extends to paradigms that do not present personality-trait adjectives. For example, in a paradigm wherein participants either formed impressions of face-statement pairs or determined the sequence in which they were presented, medial PFC activity was uniquely predictive of memory for material encoded in the impression formation task, whereas MTL regions were found to predict memory for material encoding in the non-social, sequence task (Mitchell, Macrae, & Banaji, 2004). Lastly, I note that accumulating evidence has extended the role of the medial PFC in supporting memory for self-referential information encoding. Whereas the majority of studies thus far have tested memory for individual items, recent studies have interrogated medial PFC contributions to memory for items and the contexts in which they were originally encoded. Though evidence is preliminary and requires further corroboration, it suggests that the medial PFC can support a different form of memory, contextual retrieval of previously encountered stimuli encoded in a self-referential manner (Kim & Johnson, 2012; Leshikar & Duarte, 2012). In short, a review of the literature reveals a medial PFC role in successful self-
referential memory encoding although more work is required to elucidate its role and function. Recent evidence has expanded its role in supporting different memory types but this is still preliminary in nature.

1.4.3 Autobiographical memory retrieval

1.4.3.1 Functional neural correlates of autobiographical memories

Our lives are replete with significant personal moments. From birthday milestones, to one’s first kiss, to the death of a spouse, each of these moments represents highly personally relevant memories. In the literature, events from one’s personal past are referred to as autobiographical memories. Given the inherent personal relevance of these memories, a role of the medial PFC in supporting such retrieval processes is a reasonable assumption given its previously discussed role in self-referential processing. Confirming this assumption are meta-analyses showing overlap in the medial PFC in self-referential and autobiographical memory studies (Spreng, Mar, & Kim, 2008). In further support of the role the medial PFC has in the retrieval of autobiographical memories is abundant evidence from both positron emission tomography (PET) and fMRI studies (for a review: Cabeza & St Jacques, 2007; Svoboda, McKinnon, & Levine, 2006). In order to isolate neural activity specific to autobiographical memory retrieval, early investigations compared activity elicited from auditory presentations of memories from one’s personal past (i.e. personal) versus the personal past of another (i.e. other) with medial PFC activity engaged for personal relative to other conditions (Fink et al.,
1996; Markowitsch et al., 2000). This pattern of findings persists even when testing memory for photo stimuli taken from the perspective of the participant versus that of another participant (Cabeza et al., 2004). In that study, photos taken by the participant (relative to another participant), elicited greater activity in the ventral medial PFC (see Figure 1 in Cabeza & St Jacques, 2007). Moreover, studies seeking to identify neural differences between the retrieval of autobiographical and semantic memories (memories for real-world facts) have found that the medial PFC is specific to the retrieval of the former memory type (Burianova & Grady, 2007; Graham, Lee, Brett, & Patterson, 2003; Levine et al., 2004).

Some have noted, however, that there are characteristics of autobiographical memories which make them either more similar to semantic memory retrieval (i.e. acontextual memory of real-world facts) or more similar to episodic memory retrieval (i.e. contextual retrieval of events from the past) (Cabeza & St Jacques, 2007). As discussed by Cabeza and St. Jacques (2007) on pages 223-225 of their review, autobiographical memories mirror semantic retrieval if the time between retrieval and initial experience increases (i.e. temporal distance), the event is experienced many times, or if voluntary retrieval of the event increases. Conversely, if the time between retrieval and initial experience is short, the event is rarely experienced, and is rarely if ever voluntarily retrieved, that memory becomes similar to episodic retrieval (Cabeza & St Jacques, 2007). Given that autobiographical memories can occur in the close (i.e. recent)
or distant (i.e. remote) past and can encompass characteristics of both semantic and episodic memory retrieval, it has provided fertile ground for researchers interested in examining the differences between the retrieval of episodic memories and semantic memories. This holds especially true in the arena of memory consolidation research, which attempts to elucidate the mechanisms triggered over varied timescales in the brain as soon as a memory trace is created. This will be discussed in detail in the forthcoming section.

### 1.4.3.2 Two influential theories of memory consolidation

Two prominent theories, the standard consolidation theory (SCT) and the multiple trace theory (MTT) have been proposed to describe changes that occur to memory traces as it pertains to changes in the relationship between hippocampal and neocortical brain systems (Frankland & Bontempi, 2005). The SCT asserts that during the initial encoding of material, the hippocampal complex helps to bind disparate pieces of information, initially stored in neocortical areas, into a coherent, bound unit representing specific encoding experience. Over time, however, these memory traces transition from the hippocampus to the neocortex. As such whereas recent memory retrieval relies on the hippocampus, remote memory retrieval relies on the neocortex (Dudai, 2004, 2012; Squire & Alvarez, 1995). In contrast, citing mounting neuropsychological and neuroimaging evidence, the MTT proposes that the hippocampus is critical for the retrieval of both recent and remote memories and even
more so when the memories represent the retrieval of rich or vivid contextual details inherent to the initial encoding of the event (Moscovitch, Cabeza, Winocur, & Nadel, 2016; Nadel, Samsonovich, Ryan, & Moscovitch, 2000; Nadel & Moscovitch, 1997). Of relevance to the present discussion, the MTT further posits that whereas the hippocampus supports retrieval of episodic-like information (i.e. contextual details associated with an encoded event) characteristic of recent memories, the neocortex supports retrieval of semantic-like information (i.e. acontextual, gist details of an encoded event) characteristic of remote memories. More specifically, ventral areas of the medial PFC have been proposed as a neocortical substrate in supporting memory for these gist-like, acontextual semantic memories (Moscovitch et al., 2016; Takashima et al., 2006). Recent evidence suggests that the medial PFC can support memory for remote memories associated with rich contextual details. Using multi-voxel pattern analysis techniques (Norman, Polyn, Detre, & Haxby, 2006), one study found that ventral areas of the medial PFC may support retrieval of remote memories when matched with recent memories in terms of the level of contextual retrieval (Bonnici et al., 2012). Additionally, that same study reports that the hippocampus can support both recent and remote memories. Together, these findings are in support of an MTT view of memory consolidation.
1.4.4 Processing of and-memory for schema-related content

1.4.4.1 Functional neural correlates of schema-related information processing

As human agents inhabiting a complex environment, we are often required to instantaneous judgments while simultaneously being inundated by a constant stream of information from multiple modalities. Given our inability to evaluate every piece of incoming information, our brains likely execute computations which save neural resources and lead to the best choices at the time. This has been widely known in the decision-making literature where seminal studies (e.g., Tversky & Kahneman, 1974) have shown individuals use heuristics to arrive at judgments in an expeditious manner. One such heuristic, the representativeness heuristic, describes situations wherein individuals assess the match between novel, incoming information and already obtained information to help guide future decisions. Outside the decision-making domain, an equivalent process of comparing novel information with existing information has been referred to as either schemas (Bartlett, 1932; Ghosh & Gilboa, 2014; Markus, 1977), context frames (Bar, Aminoff, Mason, & Fenske, 2007; Bar, 2004, 2007), or scripts/event-sequences (Wood & Grafman, 2003). For ease of discussion, the term schema is employed though others have used other terms referenced above. Given the exact composition of a schema is open for debate, a recent, useful framework has outlined four elements of a schema as it pertains to memory (Ghosh & Gilboa, 2014). Upon reviewing neuroimaging and neuropsychological studies, they characterize a schema (and listed on pg. 105 of the
review) as having an (a) “associative network structure”, (b) a product of “multiple episodes”, (c) a “lack of unit detail”, (d) and “adaptability” (Ghosh & Gilboa, 2014). Expanding on each of these proposed elements, schemas represent abstractions of regularly encountered real-world concepts and are (a) comprised of a network of co-occurring, related components interconnected with one another, (b) are frequently encoded together, devoid of (c) specific episodic details given the multiple encoding instances, and are able to (d) incorporate incoming, related information such that the network can expand.

Compared with the number of existing studies investigating the neural correlates underlying the schematic influences on memory, few studies have investigated the neural correlates of the processing of schema-related information. Specifically, these studies have reported medial PFC sensitivity to event sequences be they representative of daily-life activities (Krueger, Moll, Zahn, Heinecke, & Grafman, 2007) or learned sequences from an ancient language (Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013). Preliminary lesion evidence in patients with damage to ventral areas of the medial PFC have reported impairments in this patient group compared to controls when assessing whether presented words belong to one of two presented schemas (Ghosh, Moscovitch, Melo Colella, & Gilboa, 2014). Findings from another cognitive domain, self-referential processing, also support this set of evidence. As aforementioned, human neuroimaging evidence have found selective medial PFC activity for self-
referential compared to other-referential for trait-adjective stimulus evaluations (e.g. Kelley et al., 2002). Crucially, these judgments placed no mnemonic demands and thus medial PFC activity is isolated to the evaluation of the stimulus. As previously mentioned, some in the cognitive psychology literature point to an idea of a self-schema as potentially aiding the speed and consistency of self-referential judgments (Markus, 1977). In short, the medial PFC seems a prime candidate in the evaluation of schemas. Figure 2B from a meta-analysis of social cognition (Van Overwalle, 2009) supports this assumption by finding a distributed pattern of foci in ventral medial PFC areas for evaluations of social scripts.

1.4.4.2 Medial PFC supports memory of schema-related information

Motivated by landmark evidence from rodents (Tse et al., 2007, 2011) that schemas can form in the medial PFC and in-turn support memory for schema-related content, the past half-decade has seen a surge in the number of human neuroimaging investigations implicating the ventral medial PFC in memory for schema-related information. Many of these investigations share an experimental paradigm feature: schema-congruent (i.e. stimuli that naturally fit or go together) or schema-incongruent (i.e. stimuli do not naturally fit or go together) stimuli are presented to participants while requesting them to judge the degree of congruency for each stimulus pair. For both encoding and retrieval memory phases, ventral medial PFC activity contribute to memory for congruent stimulus pairs whereas MTL regions support memory for
incongruent stimulus pairs (Bein, Reggev, & Maril, 2014; van Kesteren, Rijpkema, Ruiter, & Fernandez, 2010; van Kesteren, Fernández, Norris, & Hermans, 2010a; van Kesteren et al., 2013). Additionally, greater medial PFC-MTL connectivity has been reported for incongruent compared with congruent encoding conditions (Bein et al., 2014; van Kesteren, Fernandez, Norris, & Hermans, 2010) although some have reported the reverse pattern, with medial PFC-MTL connectivity increasing (during encoding) as a function of increasing congruency for remembered items (van Kesteren et al., 2013) characteristics of a recollection-like process. Interestingly this pattern of findings persists even when using material found in the real world, for example information acquired in an academic setting (van Kesteren, Rijpkema, Ruiter, Morris, & Fernandez, 2014).

Complementing these human neuroimaging findings, recent, neuropsychological investigations have provided compelling evidence for the medial PFC in supporting memory for schema-related information. Specifically, patients with ventral medial PFC lesions exhibited fewer false memories (as indexed by intrusions committed from a canonical false memory paradigm) compared to normal controls (Warren, Jones, Duff, & Tranel, 2014) and this pattern extended to tests of recognition memory, with patients committing fewer false alarms (compared to normal controls) to items encoded congruently (Spalding, Jones, Duff, Tranel, & Warren, 2015). All together, these neuroimaging and neuropsychological evidence suggests an emerging role for the ventral medial PFC in supporting memory schema-related content. Given the infancy of
this research field, efforts to discuss these findings into a theoretical framework have been minimal but one has emerged and is discussed in the following section.

1.4.4.3 Medial PFC-MTL interactions in the encoding and retrieval of schema-related information

The schema-linked interactions between the medial PFC and MTL (SLIMM) framework has been proposed postulating the neural mechanisms underlying memory for schema-related information (van Kesteren, Ruiter, Fernández, & Henson, 2012). This framework theorizes that whereas knowledge structures such as a schema facilitate memory for schema-congruent information, memory for schema-incongruent information is facilitated by the means of a novelty mechanism. Please refer to Figures 2 and 3 in the theoretical review (Van Kesteren et al., 2012) that we will refer to in the paragraphs that follow.

During the encoding memory phase, as stimulus congruency increases, activity increases in the medial PFC which in turn inhibits MTL activity to support successful congruent encoding of congruent information. Conversely, with increasing stimulus incongruency, activity in the MTL is thought to increases, which in turn inhibits medial PFC activity to support successful incongruent encoding. Turning to Figure 2A-2C, when the bathtoy is paired with bathroom (Figure 2A, congruent pair), the medial PFC identifies this as a congruent relationship and inhibits MTL activity whereas when bathtoy is paired with an intermediate congruent scene (Figure 2B, somewhat incongruent pair) or incongruent scene (Figure 2C), the MTL comes online given the
increasing incongruency between the object (i.e. bathtoy) and scene. Concerning the retrieval memory phase, (Figure 3A-3E) the medial PFC-MTL relationship is influenced by the number of times an individual has retrieved the pair in between encoding and retrieval memory phases. As a function of increasing retrieval attempts, information originally encoded incongruently become less and less incongruent and thus increasingly (Figure 3C) and more reliant on the medial PFC. In contrast, previously encoded information that is rarely-if-ever reactivated (Figure 3B) will remain incongruent, and thus rely solely on the MTL. This framework has proven useful in helping researchers examine the precise role the medial PFC impacts memory and its larger role in the formation and retention of episodic memories.

1.4.5 An emergent role of the medial PFC in episodic memory processes

Memories are fundamental to our makeup as human beings. They allow us to execute a variety of processes including but not limited to the following: the ability to examine our core character traits, beliefs, and preferences (via self-referential processing), the ability to re-experience moments from our personal past (via autobiographical memory), and the ability to make optimal choices by evaluating novel information against preexisting knowledge (via schema processing). Paralleling the listed anecdotal benefits afforded to us by a memory system is a concomitant number of neurobiological, neuropsychological and neuroimaging studies devoted to understanding its architecture, function, and mechanisms in the mammalian brain.
While a complete overview of the memory findings hitherto is outside the scope of the present discussion, in the forthcoming sections, I review a few of the key dichotomies that proposed to evaluate the wealth memory findings.

1.4.5.1 Theoretical proposals of memory organization in the brain

In an effort to organize the wealth of findings in the memory literature, several dichotomies have been proposed. Of particular relevance to this discussion are two prominent divisions proposed in the literature including the episodic versus semantic memory division (hereafter referred to as episodic/semantic) (Tulving, 1972; Tulving, 1984) and the single (Squire, Wixted, & Clark, 2007; Squire & Zola-Morgan, 1991) versus dual-process theoretical division (hereafter referred to as single/dual-process) (Eichenbaum, Yonelinas, & Ranganath, 2007). With respect to the episodic/semantic division, Tulving (1972, 1984) proposed that episodic memories are instances when individuals retrieve previously encountered events that are single instance and associated with a specific time and place. Conversely, semantic memories are instances when individuals retrieve previously encountered events that are non-unique and consequently not bound by a specific time and place (Tulving, 1972; Tulving, 1984). According to these definitions, an autobiographical memory is considered a type of episodic memory whereas schema-congruent information (e.g. knowing that a bowling ball is found in a bowling alley) is considered a semantic memory as it represents conceptual knowledge of the world. Turning to the single/dual-process division, debate
centers on the specific roles of the MTL sub-regions (e.g. perirhinal cortex, hippocampal complex, parahippocampal cortex) in supporting different memory types. More specifically, the single-process theory (see Figure 1 in Squire, Stark, & Clark, 2004; Squire & Zola-Morgan, 1991) proposes that all of the MTL sub-regions uniformly support contextual retrieval (i.e. recollection). Memory in the form of recollection refers to the psychological process by which individuals are able to retrieve a previously encountered stimulus in addition to all of the associations (e.g. temporal/spatial) experienced during the initial event encoding. In stark contrast, the dual process-theory (Davachi, 2006; see Figure 3 in Eichenbaum et al., 2007) proposes that certain MTL sub-regions support recollection (primarily the hippocampus) whereas acontextual retrieval (i.e. familiarity-recognition memory) is supported by adjacent MTL sub-regions including the perirhinal and parahippocampal cortices. Familiarity refers to the psychological process by which individuals retrieve a previously encountered stimulus (e.g. retrieve the specific item) but do not recover the contextual details associated with the initial encoding of the event. Yonelinas (2002) provides a very nice review of the findings supporting a recollection and familiarity-based distinction for recognition memory (Yonelinas, 2002).

Although these influential theoretical dichotomies have proven useful in helping memory researchers organize the mechanisms underlying successful encoding and retrieval of memory, these proposals have predominantly focused on the precise MTL
contributions to memory. This is not without merit given its canonical role in the encoding and retrieval of memories (Milner, Squire, & Kandel, 1998; Scoville & Milner, 1957) coupled with well-cited reviews and meta-analyses consistently reporting little-to-no contribution of the medial PFC to episodic memory (Cabeza & Nyberg, 2000; Gilbert et al., 2006; Spaniol et al., 2009). Recent findings from the cognitive neuroscience of memory literature however have identified regions outside the MTL that support memory. Relevant to this discussion, an increasing number of neuroimaging investigations have highlighted a differential role for the medial PFC in episodic encoding (i.e. storage) and episodic retrieval of memories. In the sections below, we briefly review the neuroimaging evidence in support of a medial PFC role specific to recollection-based recognition memory.

1.4.5.2 Medial PFC contributions to episodic encoding

To identify neural activity during the encoding of material predictive of subsequent memory success, researchers typically use the responses provided during the retrieval phase of a paradigm to re-categorize trials at encoding as either subsequently remembered or subsequently forgotten (Paller & Wagner, 2002). Terms such as subsequent memory effects, encoding success activity, and differences in memory have been used to describe brain regions contributing to the successful episodic encoding of previously encountered material. In contrast, subsequent forgetting effects,
negative subsequent memory, or encoding failure activity have been used to describe brain regions whose activity yields the unsuccessful encoding of material.

Although findings from the self-referential literature point to a crucial role of the medial PFC in successful episodic encoding, findings from paradigms outside the self-referential and autobiographical memory domains paint a different picture. Specifically, many studies have reported that medial PFC activity during episodic encoding predicts subsequent forgetting of encoded information (Kim, 2011). Beyond the medial PFC, a similar ‘negative’ contribution towards episodic encoding has been reported for other members of the default mode network including the retrosplenial cortex and ventral parietal cortex (Daselaar et al., 2009). These set of findings are seemingly in conflict with findings from the self-referential and autobiographical memory retrieval literatures. Kim (2011), however, helps to harmonize these findings by suggesting that typical episodic memory paradigms demand an outward locus of attention whereas self-referential and autobiographical memory retrieval paradigms demand an inward locus of attention leading to differential engagement of brain regions contributing to successful episodic encoding.

1.4.5.3 Medial PFC contributions to episodic retrieval

In stark contrast to evidence during episodic encoding suggestive of an deleterious impact the default mode network (including the medial PFC) has on successful encoding, evidence suggests that during episodic retrieval, the medial PFC
contributes to retrieval success (Kim, 2010a). Complementing rodent evidence finding a medial PFC role in recollection-based memory (Farovik, Dupont, Arce, & Eichenbaum, 2008), recent fMRI investigations have supported a role of the medial PFC in supporting successful contextual retrieval of previously encoded stimuli (Johnson & Rugg, 2007; Simons, 2005; Simons, Owen, Fletcher, & Burgess, 2005; Yonelinas, Otten, Shaw, & Rugg, 2005), a key characteristic of what constitutes a recollection-based recognition memory. Moreover, this finding holds either when even matching for memory strength (i.e. memory confidence) (Kirwan, Wixted, & Squire, 2008) or when using cued-recall as the measure of successful retrieval (Hayama, Vilberg, & Rugg, 2012) instead of traditional recognition tests of memory. With this accumulating evidence in mind, Rugg and Vilberg (2013) have proposed a “general recollection network” which includes the medial PFC. The function of this network is to support recollection-based, contextual memory as opposed to familiarity-based, item memory (Rugg & Vilberg, 2013). Figure 2 in their review article presents the regions belonging to the proposed “general recollection network”. The regions of this recollection network overlap greatly with the well-described default mode network (Andrews-Hanna et al., 2010; Buckner et al., 2008) and the “contextual associations network” (Bar et al., 2007; Bar, 2007). Though the “contextual associations network” does not describe a network based on its contribution to episodic memory, it does describe regions that support the processing of contextual associations (e.g. knife-kitchen) in the real world. Collectively, the findings and recent
proposals described above emphasize a crucial role of the medial PFC in supporting processing and recollection of contextual associations. Though, to my knowledge, very little connection has been made between these findings and the emerging schema-memory literature, there is convergence in the type of information and memories supported by the medial PFC.

1.5. **Summarizing medial PFC contributions to cognition: Insights and opportunities**

While offering a new proposal, bringing together all of the findings described above, is outside the scope and expectations of the present discussion, there are indeed intriguing commonalities that emerge when stepping back to examine the constellation of experimental paradigms, task instructions, and cognitive domains reporting medial PFC engagement. In the sections below, I remark on a few of these observations and identify opportunities for future research inquiry.

Chief among these commonalities, observed across a variety of experimental paradigms, stimuli, and cognitive domains is a general role of the medial PFC in associative information processing. This has indeed been recently acknowledged by others (e.g., Euston, Gruber, & McNaughton, 2012). For example, in the case of judgment and decision-making tasks where associations of affective states and reward histories are thought to influence future choice, in self-referential and mentalizing tasks where self-related associations help to infer the intentions of others, and most recently evident in schema formation paradigms with the medial PFC exhibiting sensitivity to the nature of
inter-stimulus relationships. Further support of this observation is evident outside these discrete domains. Studies interrogating neural activity corresponding to evaluation of inter-stimulus relationships report medial PFC engagement for relationships that are well-learned and occur regularly in the environment (Bar, 2007). Importantly, these set of findings are closely linked to the cognitive operations involved in stimulus processing and not in relation to other processes (e.g. memory) suggestive of the medial PFCs innate role in evaluating stimulus associations.

A second commonality observed across cognitive domains is that medial PFC activity is reliably engaged for experimental paradigms where attention is directed inward as opposed to outward. Supporting this observation, the majority of paradigms described in the previous section have required participants to provide stimulus evaluations that are subjective and guided by their own idiosyncrasies and predilections. Brain regions including the medial PFC consistently evoked as a result of such task instructions comprise the default-mode network, a network readily shown to be more active during internally-guided thoughts compared to stimulus-guided thoughts (for a recent review see Raichle, 2015). While internally-guided thoughts have proven harmful to successful task performance in attention (e.g., Christoff, Gordon, Smallwood, Smith, & Schooler, 2009) and episodic encoding domains (see section 1.4.5.2 for specific evidence), attentional orienting to the self is beneficial in certain cases. These opposing patterns of findings provide interesting avenues for future research.
investigations crossing attentional orientation (either internally guided or externally guided) for social and non-social stimulus evaluations, assessing their impact on successful episodic memory.

Lastly, another commonality found across domains is that medial PFC activity is elicited in experimental paradigms that emphasize the evaluations of stimuli along social dimensions (e.g. judgments of congruency, action permissibility, or attractiveness). Though one can argue that medial PFC activity may just be found in these paradigms given the stimuli used in themselves are social (e.g. humans embedded in naturalistic scene pictures or moral violations), fMRI investigations comparing activity for stimulus evaluations along social compared with non-social (e.g. judging the order with which stimuli were presented) dimensions report medial PFC activity in favor of the social evaluation condition (Mitchell, Banaji, et al., 2005; Mitchell, Neil Macrae, & Banaji, 2005). These findings support a view that perhaps the medial PFC has an inherent role in cognitive operations relying on knowledge or information from our personal histories (e.g. previous interactions with the stimulus) to inform our judgments.

Despite numerous fMRI investigations devoted to the study of the medial PFC, a review of the findings reveals some areas ripe for future research investigations. In paradigms of self-referential processing where episodic memory is also examined, the tests of memory have been item-recognition memory as opposed to associative-
recognition memory (e.g., Macrae, Moran, Heatherton, Banfield, & Kelley, 2004). Given our daily lives are rich in the interactions and associations we make with others (e.g. I met Susan, at the city park and we had drinks for several hours) determining whether the medial PFC supports memories for these associations is important to uncover. Additionally, these same paradigms often employ simple stimuli (e.g. trait-adjectives) which have little correspondence with the complexity of our daily lives. As such, employing rich, complex stimuli (e.g., sociopolitical beliefs) we handle with great frequency in our lives is vital in advancing our understanding of medial PFC functions. Another area ripe for future investigations is the role of the medial PFC in supporting memory for schema-related information. While the cognitive neuroscience community has witnessed a recent flurry of human neuroimaging investigations (Bein et al., 2014; Brod, Lindenberger, Werkle-Bergner, & Shing, 2015; Liu, Grady, & Moscovitch, 2016; Sommer, 2016; van Kesteren, Fernández, Norris, & Hermans, 2010b; van Kesteren, Rijpkema, Ruiter, & Fernández, 2010; van Kesteren et al., 2013) favoring a medial PFC role in schema formation and retention, further work is required to determine its precise role in the type of associative information (i.e. conceptual or perceptual) it supports. Revisiting the example of meeting Susan in the park for a picnic, when attempting to retrieve this example from memory, there are conceptual and perceptual associations one may be able to retrieve of this previous experience. Retrieval of the perceptual associations for that event may involve the retrieval of the location or layout of the city
park whereas retrieval of conceptual associations for that event may involve the retrieval of where you may have had drinks: at the city park, at a nearby bar, or even at your own home. Consequently, elucidating the precise role of the medial PFC in associative recognition memory will help us understand its contributions to episodic memory.
2. Questions of central importance

As discussed in the review of anatomy, connectivity, and function of the medial PFC, there are fruitful research opportunities in advancing our understanding of this region in the human brain. Of specific relevance to the present discussion is the role of the medial PFC in supporting episodic memories. I discuss two neuroimaging studies examining the role of medial PFC in supporting associative-recognition memory.

Study 1 addresses the following questions: Does the role of the medial PFC extend beyond its reported role in supporting subsequent episodic, item encoding? As reviewed above, the majority of experimental paradigms in the self-referential memory and autobiographical memory retrieval paradigms for example, have reported medial PFC activity in subsequent memory for individual items. In our daily lives however, we do not encode information independently of other items in our environment but rather in relation to these other items. Thus, determining whether the medial PFC’s role extends to supporting memory for stimulus associations frequently encountered in our daily lives is an important first step to elucidating its role in episodic memory. Moreover, determining whether the medial PFC’s role in supporting memory characteristic of high confidence, recollection-based recognition memory or familiarity-based recognition memory is important to isolating the type of memories supported by this region. Behavioral and neuroimaging measures were collected from healthy young adult participants to answer these sets of questions.
Study 2 addresses the following questions: What are the neural correlates underlying visual recall of schema-congruent and schema-incongruent content? Does the use of a cued-recall memory test corroborate findings from studies using recognition memory tests? Given visual recall incorporates perceptual and conceptual elements of stimulus associations, what are the neural correlates underlying perceptual-and-conceptual components of visual recall for schema-congruent and schema-incongruent information? While accumulating evidence from neuroimaging studies has suggested the medial PFC supports retention of schema-related content, much work is required to assess whether medial PFC contributions extend to differential elements comprising a schema. Additionally, it is unclear whether the medial PFC supports memory processes that we exert on a daily basis. For example, on a daily basis, we regularly employ recall-like processes (e.g. remembering items to get at a grocery store/our agenda for the day) as opposed to recognition-like processes (e.g. judging which of several options we may have previously seen). Behavioral and neuroimaging measures were collected from healthy young adult participants to answer these questions.

The two studies described above complement each other in many ways. With respect to the type of stimulus associations presented, study 1 presented face-belief statement associations that are likely encountered on a daily basis as a result from interactions with friends, colleagues, or on the news. In study 2, we presented object-label: scene-picture pairs representing well-learned concepts, learned over multiple
episodes throughout one’s life. With respect to the phases of memory investigated, study 1 examined the medial PFC’s role in subsequent memory for personal beliefs by interrogating activity during the encoding memory phase, whereas study 2 examined the medial PFC’s role in successful visual recall of perceptual and conceptual schema-related content by interrogating activity during the cued-recall memory phase. Lastly, to capture the idiosyncrasies in subject attitudes, beliefs, and knowledge of the world, both studies collected subjective ratings of agreement and congruency respectively. This allowed confirmation that the studies described above accurately examined personal beliefs and schema-related conceptions of the world and were ecologically valid, bearing a strong relationship to how humans actually behave in real-world settings.

All together, these studies will aid in the understanding of the precise neural correlates of episodic memory, and more excitingly advance our understanding of how a non-canonical memory region, the medial PFC can support our ability to remember events from our personal past. Furthermore, by showing a role of the medial PFC in supporting successful encoding and recall of different forms of associative information, a generalized mnemonic role of the medial PFC to associative processes begins to emerge.
3. The medial PFC supports subsequent associative memory for personal beliefs

3.1 Introduction

Imagine one night after work, while getting drinks with your colleagues, conversation turns to the recent congressional passage of legislation approving certain forms of government surveillance of American citizens. You and your colleagues proceed to informally debating the implications of this legislation. While you strongly advocate for its passage in light of the constant national security threats both here and abroad, your colleagues strongly oppose such legislations, arguing it will serve as a gateway for increasing encroachment of civil liberties. Moreover, your colleague argues that the right to privacy is a fundamental human right and in-turn defines what it means to be American. The debate essentially boils down to differences in individual core belief systems as they relate to the arena of politics. On one hand, one individual has the core belief that privacy is a privilege whereas on the other hand, another individual has the core belief that privacy is a fundamental human right. Such debates, taking place on a frequent basis especially during an election season, illustrate how belief systems can play a role in our daily lives. From empowering us to determine where we land on key societal issues, to assessing whether we befriend someone or not based on the perceived preference alignment, beliefs serve as a compass, steering us during uncertain times. Consequently, examining its neural basis and the neural mechanisms underlying
memory for our personal beliefs is crucial to understanding how we operate in our daily lives.

Providing a useful framework from which to examine the precise role beliefs have in our everyday lives, Connors and Halligan (2015) outline a list of elements universally shared by beliefs (Connors & Halligan, 2015). Highlighting a subset of the elements that are of particular interest to the present study, listed are the following: “beliefs vary in their degree of personal relevance”, “beliefs can be held different levels of conviction or degrees of confidence”, and “beliefs can produce different emotional consequences” (pgs 3-4, Connors & Halligan, 2015). From their analysis, one can conclude that the emotional significance, personal self-relevance and subjective certainty associated with personal beliefs modulate their role in everyday cognition. Additionally, one can also include that with increasing emotional significance comes increases in personal relevance, which may signal these two elements of beliefs going hand-in-hand. And while, there is a scarcity of neuroimaging studies investigating the neural correlates of beliefs, available evidence from other cognitive domains reveal regions potentially supporting the underlying elements universally shared by beliefs. Specifically, findings from the domains of self-referential processing, autobiographical memory, schema, and emotional perception literatures highlight the potential role of the medial PFC and the amygdala in the processing of personal beliefs. Briefly summarized are findings in support of each region.
With respect to the medial PFC, a robust finding from the self-referential processing domain is its increased engagement during self-related stimulus evaluations as opposed to other-or-close-referential processing (Kelley et al., 2002; Moran et al., 2006). Furthermore, the medial PFC has been found to support memory for items encoded in a self-referential manner (Macrae et al., 2004). Activity in this region is also reported in paradigms instructing participants to retrieve specific memories from their personal past or engaging in autobiographical memory retrieval (Cabeza & St Jacques, 2007). Given they are retrieved from our personal past and are personally significant events (e.g. high school prom) they are often characterized as being vivid memories tinged with rich emotional associations. Complementing these findings is recent evidence pointing to a crucial role the medial PFC has in supporting memory for information that especially conforms with our knowledge and understanding of the world (van Kesteren et al., 2010; van Kesteren et al., 2010a; van Kesteren, Beul, Takashima, Henson, et al., 2013). The medial PFC is thought to use schemas, or associative knowledge structures, to evaluate the congruency of inter-stimulus relationships and to support memory of these relationships (van Kesteren, Ruiter, Fernández, & Henson, 2012). Outside the episodic memory domain, experimental paradigms examining the processing underlying social cognition have identified the medial PFC in contributing to a variety of social cognition processes from theory of mind to decision making (Amodio & Frith, 2006). In short, given the medial PFC
supports cognition that has personal meaning and is a byproduct of our everyday interactions, this seems like a prime region for the processing and retention of beliefs. Supporting this hypothesis, is preliminary evidence reporting medial PFC activity during the processing of beliefs as it pertains to the truthfulness of presented belief statements (Harris et al., 2009; Harris, Sheth, & Cohen, 2008).

Revisiting the example described at the outset, debates over sociopolitical issues such as government surveillance can elicit emotional reactions given their content and societal implications. Indeed as highlighted by the belief framework, the type of emotional associations tied to our core beliefs can modulate how they influence actions we undergo in our daily lives (Connors & Halligan, 2015). The amygdala has been a region linked to emotional processing with specific roles in evaluating the arousal (i.e. intensity) or valence (i.e. positive/negative) dimensions of emotional stimulus processing. Emotional arousal linked to lower-level affectively laden stimuli has been extensively characterized, (Cahill & McGaugh, 1998; Hamann, 2001; LaBar & Cabeza, 2006), and linked to limbic system function—particularly the amygdala, (Cahill & McGaugh, 1998; Hamann, 2001; LaBar & Cabeza, 2006), brain processes associated with belief-related emotional arousal however remain understudied though previous studies have linked greater amygdala activity in participants that report higher interest in politics compared with low interest in politics (Gozzi, Zamboni, Krueger, & Grafman, 2010). Increasingly however, studies have begun to examine the emotional aspects of
beliefs based on differences in ethnic, religious, and political affiliations (Bruneau & Saxe, 2010; Gozzi, Zamboni, Krueger, & Grafman, 2010; Harris et al., 2009, 2008).

Partially explaining this imbalance in the number of studies examining emotions evoked from belief stimuli could be that the type of emotions elicited are idiosyncratic, further speaking to the personal relevance element of individual belief systems.

Some research suggests that belief-related emotions may produce behavioral memory enhancements (Bradley, Angelini, & Lee, 2007; Civettini & Redlawsk, 2009), which have long been observed in studies using less complex emotional stimuli (Cahill & McGaugh, 1995; Dolcos, LaBar, & Cabeza, 2004; for a review see LaBar & Cabeza, 2006). Such studies typically report better memory for both positive or negative (vs. neutral) stimuli, indicating that the critical factor for mnemonic advantages may perhaps be emotional arousal, not emotional valence (Hamann, 2001; LaBar & Cabeza, 2006) although some aspects of remembering are valence-specific (e.g. Kensinger, 2007). Neuroimaging work has shown that emotional arousal enhancement on memory is associated with increased amygdala activity (Dolcos, LaBar, & Cabeza, 2004a; Dolcos et al., 2004b; Dolcos, LaBar, & Cabeza, 2005). In the case of belief-related emotion however, it is unclear if the memory-enhancing effect is primarily related to emotional arousal, or if emotional valence also plays a role.

The current study had three main goals: Our first goal was to construct and test a behavioral paradigm for investigating personal beliefs that (a) is both ecologically valid
and suitable for fMRI, (b) is internally and externally valid, (c) elicits a significant emotional reaction, and (d) enhances subsequent memory. While previous fMRI paradigms have presented belief statements (e.g. Bruneau & Saxe, 2010; Gozzi et al., 2010) these paradigm did not test memory for these beliefs. To address goals A-C, we ran a behavioral normative study to identify a set of belief statements that both covered a broad spectrum of Western socio-political issues and yielded desirable levels of internal/external validity and emotional arousal (see Methods and Results). Participants in the Agreement with Beliefs Task — ABT, were presented belief statements paired with an expressionless, unfamiliar face while participants rated the extent to which they agreed or disagreed with the statement (four-point scale encompassing strongly/weakly agree (SA/WA) or strongly disagree/weakly disagree (SD/WD)) with a separate ‘Don’t Know’ option. A memory test phase followed this evaluation phase. In the associative recognition task, participants were presented with intact face-belief pairs (identical pairs) or with pairs in which a face was accompanied by a belief originally associated with a different face (recombined pairs). In response to each of these pairs, participants made an identical-recombined decision followed by a confidence judgment, and responses to intact trials were used to identify agreement decisions trials from the evaluation phase that were either subsequently remembered or subsequently forgotten.

Our second goal was to investigate the neural correlates of belief processing for judgments that strongly (SA/SD) or weakly (WD/WA) resonated (i.e. belief resonance)
with one’s personal belief system. We hypothesized that strong versus weak judgments may reflect differences in personal relevance or differences in the emotional responses generated for these types of responses leading to a sum resonance signal. As such, we will examine activity in canonical emotional processing regions primarily the amygdala as a region-of-interest (ROI) in addition to conducting an exploratory whole-brain analysis to investigate these response types in other brain regions.

Finally, our third goal was to investigate the neural mechanisms underpinning any enhancement in associative memory formation stemming from belief-related evaluations. Using the subsequent memory paradigm (Paller & Wagner, 2002), we identified regions showing greater encoding activity for subsequently remembered than subsequently forgotten face-statement associations, or the subsequent memory effect (SME). In particular, we were interested in how the SME might vary with the extent to which other-endorsed beliefs resonate with personal belief systems. Given the overlap of medial PFC contributions to cognitive processes related to self-referential processing, autobiographical memory retrieval and schema-related content (all processes critical for belief-related processing), the medial PFC was hypothesized to support the memory enhancement observed for previously presented beliefs.
3.2 Methods

3.2.1 Participants

Twenty-one young adults (11 women; mean age = 21.52 years, SD = 2.40 years) participated in the behavioral normative study and a separate group of twenty-eight young adults in the fMRI study. fMRI participants were healthy, right-handed, native English speakers, with no disclosed history of neurological or psychiatric episodes. Eight fMRI participants were excluded from the analyses (six due to behavioral performance problems, such as too many missing or ‘don’t know’ responses (>50% across runs) or having a high percentage of no responses, and two due to excessive head motion (<65 signal-to-noise ratio)), leaving twenty participants (11 women; mean age = 22.9 years, SD = 3.68 years; years of education = 15.6 years, SD = 1.73 years). Every participant gave written informed consent for a protocol approved by the Duke University Institutional Review Board.

3.2.2 Stimuli

Stimuli consisted of 180 face-belief statement pairs. Face pictures of unfamiliar male and female individuals with neutral, expressions were obtained from an online database (http://agingmind.utdallas.edu/facedb/view/neutral-faces). All face pictures were presented in color on a black background. The belief statements, which ranged from 4-14 words (M = 9.05, SD = 1.84) and 32-89 characters (M = 58.89, SD = 10.79), consisted of an assortment of viewpoints on a spectrum of social (e.g. abortion, death
penalty, immigration, etc) and economic (e.g. welfare, taxes, etc) issues. Belief stimuli presented to participants were either modified from stimuli used in a previously published neuroimaging study (Zamboni et al., 2009), adapted from an online test serving to assess specific political attitudes (http://www.politicalcompass.org/test), or novel stimuli, created in the laboratory for the purposes of this investigation. For every belief statement (90 stimuli), statements expressing the opposing or counter-viewpoint (90 stimuli) were constructed to assess internal consistency and increase the likelihood of obtaining a sufficient number of trials to examine disagree and agree-related processing via behavioral and neural measures. For example, if the original endorsed belief read, ‘Thinks the law should limit experiments with human embryos’ its counter-viewpoint belief would read, ‘Supports increased funding for stem cell research’. Importantly for their use in memory testing, the original viewpoint and counter-viewpoint statements shared few words in common to reduce memory interference between them. All belief statements were presented in white text on a black background. Appendix A provides a list of the original and counter-viewpoint belief-statements used in the current study and their sources (Z=Zamboni, L=In-lab, and PC=political compass website).

3.2.3 Behavioral methods

Behavioral normative study. The goal of this ancillary study was to gain a better understanding of the characteristics of agreement/disagreement-related judgments. A separate group of healthy, young participants who did not take part in the imaging
study were first presented with the socio-political belief statements used in the scanned-ABT and instructed to first provide self-paced agreement responses on a similar 4-pt scale ranging from ‘strongly disagree’ to ‘strongly agree’ in addition to a ‘don’t know’ response. Instructions on using the 4-pt scale and the ‘don’t know’ response options were identical to those provided to participants in the imaging study. Unlike the imaging version described above, after making each agreement rating, participants were further instructed to provide an emotional arousal and issue knowledge rating of each belief statement the order of which was randomized. An emotional arousal rating was on a 4-pt scale ranging from 1-‘does not move me,’ to 4-‘moves me quite a bit’ with a ‘don’t know’ response option. Participants were also required to rate how knowledgeable they were about the issue topic contained in the belief on a 4-pt scale ranging from 1-‘not very knowledgeable’, to 4-‘very knowledgeable’ with a ‘don’t know’ response option. Ratings of issue importance or personal relevance were not collected from participants though others have suggested these dimensions may factor into belief judgments (Falk et al., 2012). Throughout the normative study, participants were encouraged to use the entire rating scale while making responses based on their personal political beliefs.

*fMRI study.* Prior to entering the scanner room, participants were introduced to the task and took part in an abridged, practice version of the scanned paradigm to become better acquainted with task instructions and experimental conditions. The scan
session consisted of twelve functional runs alternating between ABT and associative recognition task runs (Figure 1).

**Figure 1**: Scanned paradigm. (A) During the ABT, participants were presented with unfamiliar face-belief statement pairs and instructed to judge the extent to which they agreed or disagreed with the presented belief. Participants were instructed to respond ‘Don’t Know’ (option not shown) if they held absolutely no knowledge of the issue (i.e. death penalty) contained in the belief statement. (B) During the associative recognition task, participants were re-presented the face-belief statement pairs shown during the immediately preceding ABT run with the face-belief statement relationship either left identical (intact) or recombined (different). Upon making an intact/recombined judgment, participants judged how confident they were in their decision. An example of a face-belief statement pair left intact is denoted by the blue-dashed circle and an example of a face-belief pair that is recombined is denoted by the red-dashed circle.

During each ABT run, participants were presented with 30 unfamiliar face-belief statement pairs and instructed to rate the degree to which they either disagreed or agreed (1 = strongly disagree, 4 = strongly agree) with the particular viewpoint endorsed
by the pictured person. Participants were further instructed to choose a ‘Don’t Know’ response option if they held no knowledge of the issue contained in the statement. These types of responses were subsequently excluded from further analysis. Trials in ABT runs were presented for 6s and separated by a jittered fixation period (2s to 6s) with a mean of 4s. During associative recognition task runs, participants viewed face-belief pairs from the previous ABT run, 2/3 (20 pairs) in identical format and 1/3 (10 pairs) in rearranged format. Participants were instructed to judge whether each pair was intact or recombined (memory probe), in addition to providing a corresponding confidence rating (confidence probe). Participants were instructed to respond ‘intact’ if they judged a given face-belief statement pair to be unchanged from the immediately preceding run and were instructed to respond ‘recombined’ if they believed the face and statement had not appeared together at encoding. Each memory probe trial was presented for 4s and immediately followed (with no jittered fixation period) by a confidence probe trial of 4s during which participants provided a subjective confidence rating (1 = very low, 4 = very high) for their intact or recombined decision. Each compound retrieval trial (memory probe and confidence probe) was separated by a jittered fixation period (2s to 6s) with a mean of 4s (see Figure 1B). The faces and belief statements presented in each associative recognition run were always drawn from the immediately preceding ABT run, and the order in which each pair of runs (ABT and corresponding associative recognition)
appeared was counterbalanced across participants while the order of presentation within runs was random.

As the present investigation was interested in determining the mechanisms underlying subsequent associative recognition memory of personal beliefs, trials during ABT runs were classified according to the resonance of their judgments as either strong or weak (i.e. belief resonance), by agreement or disagreement (i.e. belief valence), and by subsequent memory performance. Agreement rating responses were analyzed in two ways: (a) belief resonance was measured by comparing strong (SA/SD collapsed) vs. weak (WA/WD collapsed) judgments and (b) belief valence was measured by comparing positive (SA/WA collapsed) vs. negative (SD/WD collapsed), judgments. With respect to subsequent memory effects (SMEs), responses to intact trials on the memory test runs were used to back-sort ABT trials allowing for the examination of neural activity associated with trials that were either subsequently remembered (correctly called intact) or subsequently forgotten (incorrectly called recombined). We note that the present investigation focuses exclusively on neural activity collected during the ABT (i.e. encoding) runs and does not address imaging data collected during the associative recognition memory task (i.e. retrieval) runs. To calculate a corrected recognition score (hit-false alarm), recombined trials incorrectly classified as intact were classified as false alarms. To ensure no instances of either 100% or 0% hit and false alarm rates, we used a procedure recommended by several studies (Quamme, Yonelinas, & Norman, 2007;
Snodgrass & Corwin, 1988): hit rate was computed as: $[(\#\text{Hits}+0.5)/(\text{total number of intact items}+1)]$ and false alarm rates computed as: $[(\#\text{FA}+0.5)/(\text{total number of recombined items}+1)]$.

### 3.2.4 fMRI methods

All MRI data acquisition was conducted with a 3-T GE scanner. Scanner noise was reduced with earplugs, and head motion was minimized with foam pads. Stimuli presented across the twelve functional runs were projected onto a mirror located at the rear of the scanner. Behavioral responses were recorded with two 4-key fiber-optic response boxes placed on the left and right hands respectively (Resonance Technology, Inc.), and when necessary, vision was corrected using MRI-compatible lenses that matched the distance prescription used by the participant. High-resolution T1-weighted structural images were collected using a 3D, T1-weighted FSPGR sequence (256 x 256 matrix, 96 slices, and 1.9 mm slice thickness). Functional images were acquired using a SENSE inverse-spiral sequence (64 x 64 matrix, TR=2000 ms, TE= 30 ms, FOV = 24 cm, flip angle = 70°). Thirty-four contiguous slices were acquired in an interleaved fashion. Slice thickness was 3.8 mm, resulting in 3.75 x 3.75 x 3.8 mm voxels.

Preprocessing and data analyses were performed using SPM5 software implemented in Matlab ([www.filion.ucl.ac.uk/spm/](http://www.filion.ucl.ac.uk/spm/)). After discarding the first five volumes of each run, functional images were corrected for slice time acquisition and motion. These images were then spatially normalized into the Montreal Neurological...
Institute (MNI) template and spatially smoothed using a Gaussian kernel of 8 mm FWHM. For each subject, evoked hemodynamic responses to event types were modeled with a delta (stick) function corresponding to the onset of stimulus presentation convolved with a canonical hemodynamic responses function in the context of the general linear model (GLM). Confounding factors (e.g. head motion) were also included in the model.

The model included 8 types of regressors corresponding to subsequently remembered and subsequently forgotten trials for every level of the ABT scale: 1 = strongly disagree (SD), 2 = weakly disagree (WD), 3 = weakly agree (WA), and 4 = strongly agree (SA). Remembered trials were defined as intact trials correctly judged intact with high or very high confidence (confidence responses 3 and 4). Forgotten trials were defined as intact trials incorrectly judged recombined, as well as intact trials judged intact but with very low confidence (confidence response 1). The latter trials were considered guesses because at the lowest level of confidence, there were as many false alarms as hits, and hence memory was at chance. In addition to the 8 trial types of interest, separate regressors were defined for trials of no interest, which included subsequently recombined trials, trials with no response or ‘Don’t Know’ responses, and intact trials classified as intact with low (confidence response 2) confidence. The latter trials were borderline between remembered and forgotten trials and were excluded to avoid diluting these two categories. Individual subject contrasts for each of the 8 trial
types of interest were generated at the fixed effects level and then submitted to a second level 2 (belief resonance: strong (SD/SA) vs. weak (WD/WA)) x 2 (belief valence: agree (SA/WA) vs. disagree (SD/WD)) x 2 (SME: remember vs. forgotten) repeated measures ANOVA. Planned contrasts were used to evaluate main effects and interactions within the 3-way ANOVA framework. Given our hypotheses about the role of the amygdala, we used a bilateral anatomical region-of-interest (ROI) defined in the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). For this analysis, the contrast (strong>weak) was thresholded at p<0.005 with a cluster extent of three. An analysis of statistical significance using the 3dClustSim program found in the AFNI software package (Ward, 2000) revealed that the threshold and cluster extent used within the bilateral amygdala ROI was equivalent to a corrected p<0.05 threshold with a cluster extent of 2.2 or greater. For other brain regions, we used a whole-brain analysis approach with a significance threshold of p<0.001 (uncorrected) and an extent threshold of 10 voxels. Identical whole-brain thresholds and extent meet suggested threshold recommendations (Lieberman & Cunningham, 2009) and is in similar fMRI studies (e.g. Harenski, Antonenko, Shane, & Kiehl, 2008; Hooker, Verosky, Germine, Knight, & D’Esposito, 2008; Wing, Marsh, & Cabeza, 2013).
3.3. Results

3.3.1 Behavioral results

Behavioral normative study. Behavioral analysis was carried out using IBM SPSS Statistics 21. Our first goal was to construct an ecologically valid fMRI-friendly paradigm, for investigating memory for personal beliefs, was internally and externally valid, and elicited a significant emotional reaction. To assess internal validity we measured the correlation between subjective agreement ratings made for original (e.g. ‘Thinks the law should limit experiments with human embryos’) and companion counter-viewpoints for each belief (e.g. ‘Supports increased funding for stem cell research’). Ratings for opposing versions of each belief were first correlated within subject and then averaged together to form a group correlation. A one-sample t-test was then performed to determine whether the group correlation was significantly different from chance (i.e. ‘0’). Supporting the internal validity of the belief stimuli, we found a negative correlation (M = -0.35, SD = 0.11) between the original and counter-viewpoint versions of each belief which was significantly different from chance (95% CI, -0.40 to -0.30), t (20) = -14.58, p (two-tailed) < 0.001. A negative correlation (M = -0.46, SD = 0.17) significantly different from chance (95% -0.54 to -0.38), t (19) = -11.91, p (two-tailed) <0.001 was also found when evaluating the subjective agreement ratings provided by those participating in the imaging study.
To assess external validity, we compared the subjective agreement ratings for participants in the normative study that were self-identified liberals (n = 14) or conservatives (n = 7). Although these groups were not matched in size, Levene’s Test for Equality of Variances was insignificant and an independent sample t-test was performed. For belief statements overlapping with a liberal stance, self-identified liberals had significantly higher subjective agreement ratings (M = 3.04, SD = 0.20) compared with self-identified conservatives (M = 2.61, SD = 0.28), t (19) = 3.967, p (two-tailed) =0.001. By contrast, for belief statements overlapping with a conservative stance, self-identified conservatives had significantly higher subjective agreement ratings (M = 2.14, SD = 0.21) compared with self-identified liberals (M = 1.82, SD = 0.281), t (19) = -2.64, p (two-tailed) =0.016. We also compared subjective agreement ratings for participants in the imaging study that were self-identified liberals (n = 11) or conservatives (n = 4). The number of participants reflects those that completed an online battery of questionnaires administered several weeks after their respective participation. An independent sample t-test revealed that for belief statements endorsing a liberal stance, self-identified liberals had significantly higher subjective agreement ratings (M = 3.23, SD = 0.29) compared with self-identified conservatives (M = 2.62, SD = 0.25), t (13) = 3.67, p (two-tailed) =0.003. By contrast, for belief statements endorsing a conservative stance, self-identified conservatives had significantly higher subjective agreement ratings (M = 2.36, SD = 0.20) compared with self-identified liberals (M = 1.73, SD = 0.19), t (13) = -5.52, p (two-tailed) <
0.001). We additionally examined levels of pre-existing knowledge associated with agreement judgments. Participants in the normative study provided ratings of how knowledgeable they were on topics contained in the belief statement (from 1-‘not very knowledgeable’, to 4-‘very knowledgeable’). A repeated measures ANOVA showed a significant main effect of judgment type on knowledge ratings \( [\text{Greenhouse-Geisser corrected } F (1.84, 36.91) = 44.095, p<0.001] \), and pairwise LSD contrasts showed significantly higher knowledge ratings for SD than for WD \( (p<0.001) \) and for SA than WA \( (p<0.001) \). Mean issue knowledge ratings along with emotional arousal ratings are plotted in Figure 2B. An independent sample t-test was conducted to determine pairwise differences between mean emotional arousal and issue knowledge ratings for SD and SA judgment types. For SD judgments, we did not find any significant differences between mean arousal and mean knowledge ratings, \( t (40) = 0.818, p \text{ (two-tailed) } =0.418 \). For SA judgments, we also did not find any significant differences between mean arousal and mean knowledge ratings, \( t (40) = 0.908, p \text{ (two-tailed) } = 0.339 \).

To assess if the ABT fulfills the requirement of eliciting significant emotional reaction, participants in the normative study rated their emotional arousal (from 1=“does not move me” to 4 = “moves me quite a bit”). We measured belief resonance by comparing strong (SA/SD) judgments to weak (WA/WD) judgments. Mean emotional arousal ratings for strongly disagree (SD), weakly disagree (WD), weakly agree (WA), and strongly agree (SA) judgments are plotted in Figure 2A. A repeated measures
ANOVA showed a significant main effect of judgment type \( F (3, 60) = 47.08, p<0.001 \), and pairwise LSD contrasts showed significantly higher emotional arousal ratings for SD than for WD \( (p<0.001) \) and for SA than WA \( (p<0.001) \). Thus, confirming our assumption that the belief statements in the ABT are effective in eliciting substantial emotional reactions, participants gave significantly higher subjective emotional arousal ratings to high-emotional arousal than low-emotional arousal judgments. Interestingly, when comparing emotional arousal ratings with ratings of issue knowledge for strong (SD/SA) judgments, the mean ratings for both responses are very close (Figure 2B) and non-significant at each agreement/disagreement level supporting the idea that both arousal and semantic knowledge contribute to potential memory enhancements observed for the extreme ends of the rating scale. In short, the constructed paradigm allowed us to examine judgments associated with high emotional arousal and high issue knowledge affording us the possibility to examine the neural correlates of belief judgments with high emotional arousal and knowledge versus judgments with low emotional arousal and knowledge.

*In-scanner behavior.* Behavioral analysis was carried out using IBM SPSS Statistics 21. Turning to the ABT in the scanner, we focused on response times (RTs), which represent the main behavioral measure given that the ABT responses are neither correct nor incorrect. As illustrated by Figure 2C, when the 4 conditions are ordered from SD to SA, RTs show a clear inverted U-shaped function. An ANOVA confirmed significant
effect of judgment type \[ F (3, 57) = 96.77, p<0.001 \], a significant quadratic function \( (p<0.001) \), and pairwise LSD tests confirmed significantly faster RTs for SD than WD \( (p<0.001) \) and for SA than for WA \( (p<0.001) \). The finding of faster responses for strong than weak agree/disagree responses is consistent with the normative study’s result that strong (SD/SA) responses are associated with greater emotional arousal and issue knowledge than weak (WD/WA) responses.

Of central interest to this study was how belief resonance produced during ABT decisions might influence later memory. Confirming the memory-related dimension of ABT judgments, a repeated measures ANOVA revealed a significant main effect of judgment type \[ F (3, 57) = 4.96, p<0.005 \] with pairwise LSD tests confirming significantly higher overall hit-rates (collapsed across all confidence levels) for SD than WD trials \( (p<0.05) \) and for SA compared to WA trials \( (p<0.01) \). The effects of ABT judgments on associative recognition were particularly clear when focusing on very high-confidence recognition responses (‘very high’ confidence level). As illustrated in Figure 2D, the proportion of very high-confidence hits shows a clear U-shaped function reflecting better memory for strong judgments (SD/SA) than for weak judgments (WD/WA). Results of a two-way repeated measures ANOVA with factors of belief resonance (strong and weak) and belief valence (agree and disagree) revealed a significant main effect of belief resonance on high-confidence hit rates \[ F (1, 19) = 19.50, p<0.001 \] however there was no significant main effect of valence \[ F (1, 19) = 0.57, p<0.001 \],
The interaction was significant \( F(1, 19) = 4.54, p=0.046 \), with a greater difference in very high-confidence hits found for strong vs. weak disagree comparisons relative to strong vs. weak agree comparisons. In sum, responses high in conditions of high belief resonance in the ABT had a significant impact on subsequent memory and this impact was mediated by strength of the belief response rather than belief valence (agree vs. disagree). Furthermore, better memory for strong (SD/SA) judgments cannot be attributed to longer encoding time because these judgments had faster RTs than weak (WD/WA) judgments (see Figure 2C). For the same reason, larger SMEs (remembered vs. forgotten activity) for strong than weak judgments cannot be attributed to differences in time-on-task.

Figure 2: Behavioral results from the normative study (A/B) and the fMRI investigation (C/D). (A) Participants who did not take part in the imaging study but
in a separate, behavioral normative study provided ratings of emotional arousal from ‘Does Not Move Me’ to ‘Moves Me Quite a Bit’ to the same belief statements used in the imaging study, *p<0.001, n.s. = not significant. (B) Mean ratings plotted for emotional arousal and issue knowledge ratings as collected in the behavioral normative study. In the issue knowledge rating, participants rated how knowledge they were on the sociopolitical issues embedded in each belief statement, n.s. = not significant. (C) Mean response times (RTs) for judgments made in the scanner during the agreement-with-beliefs task (ABT). RTs in the ABT show an inverted-U function with longer response times for weak disagree/agree judgments compared with strong disagree/agree judgments, *p<0.001, n.s. = not significant. (D) Enhancements in associative recognition memory (measured by very-high confidence hits) were found for strong disagree/agree compared with weak disagree/agree judgments, *p<0.005, **p<0.001, n.s. = not significant. All error bars represent standard error. SD: strongly disagree; WD: weakly disagree; WA: weakly agree; SA: strongly agree. For plots A, C, D, red colored bars denote disagree judgments and blue colored bars denote agree judgments.

3.3.2 Imaging results

As described above (see Methods), we analyzed fMRI data using an ROI approach for our hypothesized region (i.e. amygdala) and additionally performed whole-brain analyses to explore potential contributions from other regions. For both types of analyses, we conducted a 3-way ANOVA: belief resonance [strong (SD/SA) vs. weak (WD/WA) judgments], belief valence [agree (SA/WA) vs. disagree (SDWD) judgments], and subsequent memory (remembered vs. forgotten). Below, we consider in turn brain activity associated with belief resonance, belief valence, and the impact of these factors on subsequent memory.

Specifically, we investigated the neural mechanisms of belief resonance which we identified by comparing activity for SD/WD judgments to activity for WD/SA judgments. Given that we had a strong prediction about the amygdala, we performed an
ROI analysis on this region. As illustrated by Figure 3, the results confirmed this prediction: a cluster in the left amygdala showed greater activity for strong (SD/SA) than weak (WD/WA) judgments. After confirming this prediction, we performed a whole-brain analysis to identify other brain regions showing evoked for belief extremity.

Figure 3: Region of interest (ROI) analysis. (A) Global maxima of activation within the amygdala located at x = -19, y = -4, z = -19. (B) Bars reflect the parameter estimates for strong (SD and SA) and weak (WD and WA) judgment types respectively. Error bars denote standard error.

As listed in Table 1, regions showing greater activity for strong (SD/SA) than for weak (WD/WA) judgments included anterior and ventrolateral PFC, parahippocampal, and posterior cingulate regions. The reverse pattern of greater activity for weak (WD/WA) than strong (SD/SA) judgments was found in largely dorsal frontoparietal regions. Thus, these set of regions corresponded to belief processing for viewpoints that strongly or weakly resonated with personal belief systems.
Table 1: Main effect of belief resonance (whole-brain analysis). Up to three local maxima set 8mm apart are reported for each cluster. Regions reported reflect the nearest gray matter located to the peak cluster. R, right; L, left; BA, Brodmann area; Hem, hemisphere.

<table>
<thead>
<tr>
<th>Region</th>
<th>Hem</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
<th>Voxels</th>
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<tbody>
<tr>
<td><strong>Strong &gt; Weak</strong></td>
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<td></td>
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<tr>
<td>Anterior PFC</td>
<td>L</td>
<td>10</td>
<td>-11</td>
<td>49</td>
<td>11</td>
<td>4.41</td>
<td>65</td>
</tr>
<tr>
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<td>-34</td>
<td>34</td>
<td>-8</td>
<td>3.98</td>
<td>15</td>
</tr>
<tr>
<td>Parahippocampal Gyrus</td>
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<td>36</td>
<td>-30</td>
<td>-26</td>
<td>-19</td>
<td>4.2</td>
<td>12</td>
</tr>
<tr>
<td>Posterior cingulate</td>
<td>L</td>
<td>24</td>
<td>-19</td>
<td>-15</td>
<td>42</td>
<td>4.46</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>31</td>
<td>-4</td>
<td>-15</td>
<td>49</td>
<td>4.08</td>
<td>36</td>
</tr>
<tr>
<td><strong>Weak &gt; Strong</strong></td>
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<tr>
<td>Dorsal PFC</td>
<td>R</td>
<td>6</td>
<td>26</td>
<td>4</td>
<td>57</td>
<td>4.05</td>
<td>26</td>
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<tr>
<td></td>
<td>L</td>
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<td>-23</td>
<td>0</td>
<td>57</td>
<td>3.79</td>
<td>13</td>
</tr>
<tr>
<td>Dorsal parietal</td>
<td>R</td>
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<td>15</td>
<td>-64</td>
<td>57</td>
<td>4.68</td>
<td>19</td>
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<tr>
<td></td>
<td>R</td>
<td>7</td>
<td>41</td>
<td>-38</td>
<td>53</td>
<td>3.86</td>
<td>11</td>
</tr>
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</table>

We finally investigated the neural mechanisms of associative subsequent memory for personal beliefs. We compared differences in the size of the SMEs (subsequently remembered minus subsequently forgotten trials) as a function of belief resonance and belief valence. To this end, we found a belief resonance (SD/SA > WD/WA) x subsequent memory (remembered > forgotten) interaction in a large, ventral medial PFC (global maxima: x = 8, y = 45, z = -11) cluster (see Figure 4A). As illustrated by Figure 4B, this region showed larger SMEs for strong (SD/SA) than weak (WD/WA) judgments with a clear difference between SD and WD judgments and SA and WA judgments and marginal differences found between WD and WA judgments. No brain region showed the reverse effect of larger SMEs for weak (WD/WA) than strong (SD/SD).
judgments. Additionally, we found no brain region showing a belief valence x subsequent memory interaction, indicating that the impact of belief resonance on subsequent memory reflected may the role of emotional arousal or issue knowledge but not emotional valence. This finding parallels the behavioral findings illustrated in Figure 2D wherein we found superior memory for strong (SD/SA) than weak (WD/WA) resonance judgments. Interestingly, the amygdala did not show any belief resonance x memory interaction. Thus, whereas the amygdala has often been implicated in memory-enhancing effects of emotion in studies using more basic emotional stimuli (e.g. affective pictures), the medial PFC appears to play an important role in modulating memory for stimulus judgments characterized by high emotional arousal, high issue knowledge, and perhaps (though one cannot confirm) high personal relevance.

Figure 4: Belief resonance x subsequent associative memory interaction. (A) Activity in a large, ventral medial PFC cluster exhibited greater subsequent associative memory effects for extreme agreement judgments (SD/SA) compared with intermediate agreement judgments (WD/WA). (B) Bars reflect subsequent memory effects or encoding success activity (ESA) (hits - miss). Error bars denote standard error. For ease of comparison, bars in red denote disagree judgments and bars in blue denote agree judgments.
3.4 Discussion

In the present study, we investigated the neural correlates corresponding to personal belief processing and the neural mechanisms underlying memory for these personal beliefs. The current study had three main goals. Our first goal was to construct a paradigm that, in addition to being ecologically valid and scanner-friendly, would be internally and externally valid and would allow for the study of personal beliefs and their subsequent memory. Our second goal was to identify the neural correlates of personal belief processing. Finally, our third goal was to reveal the neural correlates of subsequent memory for personal beliefs.

The study yielded three main results. (1) Fulfilling our first goal, the ecologically valid, scanner-friendly task we developed and tested, the agreement with beliefs task (ABT), was internally and externally valid, and elicited significant an emotional reaction as indexed by emotional arousal (Figure 2A) and issue knowledge (Figure 2B) ratings, for the extreme ends of the scale which was found to exhibit the highest memory (Figure 2D). (2) In pursuit of our second goal, we observed a positive relationship between increased belief resonance (strong versus weak) during the ABT and activation of the amygdala (Figure 3). This finding indicates that the amygdala, a region strongly associated with emotional arousal driven by simple stimuli, also mediates resonance related to personal beliefs. (3) Finally, achieving our third goal, we linked the subsequent memory-enhancing effects in the ABT to the medial PFC (Figure 4A/4B). This finding
indicates that memory of personal beliefs occur via the medial PFC, a region strongly associated with self-referential processing, autobiographical memory retrieval and more recently memory for schema-congruent information. The three main results are discussed in separate sections below.

**The ABT: Contributing to fMRI paradigms investigating emotional memory**

As noted in the introduction, the vast majority of prior studies on the neural mechanisms of emotional evaluation and memory have largely neglected inquiry into emotions elicited from appraisal of abstract events such as evaluating beliefs in relation to one’s personal value system. Examples of the few studies that have employed such emotions have participants provided ratings of how much emotion they felt when viewing faces of politicians who share their ideology versus those that do not (Kaplan, Freedman, & Iacoboni, 2007), or rated the reasonability of statements matching or mismatching their particular ethnic group (Bruneau & Saxe, 2010). In general, these studies have focused mostly on social questions, such as the formation of impressions or the role of ethnic or political identity, rather than on the generation of emotional arousal (but see Gozzi et al., 2010). Emotional reactions elicited from social situations is difficult to study in the laboratory because the same event can elicit very negative, positive, or no emotions in different people. To address this issue, the ABT task measured emotional reactions by asking participants to rate the extent to which they agreed or disagreed with statements of personal beliefs about socio-political issues,
under the assumption that strongly agreeing or disagreeing with the statement would involve greater emotional arousal than only weakly agreeing or disagreeing with the statement. Consistent with this assumption, a normative study showed that higher agreement intensity (strong agree/disagree judgments) were associated with higher subjective emotional arousal ratings than weak agree/disagree judgments (Figure 2A).

To validate our assumptions that the ABT was a paradigm to investigate emotions generated from abstract stimuli, we carried out tests to measure both its internal and external validity. As a test of internal validity, we examined whether the belief-stimuli used in the study were truly tapping into opposing perspectives on a socio-political issue. Correlation analyses revealed negative relationships between subjective agreement ratings provided for opposing viewpoints of the same issue among participants in the normative and imaging studies. Thus, the belief-stimuli adequately conveyed different perspectives of a particular socio-political issue and participants were largely consistent with their agreement ratings through the course of the study. As a test of external validity, we examined the relationship between self-reported political ideology and subjective agreement ratings made for liberal or conservative belief statements. In comparing the mean ratings provided by both groups, we found that for liberal beliefs, self-identified liberals provided higher agreement ratings than self-identified conservatives and we found the reverse effect for ratings provided for conservative beliefs. We note here that in our sample, there were very few self-identified
conservatives (n=4) with all identifying themselves as merely ‘somewhat conservative’. Testing a larger number of self-identified conservatives who strongly identify themselves with this political ideology may be fruitful in terms of further testing the external validity of the ABT.

Additionally, strong (SD/SA) judgments, which presumably reflect a more pronounced version of one’s personal beliefs, were marked by higher ratings of pre-existing knowledge then weak (WD/WA) judgments (Figure 2B) serving as evidence that evaluations collected from the ABT could be considered as accurate reflections of personal belief systems. Moreover, though this group of findings seems intuitive, they do support the notion that the beliefs used in the ABT are accurately representing a diverse set of core principles advocated by individuals who identify themselves with either liberal or conservative political ideologies. They also fit within a recent belief framework and the elements of personal significance, emotion, and memory that give rise to our core belief systems (Connors & Halligan, 2015).

Taken together, the findings highlighted above point to the ABT as contributing to existing fMRI paradigms investigating emotional memory in their use of ecologically-valid stimuli, that evoke emotions frequently experienced and evoked through interactions with those that belong to or are outside one’s social groups.
Neural mechanisms underlying personal belief processing

Our second goal was to investigate the neural mechanisms of belief resonance triggered by social situations, which we identified by comparing activity for strong (SA/SD) judgments vs. weak (WA/WD) judgments. Given a hypothesized effect in the amygdala, we focused on this region as an ROI. Confirming our hypothesis, amygdala activity was greater for SA/SD than for WA/WD judgments (Figure 3). This finding generalizes the link between the amygdala and emotional arousal found in many emotions triggered by non-social situations (Cahill & McGaugh, 1998; Hamann, 2001; LaBar & Cabeza, 2006) to the domain of emotions triggered by social situations. An important difference between these effects is that in typical studies the amygdala generally responds to the same stimuli across participants (e.g., pictures of dangerous animals), whereas in the case of the ABT, amygdala responses are generated by the comparison of pre-existent personal beliefs to an external statement. The beliefs that elicited SD judgments in some participants, elicited WD or WA judgments in other participants, and vice-versa. Thus, in the ABT, amygdala activity did not track properties of the stimuli themselves but instead related to how strongly each belief matched each participant’s personal belief system.

In the whole-brain analyses, we also found greater activity linked with high belief resonance (SD/SA) compared with low belief resonance (WD/WA) in anterior and ventrolateral PFC, parahippocampal, and posterior cingulate regions (Table 1). This
network of regions is often associated with episodic memory retrieval (Spaniol et al., 2009). One possibility is that high belief resonance judgments involve the retrieval of personal memories consistent or supporting the judgments. For example, while assessing one’s personal view on the use of human embryos, a participant could try to remember how they felt the last time they encountered while watching a news commentator espousing an alternative view. We posit remembering a strong negative feeling would support a “strongly disagree” judgment, whereas failing to remember a specific emotion could lead to an intermediate judgment. Thus, although evaluation of personal belief system share an amygdalar component with emotional arousal elicited by emotions generated from non-social situations, it may also involve other components, such as episodic memory retrieval. Concerning the anterior PFC (BA 10) region found from this contrast, it may reflect ratings of increased knowledge found in the normative study for high versus low belief resonance judgments (Figure 2B). Increasing knowledge may also reflect the retrieval of personal memories given the issue topics are more familiar to the participant and may also reflect retrieval of schema-related information (e.g. van Kesteren et al., 2012) or the detection of well-learned contextual associations with issue beliefs paralleling findings of medial PFC sensitivity for associations that are linked with a well-established (e.g. knife-kitchen) versus weak (e.g. knife-beach) environmental context (e.g., Bar, 2007). Finding additional components generated from abstract, complex stimuli makes intuitive sense given that such emotions are less
automatic and involve greater elaboration (Knutson, Wood, Spampinato, & Grafman, 2006; Sakaki, Niki, & Mather, 2012). With respect to the normative finding of increased issue knowledge for SD/SA judgments, we also found activity in the ventrolateral prefrontal cortex which has previously been linked to semantic processing and retrieval (Binder, Desai, Graves, & Conant, 2009). Ultimately, deciding how one feels about complex issues such as embryo usage or privacy is likely to involve a more complex network than a simple emotional arousal response elicited by viewing a picture of a snake. Additionally, such response types as found in the present study are characterized by high emotional arousal and issue knowledge. Moreover, the finding that high belief-resonance judgments (i.e. SA/SD) are characterized by high emotional arousal and issue knowledge ratings is consistent with evidence reporting that measures of emotional arousal (from self-report and skin-conductance) increased as a function of increasing experimental familiarity (van den Bosch, Salimpoor, & Zatorre, 2013). Furthermore, it corroborates evidence showing that information that is semantically related and highly emotionally arousing leads to greater memory enhancements compared with information that is moderately semantically related and high in emotional arousal (Buchanan, Etzel, Adolphs, & Tranel, 2006).

We also conducted whole brain analyses identifying brain regions that showed greater activity for low (WD/WA) resonance judgments. These regions included dorsal PFC and parietal regions (Table 1). These dorsal fronto-parietal regions are often
activated during demanding tasks and decisions and are attributed to top-down
attention processes (Corbetta & Shulman, 2002). The idea that low agreement resonance
(WD/WA) judgments are more demanding than high agreement resonance (SD/SA)
judgments is consistent with RTs in the ABT, which were found to be slower for
WD/WA than SD/SA judgments (Figure 2C). A similar inverted-U function with longer
RTs for intermediate than extreme judgments has been observed for other scales with
opposing extremes for facial attractiveness (Tsukiura & Cabeza, 2011), food preferences
(Litt, Plassmann, Shiv, & Rangel, 2011), and in personality measures that have measured
RTs for items deemed to be highly congruent or incongruent with one’s schema
(Akrami, Hedlund, & Ekehammar, 2007). One possible interpretation is that
intermediate judgments are more demanding because they are close to the boundary
between two qualitatively different judgments (e.g., congruent vs. incongruent,
attractive vs. unattractive), and are characterized by low issue knowledge and therefore
require greater monitoring. Alternatively, intermediate judgments reflect a lack of
knowledge about the topic, leading to greater indecision. Consistent with this idea, in
the normative study, participants rated their levels of knowledge about topics to which
they made intermediate WD/WA judgments to be less than for topics in which they
made extreme SD/SA judgments (Figure 2B).
Neural mechanisms underlying memory for personal beliefs

Our third goal was to investigate the neural mechanisms of subsequent memory for personal beliefs. Our results showed that, compared to low resonance (WA/WD) judgments, high resonance (SA/SD) judgments yielded a larger subsequent memory effect (SME) in the medial PFC. In this region, SMEs displayed the same U-shaped function (Figure 4A) as the behavioral effects showed for subsequent memory. No region showed the opposite effect of greater SMEs for low resonance (WD/WA) than high resonance (SD/SA) judgments.

The behavioral finding that emotion increases in the ABT significantly enhanced associative recognition performance suggests that the memory-enhancing power of emotions is not limited generalizes to emotions triggered by evaluation of personal beliefs. The argument of why our memory systems evolved to better remember events associated with negative or positive emotions from situations such as encountering a dangerous animal is straightforward: these emotions signal events that are critical for survival (e.g., the fear of encountering a predator; the happiness of finding food).

Indeed, an evolutionary account of the mnemonic benefits for stimuli associated with high emotional arousal has been similarly posited in the emotional memory literature (Adolphs, Russell, & Tranel, 1999; Hamann, 2001). The argument, however, of why we better remember information that is associated with emotions from personal beliefs is less obvious. One possibility is that these emotions are indirectly related to survival
through interactions with surrounding social groups. In the case of the ABT, remembering who agrees with us and who disagrees with us could be essential for distinguishing between friends (close to the self) and foes (others) and/or defining our position within the group. Given the scarcity of research on emotions generated from evaluations of personal beliefs, it is difficult at present to address the basic question of why these emotions enhance memory.

The lack of memory-enhancing effects in the amygdala cannot be attributed to a low fMRI signal in this region, because we found significant amygdala activity when comparing strong (SD/SA) to weak (WD/WA) trials independently of memory (Figure 3). One possible explanation of why the amygdala did not influence subsequent memory is that our measure was associative recognition of face-belief statement pairs. Most studies linking the amygdala to enhance memory formation have focused on memory of items (e.g., words, pictures) rather than on binding between very different items, such as faces and beliefs. According to one view, arousal (as elicited by survival-related emotional stimuli) can enhance binding between an object and its features (e.g., color) but not between an object and other distinct objects or background contextual information (Mather, 2007). Consistent with this theory, there is evidence that arousal-related amygdalar activity enhances the vividness of subsequent item recognition but not context memory (Dougal, Phelps, & Davachi, 2007; Kensinger & Schacter, 2006). In
contrast, medial PFC activity in the current study was associated with better associative recognition for face-belief pairs.

The finding that medial PFC activity enhanced subsequent memory is broadly consistent with but extends the results of several previous lines of fMRI investigations. First, our finding is consistent with the results of Macrae and colleagues (2004). Using a trait adjective paradigm (Does this adjective describe you?) (Heatherton et al., 2006; Kelley et al., 2002), Macrae and collaborators found a medial PFC region that showed greater activity for self-relevant than not-relevant adjectives and for subsequently remembered than forgotten adjectives (see also Fossati et al., 2004). Our findings extend this result by showing that the relation between self-relevance and subsequent memory in medial PFC is nonlinear (Figure 4B): medial PFC show a larger SME for beliefs that are relevant (SA) than non-relevant (WA/WD) to the self-but, it also shows a large SME for beliefs that very discordant with self (SD). To assess whether our ventral medial PFC cluster overlapped with previous studies examining self-referential processing, we entered the coordinates for the maxima (x = 8, y = 45, z = -11) into Neurosynth, an online meta-analytic tool (Yarkoni et al., 2011). Entering the search term “self referential” we find our cluster overlaps with a pattern of foci generated from an online meta-analysis of 127 neuroimaging studies (http://neurosynth.org/analyses/terms/self%20referential/). This observation may in part explain the idea of self-referential processing potentially leading to memory enhancements.
Second, our finding is consistent with recent evidence from Leshikar and Duarte (2012) who found that medial PFC activity predicted subsequent memory for object-scene pairs when participants focused on pleasantness rather than color (Leshikar & Duarte, 2012). Our finding extends this result by showing that medial PFC contributions to relational memory do not only depend on an orientation towards the self but also on the match between the stimulus and the self.

Third, our finding is consistent with the results of Mitchell and colleagues (2004), who had participants associate faces with actions consistent with a personality trait (e.g., *He refused to loan his extra blanket to the other campers* for the "inconsiderate" trait) while focusing either on forming an impression about the person or to pay attention to the sequence in which actions were presented on the screen. When focusing on forming an impression, activity in a dorsal medial PFC region predicted associative memory for face-sentence pairs. Our finding extends this result by showing that when the focus is on personal beliefs, SME’s can occur in the ventral medial PFC and its contribution varies with the strength of the match with one’s personal belief system.

Fourth, our findings of the medial PFC as a region supporting memory for content encoded in a social context is consistent with previous findings implicating the medial PFC as a region supporting subsequent memory for impression formation (Gilron & Gutches, 2012), stimuli included in an socio-emotional context (Somerville,
Wig, Whalen, & Kelley, 2006), and finally with increasing working memory load demands for social content (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012).

Lastly, our findings of the medial PFC as a region important for beliefs resonating strongly (as opposed to weakly) with participants aligns well with studies in the judgment and decision making literature showing that this region tracks increases in subjective stimulus reward value (O’Doherty, 2004). In the present study, though we cannot confirm, beliefs containing issues that participants were knowledgeable about potentially tagged with greater stimulus value also contributing to medial PFC activity.

Beyond the role of the medial PFC in self-referential processing, the current findings is also related to a very different literature regarding the contributions of medial PFC to processing of pre-existing knowledge or "schemas" (Knutson et al., 2006; van Kesteren et al., 2010, 2012; van Kesteren, Beul, Takashima, Henson, et al., 2013). Citing rodent evidence (Tse et al., 2007, 2011), a recent theory postulates that information congruent with pre-existing schemas is encoded primarily by medial PFC whereas information incongruent with pre-existing schemas is encoded primarily by the medial temporal lobe (MTL) regions (van Kesteren et al., 2012). Consistent with this theory, a recent fMRI study found greater SMEs in medial PFC for congruent object-scene pairs (e.g., tennis court – tennis racket) than for incongruent pairs (e.g., tennis court – umbrella) whereas MTL showed the opposite effect (van Kesteren, Beul, Takashima, Henson, et al., 2013). At first blush, the current findings seem inconsistent
with this theory because, compared to intermediate beliefs, we found larger SMEs in medial PFC not only for beliefs that were highly congruent with the self but also for beliefs that highly incongruent with the self. However, this finding is harmonized with the schema theory given that people’s schemas about political issues include not only the position they support but also the position they do not support. In this sense, having a schema about an issue would be equivalent to having a strong opinion about the issue, which is required for both SA and SD judgments. This interpretation fits with evidence from our normative study that the issues for which participants produced strong agree/disagree ratings from participants as issues they know more about.

3.5 Study conclusion

In order to address a relatively neglected area of the emotional memory and social neuroscience literatures, we constructed a paradigm investigating emotions triggered from social situations, the Agreement with Beliefs Task. The present paradigm provided measures of belief resonance (strong vs. weak judgments) and belief valence (agree vs. disagree judgments) and revealed how these two factors affected subsequent associative recognition memory (remember versus. forgotten). The study yielded three main findings. First, behavioral results showed that the ABT is internally and externally valid and that SA/SD judgments elicited greater subjective measures of emotional arousal and issue knowledge leading to better subsequent memory than WA/WD judgments. Second, fMRI analyses of the judgment phases showed that the judgment
types characterized by high emotional arousal and issue importance were associated
with greater activity in the amygdala. Finally, subsequent memory fMRI analyses
showed that SMEs in the medial PFC but not in the amygdala. This finding is consistent
with accumulating evidence highlighting the medial PFCs role in associative recognition
memory and consistent with its well-established role in self-referential processing,
autobiographical memory retrieval, emergent role in processing and memory for
schema-related content.
4. The medial PFC supports visual recall and recognition of schema-related content

4.1 Introduction

On a daily basis, across a variety of contexts, we are bombarded by incoming information from our external environment. Making sense of this incoming information on the dimensions of event relevance (critical/trivial) and/or familiarity (previously experienced/novel) is essential to our decision-making process. Oftentimes, when we encounter novel, never-before experienced scenarios, our actions are influenced by how we have acted in similar but non-identical situations in the past. This is apparent when considering the following example. Imagine you are at a party hosted by one of your work colleagues. You are introduced to a particular individual at the party and as you are walking over to meet him, you form a quick impression. Based on the clothes he is wearing, his hairstyle, and how he comports himself with others, you generate an expectation of what type of person he may be, the values he espouses and the likelihood of you befriending him. This expectation is a product of previous encounters with individuals who match the outward characteristics of the person you are going to meet. This sequence of evaluating our external environment, comparing it against similar, well-established templates, and producing an expectation or judgment is a process we undertake on a frequent basis. Certainly, this process extends well beyond the described example.
These templates, allowing us to link novel experiences with previously experienced events, is referred to in the literature as context frames (Bar et al., 2007; Bar, 2007), scripts/event sequences (Krueger et al., 2007; Wood & Grafman, 2003), and schemas (Ghosh & Gilboa, 2014; van Kesteren et al., 2012). In the present study, we will use the term schema given its traditional use in the cognitive neuroscience of memory literature. What defines a schema has been a challenge for researchers but a recent framework (Ghosh & Gilboa, 2014) provides elemental characteristics relevant to the present discussion. On pg. 105 of that review, the authors specifically describe a schema as the following: a network of elements that is (a) interconnected and related formed over (b) multiple encoding experiences, (c) absent of specific elements to any one encoding experience but a generalized abstraction, (d) flexible in its incorporation of novel yet related incoming information. Until recently, the neural mechanisms underlying its processing, formation, and influence on episodic memory were unclear but emerging evidence suggests a role for the medial PFC. Inspired by seminal evidence in the rodent literature showing that the medial PFC can store schema-related knowledge information and in-turn can function independently of the hippocampus (Tse et al., 2007, 2011), the past five years has seen a flurry in the number of human neuroimaging investigations of schemas (Bein et al., 2014; Brod et al., 2015; Sommer, 2016; van Buuren et al., 2014; van Kesteren et al., 2014; van Kesteren, Fernández, et al., 2010b; van Kesteren et al., 2010; van Kesteren, Beul, Takashima, Henson, et al., 2013).
Shared by many of these investigations is the methods used to examine schema processing and retention. Participants are presented with stimulus pairs whose inter-stimulus relationship is either congruent or incongruent. Congruent stimulus relationships are defined as relationships that are regularly co-occur in the natural environment (e.g., rental shoes-bowling alley) whereas incongruent stimulus relationships are defined as relationships that are rarely-if-ever co-occur in our natural environment (e.g., saw-adult bedroom). These relationships have been presented as word pairs (Bein et al., 2014), object-location pairs (Sommer, 2016; van Buuren et al., 2014), abstract-shape pairs (Brod et al., 2015), picture pairs (Liu et al., 2016; van Kesteren, Beul, Takashima, Henson, et al., 2013) or as picture-word pairs (van Kesteren et al., 2010a). Additionally, in examining the differential effects of stimulus congruency on later memory processes, tests of item and associative recognition memory are employed. Consistent across encoding (van Kesteren, et al., 2014; van Kesteren, Fernández, et al., 2010b; van Kesteren, Beul, Takashima, Henson, et al., 2013), post-encoding (van Kesteren, Fernández, et al., 2010b), and retrieval (Brod et al., 2015; van Buuren et al., 2014; van Kesteren et al., 2010a) memory phases is a role for the medial PFC in supporting memory for schema-congruent information. Complementing this evidence are studies from the neuropsychological literature. Two very recent studies of note have found that patients with lesions focal to ventral areas of the medial PFC exhibit declines in the ability to assess whether information conforms to a schema (Ghosh et al., 2014).
and commit fewer false alarms (as indexed by a false-memory paradigm) compared to normal controls (Spalding et al., 2015). In sum, emerging evidence supports a role of the medial PFC in episodic memory of information concordant with previously acquired knowledge.

A theoretical framework, termed the schema-linked interactions between medial prefrontal and medial temporal regions (SLIMM), has been proposed to help explain these consistent findings (van Kesteren et al., 2012). In this proposal, the authors postulate that there is a push-and-pull mechanism between the medial PFC and MTL sub-regions modulated by the level with which newly, acquired information relates to previously acquired information. As newly acquired information becomes increasingly incongruous in the face of preexisting information, it is identified as novel by the brain, triggering greater engagement of the MTL and in-turn suppressing medial PFC engagement. Conversely, as newly acquired information becomes increasingly congruous with previously acquired information is identified as conforming to an existing schema by the brain, triggering greater engagement of the medial PFC and in-turn suppressing MTL engagement. At the retrieval memory phase, this push-and-pull dynamic changes as a function of the strengthening of the incongruent information. Specifically, it is postulated that schema-incongruent material is increasingly treated as congruent as the frequency of retrieval attempts increases and thus shifts its reliance
from the MTL to the medial PFC. On the other side, schema-incongruent material that is rarely-if-ever retrieved remains incongruent and continues to rely on MTL regions.

While accumulating evidence supports the medial PFC in supporting schema-congruent information, a few issues regarding this emergent role remain outstanding. *First*, although the studies described above have extended a role of the medial PFC to the domain of episodic memory, in particular associative-recognition memory, it is unclear how the medial PFC supports different aspects of recall and associative recognition memory: perceptual (i.e. specific visual details of a stimulus association) compared with conceptual (i.e. specific semantic details of a stimulus association). *Second*, the experimental designs employed thus far are less than ideal for examining encoding-retrieval relationships. A cued-recall experimental paradigm is potentially well suited to examining encoding-retrieval relationships and the precise neural reinstatement (at retrieval) of processes undertaken during encoding (Danker & Anderson, 2010; Rugg, Johnson, Park, & Uncapher, 2008). Studies have taken advantage of such paradigms to examine the trial-specific neural similarity between encoding and retrieval phases, reporting a positive relationship between increasing neural similarity and successful memory retrieval (Ritchey, Wing, LaBar, & Cabeza, 2013; Staresina, Henson, Kriegeskorte, & Alink, 2012; Wing, Ritchey, & Cabeza, 2015). *Third*, a subset of the investigations reviewed above have tested memory 24-hours after initial episodic encoding (van Kesteren, Fernández, et al., 2010b; van Kesteren et al., 2010; van Kesteren,
Beul, Takashima, Henson, et al., 2013) leading to potential influences from memory consolidation processes. In fact, preliminary evidence finds that increases in the delay between encoding and retrieval can modulate the differences in associative recognition memory performance found for previously encoded congruent and incongruent material. Specifically, the memorial advantages found for schema-congruent information (as opposed to schema-incongruent information) dissipate with increasing encoding-retrieval delay (van Kesteren, Rijpkema, Ruiter, & Fernández, 2013). Thus, avoiding this delay is critical in examining the potential medial PFC contributions to associative recognition memory. Fourth, to the author’s knowledge, hitherto, no fMRI investigation in healthy adults has established a link between ventral medial PFC and conceptual false memories for schema-related content. This would link the human neuroimaging and neuropsychological literatures together by confirming findings that patients with lesions to the ventral medial PFC commit fewer conceptual false alarms (Warren, Jones, Duff, & Tranel, 2014). A possible first step towards this would be to demonstrate a role of ventral areas of the medial PFC to conceptual associative recognition. Fifth, while evidence suggests that the medial PFC supports schema-congruent memory during off-line, post-encoding periods (van Kesteren, Fernández, et al., 2010b) there is scant evidence in support of this and thus future studies should examine medial PFC-MTL interactions during post-encoding rest periods as it relates to memory for schema-congruent and schema-incongruent information.
As reviewed above, there are indeed several lines of research inquiry possibly reflective as the medial PFC’s role in the processing and retention of schema-related information is emerging. Our first goal was to assess behaviorally, whether we would observe schema-congruent enhancements for associative recognition of schema-related material that was perceptual or conceptual in nature. Hypothesized was the following: (1) better conceptual associative recognition memory performance for schema-congruent then schema-incongruent encoded information and (2) better perceptual associative recognition memory performance for schema-incongruent then schema-congruent encoded information, which would align with the SLIMM framework predictions.

Our second goal was to investigate the neural correlates underlying successful visual recall of schema-congruent and schema-incongruent information. Based on the preliminary set of findings reviewed above and available theoretical proposals, we hypothesized that the medial PFC would support successful recall of schema-congruent information whereas the MTL would support successful recall of schema-incongruent information.

Our third goal was to investigate the neural correlates underlying successful recall of conceptual and perceptual associative elements of schema-congruent and schema-incongruent pairs. We hypothesized that the medial PFC would support successful retrieval of conceptual schema-related content whereas the MTL would support successful recall of schema-related content given these associations are not inherent to
the schema. This would support notions that recognition memory for information not anchored to a schema may benefit from schema-incongruent encoding (van Kesteren et al., 2012).

Collectively, the present study will add to a small, but accumulating group of studies by (1) extending a mnemonic role of the medial PFC to successful visual recall and (2) identifying its precise role in the successful recall of either or both conceptual- and-perceptual elements of schema-related content.

4.2 Methods

4.2.1 Participants

Twenty-two healthy, young adults (15 women; mean age=23.77 years, SD=3.14 years; years of education= 15.77 years, SD= 1.65 years) participated in the imaging study. Study participants were healthy, right-handed, native English-speakers, with no disclosed history of neurological or psychiatric episodes. Four participants were excluded from subsequent behavioral and imaging analyses. One participant was excluded for several reasons including at-or-below chance performance (<25%) on the conceptual recognition test, a high percentage of object-labels marked as Don’t Know/Unfamiliar (~5%), and a perceived failure to understand the in-scan task instructions. Another participant was excluded due to a high percentage of object label cues marked as Don’t Know/Unfamiliar (~8%) coupled with low subjective agreement ratings (64.8% for congruent pairs and 85% for incongruent pairs) with experimenter
determinations of stimulus congruency. Two participants were excluded as data could not be collected either due to a technical error with the experimental script or voluntary withdrawal from the study. This resulted in 18 participants (12 women; mean age= 24.27 years, SD= 3.00 years; years of education= 15.94 years, SD= 1.55 years). Every participant gave written informed consent for a protocol approved by the Duke University Institutional Review Board.

4.2.2 Stimuli

The experimental protocol consisted of the following phases: an object-assignment encoding task, a conceptual recognition test, a perceptual recognition test, and a congruency-validity task. Additional measures were collected after the experimental session including participant identification of object-label cues they were unfamiliar with/did not have any knowledge about and a debrief questionnaire. Stimuli employed for each phase of the experimental protocol are discussed in separate sections below.

(1) Object-Assignment Encoding Task. Over the course of ten functional runs, 200 object-label: scene-picture pairs were presented to the participant, 100 of which were presented in a schema-congruent condition and 100 of which were presented in a schema-incongruent condition. The experimenter predetermined the schema-congruent and schema-incongruent pairs. Schema-congruent pairs consisted of objects deemed to fit well with an associated scene-picture (e.g. the pair of diploma (object-label):
graduation ceremony (scene-picture). Schema-incongruent pairs consisted of objects deemed to fit poorly with an associated scene-picture (e.g. saw (object-label): bedroom (scene-picture)). Ideas for congruent/incongruent pairs were obtained from a previous fMRI investigation (van Kesteren et al., 2013) or were formed in the laboratory.

Given the present study employed a cued-recall paradigm, short, verbal labels for the objects were created in-lab and scene-pictures were found via online searches on Google Images. To minimize overlap between object-label cues and spontaneously generated labels for scene-pictures, steps were taken to ensure the objects corresponding to the object-labels were not visible in the scene and composed of words absent from potentially generated scene-labels. Two-hundred object-labels used in this study ranged from 1-2 words in length (M=1.32 words, SD=0.46) and ranged from 3-17 characters in length (M=8.24 characters, SD=3.13). Two-hundred scene-pictures were 400x300 pixels in size and presented in color (along with the object-label in black text) against a grey background.

(2) Conceptual Recognition Post-Scan Test. Scene-labels were constructed by the experimenters for each of the two-hundred scene-pictures presented in the object-assignment encoding task. Scene-labels served as short descriptions of the scene-pictures presented to participants while in the scanner. Scene-labels were constructed in such a way as to provide enough detail to describe the companion scene-picture. Scene-labels
ranged from 1-4 words (M=1.92 words, SD=0.54) and ranged from 3-23 characters (M=12.52 characters, SD=3.98).

(3) Perceptual Recognition Post-Scan Test. Two-hundred scene-picture quartets were presented to the participant. Scene-picture quartets consisted of scene-pictures presented to the participant during the object-assignment task along with three additional scene-pictures, which served as visually similar distracters. Distracter scene-picture stimuli were gathered from Google Images. Scene-pictures were 400x300 pixels in size and presented in color against a grey background.

4.2.3 Behavioral methods

fMRI study. The scan session took place over two-hours and consisted of the following components: a (1) five-minute awake resting state scan, the (2) a face-scene localizer task, and (3) ten functional runs each consisting of three different block types: the object-assignment task block, a three-minute awake resting state block, and a covert cued-visual recall task block. In the sections that follow, a detailed discussion of relevant components of the scanned paradigm is provided.

Primary functional task. The bulk of the in-scan session took place over ten functional runs. Each run consisted of three different blocks: The object-assignment encoding block, a 3-minute post-encoding awake resting state block, and a covert cued-visual recall block. Before discussing each block, we note here that the run order and trials presented within each block was randomized. Additionally, there were two
counterbalances in the present study designed so that every object-label: scene-picture pair was either presented in an congruent or incongruent encoding condition. During the object-assignment encoding task block (Figure 5A), participants were shown twenty object-label: scene-picture pairs with half of the presented in the schema-congruent condition and the other half presented in the schema-incongruent condition. For each pair, participants constructed a mental image of the object (corresponding to the object-label) and assigned the object to a quadrant of the associated scene-picture (BL=Bottom-Left, TL=Top-Left, TR=Top-Right, BR=Bottom-Right) judged to be the best fit for the object. Each pair was presented for 4000ms. Immediately following each pair was an active baseline task. In this task, a series of numbers (ranging from 1-9) were individually presented for 1000ms. The average duration was 3000ms and ranged from 2000ms-6000ms sampled from a quasi-exponential distribution. For each number, participants provided an odd/even judgment. Immediately following this task block, a 3-minute post-encoding awake resting-state block (Figure 5B) commenced. Participants then proceeded to the covert cued-visual recall block (Figure 5C). Object-labels presented in the first task block served as cues. Participants were instructed to covertly recall the scene-picture originally associated with the object-label cue and rate the vividness of the recalled associate on a 4-pt scale ranging from ‘Not Very Well’=1 to 4=’Very Well’. This scale was employed, as ratings would reflect recall of the perceptual and conceptual details of the scene associate. Each of these trials was presented for
3000ms and separated by an active baseline task similar to the baseline-task used in the first task block.

*Post-scan tests.* To (1) assess differential influences of congruency on associative recognition, (2) validate the in-scan covert cued-visual recall ratings, and to (3) determine the extent to which within-subject congruency ratings matched experimenter classification of congruency, a series of post-scan tests were administered to participants. The post-scan experimental phase consisted of the following components: the (1) concept recognition test, the (2) perceptual recognition test, and the (3) congruency-validity test. These tasks are described in detail below. Though each post-test task was self-paced, there was a 6000ms response deadline to prevent exhaustive deliberation.

(1) *Conceptual recognition test:* A schematic of this test is provided in Figure 5D. Participants were presented with any of the object-labels along with four scene-label options and instructed to select the scene-label option previously associated with the object-label. The four scene-labels consisted of a target option and three distracters options. If the object-label: scene-picture pair was originally encoded congruently (i.e. schema-congruent condition) then the four scene-label options comprised of a target, a congruent scene-label lure, and two-incongruent scene-label lures. Conversely, if the object-label: scene-picture pair was encoded incongruently (i.e. schema-incongruent condition), the four scene-label options comprised of a target, an incongruent scene-label distracter and two congruent scene-label distracters. Participants then rated how
confident they were in their selection on a 4-pt scale ranging from 1=‘Very Low’ to
4=‘Very High’. Immediately after their confidence rating, participants were re-presented
the object-label from the first phase of the trial along with their selected scene-label
option. Participants were instructed to select the location selection that matched their
location judgment during the object assignment task. Upon making their response, they
proceeded to rate their confidence-level on a 4-pt scale ranging from 1= ‘Very Low’ to 4=‘Very High’. Though self-paced, there was a 6000ms response deadline.

(2) Perceptual recognition test. A schematic of this test is provided in Figure 5E.
Participants were presented with four visually similar scene-pictures comprised of a
target scene-picture (the scene picture presented during the object assignment task) and
three scene-picture distracters. Participants were instructed to select the scene-picture
they believed was presented while in the scanner. After making their selection, they
proceeded to judging their confidence on a 4-pt scale ranging from 1= ‘Very Low’ to 4=‘Very High’. Though self-paced, there was a 6000ms response deadline.

(3) Congruency-validity task. A schematic of this task is provided in Figure 5F. To
assess the correspondence between experimenter classifications of stimulus congruency
and participant classifications of stimulus congruency, participants were re-presented
the two-hundred object-label: scene-picture pairs from the object assignment task and
this time asked to rate the congruency of each pair. Specifically, participants provided
‘fitness’ judgments, evaluating how well the object-label fits with the associated scene-
picture (and vice versa) on a 4-pt scale ranging from 1= ‘Very Incongruent’ to 4= ‘Very Congruent’. Though self-paced, there was a 6000ms response deadline.

Upon concluding the experimental session, participants identified which of the two-hundred object-labels shown in the scanner presented difficulties to them due to a lack of knowledge or unfamiliarity. Additionally, participants completed an experimental debrief questionnaire providing feedback and answering specific questions of the clarity of the task instructions. Given the present investigation was interested in examining the extent to which stimulus congruency has on associative recognition memory, we examined neural data via an ANOVA framework and by means of parametric analyses. We describe these models in detail in the sections that follow.

Figure 5: Scanned paradigm and post-scan phase. (A) Participants commenced each functional run with the object-assignment task block. In this task block, twenty
object-label: scene-picture pairs were presented with half of the pairs presented in the congruent encoding condition and half of the pairs presented in the incongruent encoding condition. For each pair, participants were instructed to construct a mental image of the object corresponding to the object-label and select the quadrant (BL: Bottom Left; TL=Top Left; TR=Top Right; BR=Bottom Right) of the scene-picture they believed the object best fits. Each of these trials lasted for a duration of 4s. In-between pair presentation, there was an active baseline task. During this active baseline task, numbers ranging from 1-9 were presented one-by-one. Participants provided odd/even judgments. Each of these numbers was presented for 1s and the active baseline duration ranged from 2-6s. (B) A three-minute awake resting-state block immediately followed this block. In this block, participants were instructed to attend to a black cross-found in the middle of the screen while keeping their eyes open. No explicit response was required. (C) Participants then proceeded to the covert-visual recall block. In this block, participants were re-presented all of the object-labels presented in the object assignment task block of the same run. On each trial, which lasted a duration of 3s, participants were instructed to covertly retrieve the scene-picture previously associated with the object-label cue and subsequently provide a rating of how well they could describe the retrieved scene-picture (‘Not Very Well’=1, 2, 3, 4=’Very Well’). The post-scan phase (D-F) immediately followed the in-scan task. (D) Participants first completed the conceptual recognition test. Object-label cues were presented along with four scene-label options. Participants were instructed to select the scene-label corresponding to the scene-picture that was originally associated with the object-label. They then proceed to rating their confidence level in this response (‘Very Lo’=1, 2, 3, 4=’Very Hi). Following this, the selection scene-label option was re-presented and this time participants retrieved the location of the scene-picture originally selected while in the scanner. Confidence ratings for this judgment were recorded. (E) Participants then completed the perceptual recognition test. Four perceptually similar scene-pictures were presented to the participant with instructions to select the scene-picture believed to have been presented to them while in the scanner. Confidence ratings for this judgment were recorded. (F) Subjective congruency ratings were collected via the congruency-validity test. Participants were re-presented the entire set of object-label: scene-picture pairs presented in the scanner and instructed to rate how well the object corresponding to the object-label ‘fits’ with the associated scene-picture.

4.2.4 fMRI methods

All MRI data acquisition was conducted with a 3-T GE scanner. Scanner noise was reduced with earplugs, and head motion was minimized with foam pads. Stimuli
presented across the ten functional runs were projected onto a mirror located at the rear of the scanner. Behavioral responses were recorded with a 4-key fiber-optic response boxes placed on the right hand (Resonance Technology, Inc.), and when necessary, vision was corrected using MRI-compatible lenses that matched the distance prescription used by the participant. To gauge whether participants stayed awake throughout the course of the experiment, an eye-tracker was used to track eye movements. High-resolution T1-weighted structural images were collected using a 3D, T1-weighted FSPGR sequence (256 x 256 matrix, 96 slices, and 1.9 mm slice thickness). Functional images were acquired using a SENSE inverse-spiral sequence (64 x 64 matrix, TR=2000 ms, TE= 30ms, FOV = 24 cm, flip angle = 70°). Thirty-four contiguous slices were acquired in an interleaved fashion. Slice thickness was 3.8 mm, resulting in 3.75 x 3.75 x 3.8mm voxels.

Preprocessing and data analyses were performed using SPM5 software implemented in Matlab (www.fil.ion.ucl.ac.uk/spm). After discarding the first five volumes of each run, functional images were corrected for slice time acquisition and motion. These images were then spatially normalized into the Montreal Neurological Institute (MNI) template and spatially smoothed using a Gaussian kernel of 8 mm FWHM. For each subject, evoked hemodynamic responses to event types were modeled with a delta (stick) function corresponding to the onset of stimulus presentation convolved with a canonical hemodynamic responses function in the context of the
general linear model (GLM). Confounding factors (e.g. head motion) were also included in the model. Analysis was conducted at the whole-brain level and specific significance level and cluster extent thresholds are presented in each of the sections below.

Moreover, the imaging analysis focused exclusively on activity collected during the covert-visual recall task. Several factors went into this decision including the following: (1) few studies investigating schema-related memory effects have used a cued-recall paradigm, (2) visual recall-related activity should be strongest during this phase, (3) our primary goal was to examine effects of schema-congruency on cued recall, (4) correspondence with previous neuroimaging investigations of cued-recall, and (5) the ability to examine process-pure activity linked to the recall of scene-pictures (activity collected during the object-assignment encoding task could potentially be adulterated by other processes including stimulus evaluation). Common to the models were separate regressors for trials of no interest including trials with no response, trials that contained object-label cues that participants had no knowledge or were unfamiliar with, and trials where participant classifications of congruent/incongruent did not match our predetermined classifications of congruent/incongruent.

*Neural correlates underlying visual recall.* To identify the neural correlates of successful scene-picture recall effects, we employed a repeated measures 2 \((\text{congruency})\) x 4 \((\text{cued recall rating})\) ANOVA model on neural activity measured during the CCP-R task. This model
contained 8 types of regressors with separate regressors defined for trials of no interest. Individual participant contrasts for each of the 8 trial types of interest were generated at the fixed effects level and submitted to the second level. A whole-brain significance threshold of p<0.001 (uncorrected) with a cluster extent threshold of 5 voxels was used for the 2x4 ANOVA framework.

**Neural correlates underlying perceptual components of visual recall.** To identify the neural correlates of perceptual elements of visual recall (as indexed by the perceptual recognition test), we employed a 2 (congruency: congruent, incongruent) x 3 (perceptual recognition memory: Miss, Low/Medium Confidence Hits, High-Confidence Hits) ANOVA model on activity measured during the covert-visual recall task. We treated misses separately, pooled together hit trials associated with ‘Very Low’, Level 2, and Level 3 confidence, and treated hits associated with ‘Very High’ confidence as a separate regressor. Consequently, this model contained 6 types of regressors with separate regressors defined for trials of no interest. Individual participant contrasts for each of the 6 trial types of interest were generated at the fixed effects level and submitted to the second level. A whole-brain significance threshold of p<0.005 (uncorrected) with a cluster extent threshold of 8 voxels was used for the 2x3 ANOVA framework.

**Neural correlates underlying conceptual components of visual recall.** To identify the neural correlates of conceptual elements of visual recall (as indexed by the conceptual recognition test), we employed a 2 (congruency: congruent, incongruent) x 3
(conceptual recognition memory: Miss, Low/Medium Confidence Hits, High-Confidence Hits) ANOVA model on activity measured during the CCP-R task. We treated misses separately, pooled together hit trials associated with ‘Very Low’, Level 2, and Level 3 confidence, and treated hits associated with ‘Very High’ confidence as a separate regressor. Consequently, this model contained 6 types of regressors with separate regressors defined for trials of no interest. Individual participant contrasts for each of the 6 trial types of interest were generated at the fixed effects level and submitted to the second level. A whole-brain significance threshold of p<0.005 (uncorrected) with a cluster extent threshold of 5 voxels was used for the 2x3 ANOVA framework.

Neural correlates underlying perceptual-and-conceptual components of visual recall. To identify the neural correlates of visual recall of conceptual-and-perceptual recognition, we employed a repeated measures 2 (congruency: congruent, incongruent) x 4 (conceptual/perceptual recognition: MM, MH, HM, HH). For clarification in the MH trial type, the ‘M’ corresponds to concept recognition performance (i.e. a miss trial on the conceptual recognition test) and the ‘H’ corresponds to picture recognition performance (i.e. a hit trial on the perceptual recognition test). For this model, recognition performance was collapsed across confidence level ratings. Consequently, this model contained 8 types of regressors with separate regressors defined for trials of no interest. Individual participant contrasts for each of the 6 trial types of interest were generated at
the fixed effects level and submitted to the second level. A whole-brain significance threshold of $p<0.001$ (uncorrected) with a cluster extent threshold of 5 voxels was used for the 2x3 ANOVA framework.

4.3 Results

4.3.1 Behavioral results

Congruency-validity task. Behavioral analysis was carried out using IBM SPSS Statistics 21. Essential to our subsequent behavioral and imaging analyses was determining whether our construction of congruent and incongruent object-label: scene-picture pairs conformed to participant ratings of stimulus congruency. Consequently, we obtained ratings of congruency from participants for all of the object-label: scene-picture pairs presented to them while in the scanner. When analyzing the mean response ratings provided in this task, participants indeed judged predetermined congruent pairs as congruent and judged predetermined incongruent pairs as incongruent (Figure 6). An independent samples t-test revealed that the mean ratings of congruency during was significantly different for the congruent and incongruent encoding conditions, $t(34) = 25.851, p$ (two-tailed) $<.001$. Moreover, we found no differences with respect to time-on-task between congruent and incongruent encoding conditions. An independent samples t-test confirmed no significant differences $t(34) = -.712, p$ (two-tailed) $=.481$. Lastly, when evaluating the extent to which participant ratings agreed with experimenter classification of congruency, we found high agreement percentage across
participants with 87.8% agreement for congruent pairs and 91.9% agreement for incongruent pairs.

Figure 6: Behavioral results from the congruency-validity task. Mean subjective congruency ratings provided on a 4-pt scale ('Very Incongruent' = 1, 2, 3, 4='Very Congruent') for object-label: scene-picture pairs for congruent and incongruent conditions respectively.

Object-assignment encoding task. Behavioral analysis was carried out using IBM SPSS Statistics 21. Visual inspection of the distribution of location selections revealed marginal differences between congruent and incongruent conditions. This was confirmed by a repeated measures ANOVA with factors of congruency (congruent, incongruent) and object location (BL, TL, TR, and BR). A Greenhouse-Geisser correction revealed no significant differences in encoding conditions $F(1, 17) = 1.292, p=0.271)$. Additionally, there was no significant encoding condition x location interaction $F(3, 51) = 0.679, p=0.569)$. Post hoc tests using the Bonferroni correction revealed TL selections (averaged across encoding condition) were significantly different from BL ($p=0.028$) and
TR ($p=0.022$) selection options respectively. After consulting our gallery of scene-pictures, potential reasons for the relatively fewer number of TL location selections could be due to the following: this quadrant of the scene-picture was in the distant background, comprised primarily of environmental elements including the sky or vegetation or were elements deemed irrelevant to the understanding of the associated scene-picture.

Turning to mean response times, visual inspection revealed no differences between encoding conditions at each location. A repeated measures ANOVA with factors of congruency (congruent, incongruent) and object location (BL, TL, TR, BR) confirmed no significant difference found in encoding conditions $F(1,17)=2.263, p=0.151$). Additionally, after a Greenhouse-Geisser correction, we found no significant encoding condition x object location interaction $F(1.784, 30.333) =.710, p=0.485)$. Post hoc tests using the Bonferroni correction revealed significant response time differences (averaged across encoding condition) between BL and TR location selections ($p=0.032$).

Covert cued-visual recall task. Behavioral analysis was carried out using IBM SPSS Statistics 21. To examine the influence of schema-congruent and schema-incongruent encoding conditions on covert cued picture recall, we plotted the mean number of responses for each level of covert cued recall rating (‘Not Very Well’=1, 2, 3, 4=‘Very Well’). Visual inspection of the behavioral output (Figure 7) revealed an increase in the mean number of responses as a function of the increasing covert cued visual recall rating.
for schema-congruent pairs, a pattern absent for schema-incongruent encoded pairs. Separate 1x4 repeated measures ANOVA for the schema-congruent condition revealed a significant linear effect $F(1, 17) = 24.819, p<0.001$ and a weaker but significant quadratic effect $(F(1, 17) = 4.884, p<0.05$. Meanwhile, a 1x4 repeated measures ANOVA for the schema-incongruent conditions revealed an insignificant linear effect $F(1, 17) = 1.706, p=0.209$.

Turning to mean response times, visual inspection of the behavioral output revealed fastest response times for the highest levels of covert cued picture recall rating for both schema-congruent and schema-incongruent conditions. Confirming this, a 1x4 repeated measures ANOVA for the schema-congruent condition revealed a significant linear effect $F(1, 17) = 6.662, p<0.05$ and a stronger significant quadratic effect $F(1, 17) = 28.263, p<0.001$. A separate 1x4 repeated measures ANOVA for the schema-incongruent condition revealed a significant quadratic effect $F(1, 17) = 26.223, p<0.001$. Paired samples t-test were performed on the extreme ends of the in-scan cued-recall rating scale comparing schema-congruent and schema-incongruent conditions for the ‘Not Very Well’ rating response and ‘Very Well Rating’ response. We found significant differences for the ‘Not Very Well’ response $(t(1, 17) = -4.187, p \text{ (two-tailed)} = 0.001)$ and for the ‘Very Well’ rating response $(t(1, 17) = 7.246, p \text{ (two-tailed)} < 0.001)$. 
Figure 7: Behavioral results from the in-scan covert-cued visual recall task. Mean number of responses for each covert cued visual recall rating level for congruent and incongruent conditions respectively.

Conceptual recognition post-scan test. Behavioral analysis was carried out using IBM SPSS Statistics 21. To assess the differential stimulus congruency effects on conceptual associative recognition, we administered the conceptual recognition post-scan test. Participants were instructed to select the scene-label corresponding to the scene-picture (previously presented to them) originally associated with the object-label. We note here that 16 out of the 18 participants were entered into this analysis as 2 participants had below chance (<25%) performance on either the congruent or incongruent condition. An independent samples t-test revealed that the mean hit-rate on the conceptual recognition test (Figure 8A) was significantly different for congruent and incongruent encoding conditions, $t(30) = 7.881$, $p$ (two-tailed) $< 0.001$. In Figure 8B, mean hit
rates for each level of the in-scan visual recall ratings is plotted separately for schema-congruent and schema-incongruent conditions. Separate 1x4 repeated measures ANOVA revealed a significant linear effect for schema-congruent (F (1, 15) = 14.307, p<0.005) and a significant linear effect for schema-incongruent conditions (F (1, 15) = 40.025, p<0.001). To complement these results, we examined confidence ratings for each visual recall rating level. Separate 1x4 repeated measures ANOVA revealed a significant linear effect of in-scan visual recall ratings on high-confidence hits F (1, 15) = 81.597, p<0.001. A similar analysis for schema-incongruent pairs also revealed a significant linear effect F (1, 15) = 103.364, p<0.001 and a weaker but significant quadratic effect F (1, 15) = 7.888, p<0.05. With respect to hits associated with low confidence a 1x4 repeated measures ANOVA for schema-congruent pairs reveals a significant linear effect F (1, 15) = 20.082, p<0.001 and a significant quadratic effect F (1, 15) = 5.670, p<0.05. For schema-incongruent pairs, we found a significant linear effect F (1, 15) = 36.928, p<0.001. Paired samples t-test were performed on the extreme ends of the confidence rating scale revealed significant differences between schema-congruent and schema-incongruent encoding conditions for ‘Very Low’ (t (1, 14) = -2.195, p_{two-tailed} < 0.05) and for ‘Very High’ (t (1,15) = 3.410, p_{two-tailed} < 0.005).
Figure 8: Behavioral results from the conceptual recognition test. (A) Mean hit-rates for congruent and incongruent encoding conditions. Dashed line denotes chance-level performance (25%). (B) Mean hit rate for each level of the covert cued-visual recall in-can task plotted separately for the schema-congruent and schema-incongruent conditions respectively. Error bars denote standard error.

Perceptual recognition post-scan test. Behavioral analysis was carried out using IBM SPSS Statistics 21. To assess the differential stimulus congruency effects on perceptual associative recognition, we administered the perceptual post-scan test. According to theoretical proposals, schema-incongruent relationships should confer a memorial advantage for information not essential to a schema. Participants were instructed to select the scene-picture that they believed was previously presented to them while in the scanner. An independent samples t-test revealed that the mean hit-rate on this test (Figure 9A) was significantly different for congruent and incongruent encoding conditions, \( t(34) = 2.533, p \text{ (two-tailed) } < 0.05 \). In Figure 9B, mean hit rates for each level of the in-scan visual recall rating is plotted separately for schema-congruent and schema-
incongruent conditions. Separate 1x4 repeated measures ANOVA revealed a significant linear effect for schema-congruent (F (1, 15) =33.219, p<0.001) and a significant linear effect for schema-incongruent conditions (F (1, 15) =14.306, p=0.001). To complement these results, we examined confidence ratings for each visual recall rating level. Separate 1x4 repeated measures ANOVA revealed a significant linear effect of in-scan covert visual recall ratings on high-confidence hit F (1, 17) =15.654, p=0.001. A similar analysis for schema-incongruent pairs revealed a significant linear effect F (1, 17) =15.759, p=0.001. With respect to hits associated with low confidence a 1x4 repeated measures ANOVA for schema-congruent pairs and for schema-incongruent pairs did not reveal significant linear or quadratic effects. Paired samples t-test were performed on the extreme ends of the confidence rating scale revealed significant differences between schema-congruent and schema-incongruent encoding conditions for ‘Very Low’ (t (1, 13) =−4.080, p(two-tailed)=0.001) and for ‘Very High’ (t (1,17) =4.936, p(two-tailed) <0.001).
Figure 9: Behavioral results from the perceptual recognition test. (A) Mean hit-rates for congruent and incongruent encoding conditions. Dashed line denotes chance-level performance (25%). (B) Mean hit rate for each level of the covert cued-visual recall in-scan task plotted separately for the schema-congruent and schema-incongruent conditions respectively. Error bars denote standard error.

Recognition performance (as indexed by hit rate) for the conceptual and perceptual tests for every object-label: scene-picture pair was first correlated within participant and then averaged together to form a group correlation. When correlating overall hit rate for conceptual and perceptual tests, we found a weak correlation (Mean $r = 0.168$, SD = 0.09). We also found a weak correlation when examining schema-congruent (Mean $r = 0.125$, SD = 0.128) and schema-incongruent (Mean $r = 0.147$, SD = 0.10) conditions respectively. With this in mind, we examined the underlying neural correlates of conceptual-and-perceptual components of visual recall presented in sections that follow.
4.3.2 Imaging results

Neural correlates underlying visual recall. To address one of our study goals, we conducted a 2 (congruency: congruent, incongruent) x 4 (cued recall rating: ‘Not Very Well’, 2, 3, ‘Very Well’) repeated measures ANOVA to identify regions critical for successful visual recall. Given we were using a 4-pt cued-recall rating scale, we weighed each of the rating levels according to a linear function (congruent condition: -1.5, -0.5, 0.5, 1.5; incongruent condition: -1.5, -0.5 0.5, 1.5). Table 2 contains regions resulting from this analysis.

<table>
<thead>
<tr>
<th>Region</th>
<th>Hem</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
<th>Voxels</th>
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<td>4</td>
<td>49</td>
<td>-8</td>
<td>3.69</td>
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</tr>
<tr>
<td></td>
<td>R</td>
<td>11</td>
<td>0</td>
<td>34</td>
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<tr>
<td></td>
<td>L</td>
<td>10</td>
<td>-4</td>
<td>45</td>
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<td>Posterior cingulate</td>
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<td>-45</td>
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<td>-23</td>
<td>-60</td>
<td>34</td>
<td>3.51</td>
<td>9</td>
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</table>
As expected, we found regions corresponding to the ‘core recollection network’ including the posterior cingulate and parahippocampal gyrus. Additionally, we find activity in the ventral areas of the medial PFC and MTL sub-regions including the rhinal cortices. Given we found no congruency x cued recall interactions, we next examined congruency-specific effects on visual recall. Linear increases in memory for schema-congruent and schema-incongruent conditions were found in several regions (see Table 3).

**Table 3: Linear increases in (I) schema-congruent and (II) schema-incongruent memory (whole-brain analysis).** Up to three local maxima set 8mm apart are reported for each cluster. Regions reported reflect the nearest gray matter located to the peak cluster. R, right; L, left; BA, Brodmann area; Hem, hemisphere.

<table>
<thead>
<tr>
<th>Region</th>
<th>Hem</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
<th>Voxels</th>
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<tr>
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<td>L</td>
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<td>-4</td>
<td>41</td>
<td>-11</td>
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<td>-27</td>
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<tr>
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<td>-19</td>
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<td>-11</td>
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<td><strong>II.</strong></td>
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<td>4.67</td>
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</table>
Entorhinal cortex    L    28    -23    -19    -23    3.87
Precentral gyrus     L    6    -34    -15    68    4.07    25
Middle frontal gyrus L    6    -19    19    57    3.55    10
Cingulate gyrus      R    31    23    -53    27    3.43    5

Figure 10A/10B present the activity profiles within the local maxima of a medial
PFC cluster \((xyz = 4, 38, -15)\) and within the MTL, the local maxima of a cluster within
the entorhinal cortex \((xyz = 23, -15, -27)\). Activity from these two regions is presented
given they are core regions discussed in the context of the SLIMM framework.

Conversely, when turning to regions shown increases in activity as a function of
increasing recall for schema-incongruent pairs, we find several MTL regions including
the perirhinal cortex. Figure 11A contains the activity profile within the local maxima of
a perirhinal cluster \((xyz = 23, -11, -30)\). Noticeably absent was activity from the medial
PFC, which is consistent with SLIMM predictions but extends these findings to the
realm of cued recall.
Figure 10: Linear increases in neural activity corresponding to visual recall for the schema-congruent condition. (A) Local maxima of activation within the medial PFC located at x=4, y=38, z=-15. Bars reflect the parameter estimates for each level of the in-scan covert cued picture recall rating (1='Not Very Well', 2, 3, 4='Very Well'). Activity for the schema-incongruent condition is presented for comparison. (B) Local maxima of activation within the entorhinal cortex located at x=23, y=-15, z=-27. Bars reflect the parameter estimates for each level of the in-scan covert cued picture recall rating (1='Not Very Well', 2, 3, 4='Very Well'). Activity for the schema-incongruent condition is presented for comparison. Error bars denote standard error.
Neural correlates underlying perceptual components of visual recall. To identify the neural correlates underlying the visual recall of perceptual elements for schema-related content we conducted a 2 (congruency: congruent, incongruent) x 3 (perceptual recognition memory: Miss, Low/Medium Confidence Hits, High-Confidence Hits) repeated measures ANOVA. Within this framework, we proceed to search for interactions. To accomplish this we looked for opposing linear effects by assigning contrasting weights for increasing (e.g. Miss=1.5, LCH=0.5, HCH=1.5) and decreasing (e.g. Miss=1.5, LCH=0.5, HCH=1.5) levels of perceptual recognition memory. We first sought brain regions exhibiting a linear increase in perceptual recognition memory for schema-congruent and an opposite for schema-incongruent [(Congruent:
HCH>LCH>Miss) x (Incongruent: HCH<LCH<Miss)] pairs. We also examined the reverse interaction [(Congruent: Miss>LCH>HCH) x (Incongruent: Miss<LCH<HCH)].

Table 4 presents the regions found for the interactions that were setup within the ANOVA framework.

<table>
<thead>
<tr>
<th>Region</th>
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<th>MNI Coordinates</th>
<th>t</th>
<th>Voxels</th>
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<tr>
<td>(Congruent&gt;Incongruent) x (HCH&gt;LCH&gt;Miss) (whole-brain analysis)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>-</td>
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<td>-</td>
<td>-60 -49 -42</td>
<td>3.66</td>
<td>16</td>
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<td>-49 -53 49</td>
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</tr>
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<td>-4 -15 42</td>
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<tr>
<td></td>
<td>R</td>
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<td>56 -56 19</td>
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<td>4</td>
<td>30 -23</td>
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<td>-56 -64 19</td>
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<tr>
<td></td>
<td>L</td>
<td>22</td>
<td>-60 -56 19</td>
<td>3.03</td>
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<tr>
<td>-</td>
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<tr>
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<td>-4 41 19</td>
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</table>

(Incongruent>Congruent) x (HCH>LCH>Miss) (whole-brain analysis)

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<th>Region</th>
<th>Hem</th>
<th>BA</th>
<th>MNI Coordinates</th>
<th>t</th>
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<td>8 30 15</td>
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<tr>
<td></td>
<td>L</td>
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<td>-4 30 11</td>
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</tr>
<tr>
<td>Region</td>
<td>Side</td>
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<td>Y</td>
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</tr>
<tr>
<td>Anterior cingulate/medial frontal gyrus</td>
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<td>10,32</td>
<td>-15</td>
<td>41</td>
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</tr>
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</tr>
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<td>Inferior parietal lobule</td>
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<td>Precuneus</td>
<td>R</td>
<td>31</td>
<td>8</td>
<td>-49</td>
<td>38</td>
</tr>
</tbody>
</table>

Regions marked in bold are those we further examined to determine the precise patterns of activity displayed in Figure 12.

**Figure 12:** Congruency x perceptual recognition interactions. Linear increases in perceptual recognition for the schema-congruent condition and the reverse for the schema-incongruent condition. (A) Local maxima of activation within the medial PFC located at x=4, y=38, z=-19. (B) Bars reflect the parameter estimates for recognition performance on the perceptual recognition in medial PFC cluster. (C) Activation within a parahippocampal/hippocampal region located at x=38, y=-11, z=-15. (D) Bars reflect the parameter estimates for recognition performance on the perceptual
recognition test in parahippocampal/hippocampal cluster. Error bars denote standard error.

Whereas a ventral-orbital region of the medial PFC (Figure 12A/12B) exhibited an interaction for increasing perceptual recognition for schema-congruent content, activity in the parahippocampal gyrus/hippocampus (Figure 12C/12D) resulted from the reverse interaction setup (bottom-half of Table 4). These pattern of findings fits well with the SLIMM framework, which posits that the medial PFC supports retrieval of schema-congruent information whereas MTL sub-regions should support retrieval of schema-incongruent information.

Neural correlates underlying conceptual components of visual recall. For sake of completeness, we identified the neural correlates underlying the visual recall of conceptual elements for schema-related information. We conducted a 2 (congruency: congruent, incongruent) x 3 (conceptual recognition memory: Miss, Low/Medium Confidence Hits, High-Confidence Hits) repeated measures ANOVA. Similar to our previous analysis on perceptual components of visual recall, we examined two specific interactions: regions exhibiting increasing memory specific for schema-congruent or schema-incongruent conditions. Table 5 lists the regions resulting from these two interactions.
Table 5: Congruency x conceptual recognition interactions (whole-brain analysis). Up to three local maxima set 8mm apart are reported for each cluster. Regions reported reflect the nearest gray matter located to the peak cluster. R, right; L, left; BA, Brodmann area; Hem, hemisphere.

<table>
<thead>
<tr>
<th>Region</th>
<th>Hem</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
<th>Voxels</th>
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</thead>
<tbody>
<tr>
<td>Medial frontal gyrus</td>
<td>R</td>
<td>11</td>
<td>4</td>
<td>38</td>
<td>-19</td>
<td>3.25</td>
<td>8</td>
</tr>
<tr>
<td>Claustrum</td>
<td>R</td>
<td>-</td>
<td>38</td>
<td>-26</td>
<td>-4</td>
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<td>Postcentral gyrus</td>
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<td>40</td>
<td>68</td>
<td>-30</td>
<td>19</td>
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<td>8</td>
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<td>Fusiform gyrus</td>
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<td>23</td>
<td>2.97</td>
<td>9</td>
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<tr>
<td>Inferior parietal lobule</td>
<td>L</td>
<td>40</td>
<td>-60</td>
<td>-34</td>
<td>23</td>
<td>2.95</td>
<td>9</td>
</tr>
</tbody>
</table>

As expected from the SLIMM framework, activity in the medial PFC tracked successful conceptual recognition specific to schema-congruent conditions. Keeping in mind the pattern of findings from the previous analysis, the medial PFC was found to support perceptual and now conceptual components of visual recall. Interestingly, we found no activity in the MTL for the interaction emphasizing increases in schema-incongruent memory. An absence of MTL activity for schema-incongruent conditions differs from our previous finding and possibly suggests that memory for conceptual information, which is bound to a pre-existing schema, may rely more on the medial PFC than MTL. In fact, the SLIMM framework proposes that the MTL supports information that is unbound to a schema and thus may explain its absence in this analysis.
Neural correlates underlying conceptual-and-perceptual components of visual recall.

Lastly, to identify the neural correlates underlying joint, successful visual recall of conceptual-and-perceptual components of schema-related content, we conducted a repeated measures 2 (congruency: congruent, incongruent) x 4 (conceptual/perceptual recognition: MM, MH, HM, HH). We setup interactions to identify regions critical for either conceptual or perceptual recognition in schema-congruent and schema-incongruent conditions respectively. With respect to conceptual recognition, we found an interaction solely in the medial PFC (Figure 13A) driven by conceptual recognition memory in the schema-congruent condition relative to the schema-incongruent condition (Figure 13B). When examining the reverse interaction, we only found activity when using a very liberal threshold at p<0.05. With respect to perceptual recognition, we did not find any regions exhibiting an interaction with congruency either for schema-congruent or schema-incongruent conditions respectively.
Figure 13: Congruency x conceptual/perceptual recognition performance. Interaction driven by linear increases in conceptual and perceptual recognition performance for the schema-congruent relative to schema-incongruent condition. (A) Glass brain depicting whole-brain activation and the local maxima of activation within the medial PFC located at \(x=0, y=41, z=-19\). (B) Bars reflect the parameter estimates for joint recognition performance on both the conceptual and perceptual recognition tests. Error bars denote standard error.

4.4 Discussion

In the present study, we investigated the neural correlates underlying successful recall of information concordant (i.e. schema-congruent) or discordant (i.e. schema-incongruent) with previously acquired knowledge. Furthermore, we identified brain regions whose activity corresponded to the recall of either the conceptual or the perceptual components associated with schema-related content. To this end, our study had three main goals. Our first goal was to behaviorally assess the differential effects of stimulus congruency on the conceptual and perceptual components of schema-related
content. Our second goal was to investigate the neural correlates underlying successful recall of schema-congruent and schema-incongruent information. Lastly, our third goal was to investigate the neural correlates underlying the recall of conceptual and perceptual components of schema-congruent and incongruent information. We discuss each of these goals and our findings in sections that follow.

**Stimulus congruency effects on visual recall and associative recognition memory**

To address our first goal, we behaviorally examined the differential effects of stimulus congruency on visual recall and conceptual/perceptual associative recognition memory respectively. The effects of stimulus congruency on visual recall were assessed via the distribution of responses at every level of the cued recall rating scale. With respect to perceptual recognition performance, two differential patterns for schema-congruent and schema-incongruent encoding conditions emerged. A significant linear increase in the number of endorsed responses as a function of visual recall was found for schema-congruent pairs (**blue bars: Figure 7A**) and a non-significant linear function found for schema-incongruent pairs (**red bars: Figure 7A**). Hence, recall benefits were found for schema-congruent but not for schema-incongruent pairs. Although the behavioral evidence highlights inconsistent findings of schema-congruency enhancements on recall and recognition memory tests (Rojahn & Pettigrew, 1992), the
present findings are consistent with behavioral evidence finding schema-congruency enhancements for both tests of recall and recognition memory (Brewer & Treyens, 1981; Goodman, 1980). Additionally a more recent behavioral study finds that the recall of new definitions assigned to previously learned words is better when the new definitions are semantically related to definitions already learned, further suggestive of a semantic congruency enhancement on recall tests of memory (Rodd et al., 2012).

Turning to the differential stimulus congruency effects on conceptual and perceptual associative recognition, we examined the behavioral performance in the conceptual and perceptual recognition tests respectively. Paralleling the schema-congruency enhancement effect on visual recall, we see a similar schema-congruency enhancement for overall conceptual recognition performance (Figure 8A). Validating our in-scan visual recall ratings, we found that mean hit rate increased as a function of visual recall ratings for both schema-congruent and schema-incongruent conditions (Figure 8B). Given conceptual associative recognition is likely to rely on existing schemas as the associated information is critical to the schema (e.g. retrieving the scene concept); it is unsurprising we see such a robust schema-congruent enhancement effect on conceptual recognition.

Concerning perceptual recognition performance, while we do find significant differences in overall hit rate between schema-congruent and schema-incongruent encoding conditions (Figure 9A), the differences are far less than what was observed for
conceptual recognition. Validating our in-scan visual recall ratings, we found an increase in the mean hit rate as a function of visual recall ratings for both schema-congruent and schema-incongruent conditions (Figure 9B). These findings were surprising given the assumption shared by others (pg. 216, Van Kesteren et al., 2012) that memorial benefits conferred by schema-incongruent (relative to schema-congruent) stimulus relationships would arise when testing memory for information inherently unrelated to an existing schema. Given perceptual-recognition (e.g. picture of a graduation ceremony) is not a core component of the concept of ‘graduating’, memory would not rely on retrieval of schema-congruent information. We note here that several recent neuroimaging investigations examining memory for schema-congruent and schema-incongruent materials have failed to find memorial advantages for schema-incongruent relative to schema-congruent conditions (see Table 1: Bein et al., 2014; see Figure 2: Van Kesteren, Fernández, et al., 2010a; van Kesteren et al., 2010; see Figure 2: van Kesteren, Beul, Takashima, Henson, et al., 2013). In the present study, several unintended design factors may have shifted the memorial advantage to schema-congruent relationships. Before the scan session commenced, participants were informed that some of the relationships would be unrelated (i.e. incongruent), participants intentionally encoded materials potentially interfering with the evaluations of incongruent stimulus processing, participants interacted with elements of each congruent/incongruent pair up to five times: once during the object-assignment task,
once during the covert, visual recall task, once during the conceptual recognition test, once during the perceptual recognition test, and finally during the congruency-validity task. Lastly, post-test questionnaires revealed a tendency to overestimate the percentage of congruent pairs in the study; possibly reflective of a congruency bias that reflects how we operate in the environment (i.e. we encounter very few incongruous situations in our environment). Analysis of miss responses for the conceptual recognition test confirm a congruency bias as participants were more likely to select congruent lure distracters for both schema-congruent (50.1% congruent lure selection) and schema-incongruent conditions (76.7% congruent lure selection).

In short, the behavioral findings are consistent with behavioral evidence of a schema-congruent enhancement on cued recall and associative recognition tests of memory. Additionally, while we found a large schema-congruency enhancement for concept associative recognition, this was partly diminished when testing memory for information unbound to a schema (i.e. picture associative recognition). We next examine these effects in the brain.

**Differential stimulus congruency effects on the neural correlates of visual recall**

According to the schema-linked interactions between medial prefrontal-medial temporal lobe (SLIMM) framework, whereas the medial PFC is proposed to support
retrieval of schema-congruent information, sub-regions in the MTL support retrieval of schema-incongruent information (van Kesteren et al., 2012). Given the SLIMM framework is informed largely by neuroimaging studies devoid of a cued-recall component, we first employed a whole-brain analysis to identify brain regions tracking increases in visual recall. Increases in visual recall were indexed by ratings in the visual recall task on the 4-pt scale ranging from ‘Not Very Well’ to ‘Very Well’ (Figure 5C). Table 2 lists regions found for this analysis. Noteworthy are regions in the MTL (rhinal cortices, parahippocampal gyrus), posterior mid-line cortical regions (posterior cingulate) and in the medial PFC. This network of regions overlaps with the proposed “core recollection network” proposed to come online during retrieval of previously encoded materials (Rugg & Vilberg, 2013). Moreover, we found a group of regions, including the fusiform gyrus, precentral gyrus, superior frontal gyrus, and the precuneus, linked with subjective ratings of recollection associates (Spaniol et al., 2009). One can assume that participants provided subjective ratings of recall, which would make the present finding harmonious with existing findings.

Next, we identified regions whose activity increased with visual recall of previously schema-congruent or schema-incongruent pairs. With respect to the schema-congruent condition, we found regions in the MTL and, the medial PFC (Figure 10A/10B), whose activity tracked with increases in successful recall. Table 3 lists other regions found for this analysis. Whereas medial PFC was hypothesized given its role in
memory for schema-congruent information (e.g., van Kesteren, Fernández, et al., 2010; van Kesteren et al., 2010a), on the other hand, observing activity from MTL sub-regions for this analysis was unexpected. Complementing this analysis, we also identified regions whose activity increased with visual recall of previously schema-incongruent pairs. The bottom-half of Table 3 lists regions coming from this analysis. In accordance with predictions made by the SLIMM framework, we observed robust activity from several MTL sub-regions (Figure 11A) and a noticeable absence of activity from the medial PFC.

All together, when examining activity corresponding to increasing visual recall memory, we confirmed predictions made by the SLIMM framework. Specifically, we found increasing activity in the medial PFC for schema-congruent pairs as a function of increasing visual-recall ratings and conversely, we found increasing activity from MTL sub-regions for schema-incongruent pairs as a function of increasing visual-recall ratings. Inconsistent with the SLIMM framework, however, was the observation of MTL activity tracking visual recall for schema-congruent pairs. First, this finding could reflect a broader MTL contribution to visual recall irrespective of whether material is congruent or incongruent with preexisting knowledge structures. Second, given participants were aware that recall of the scene-picture would be tested, an unintended reduction in the potential differences between schema-congruent and schema-incongruent pairs may have resulted in similar neural activity profiles. Third, we cannot rule out with certainty
that during schema-incongruent conditions, participants covertly generated congruent object-labels further minimizing potential differences between schema-congruent and schema-incongruent conditions. Lastly, during the post-encoding phase (preceding the covert cued-visual recall task), the retrieval of schema-incongruent information may have resulted in the increasing congruency of these pairs thus evoking MTL activity for schema-congruent and schema-incongruent pairs.

**Neural correlates underlying perceptual components of visual recall**

To partly validate the in-scan visual recall rating, we administered a perceptual recognition test. Behavioral results revealed increases in the mean hit rates as a function of increasing visual recall for schema-congruent and schema-incongruent conditions (**Figure 9B**). To uncover the neural correlates underlying perceptual components of visual recall, we searched for interactions in the brain between perceptual recognition performance and stimulus congruency.

Perceptual recognition performance consisted of three levels: high confidence hits (HCH), low/medium confidence hits (Low/Med Hits) (‘Very Low’/’2’/’3’), and miss trials. Strikingly, when examining visual recall activity increasing as a function of perceptual recognition for schema-congruent conditions (and the opposite pattern for schema-incongruent conditions), we found activity from the local maxima of a cluster residing in the medial PFC (xyz =4, 38, -19) (**Figure 12A**) driven by HCH hits (**Figure**
When looking at the reserve interaction (i.e. Schema-Congruent: HCH<Low/Med Hits<Miss x Schema-Incongruent: HCH>Low/Med Hits>Miss) we found no activity in the medial PFC (bottom-half of Table 4) but did find activity in MTL sub-regions (Figure 12C) whose activity was driven for HCH trials in the schema-incongruent condition (Figure 12D). MTL activity found for schema-incongruent (but not schema-congruent) conditions fits well with predictions of the SLIMM framework and additionally, fits with assumptions that MTL activity supports memory for information that is unbound to a preexisting schema. In this case, memory for perceptual associates (e.g. graduation scene) is trivial to the schema of a graduation ceremony and thus may explain MTL activity for schema-incongruent content.

In addition to the medial PFC and MTL, Table 7 lists several other regions whose activity has been linked to semantic retrieval. An exhaustive meta-analysis of the semantic memory literature (Binder, Desai, Graves, & Conant, 2009) found a network of regions including the dorsal medial PFC, middle temporal gyrus, precuneus, and inferior parietal lobule which overlap with the regions we found for the reverse interaction. These regions are potentially crucial in the semantic processing and retrieval for schema-incongruent pairs. Additionally, the finding of activity in the anterior cingulate for the reverse interaction aligns well with its well-established role in conflict detection and monitoring (Botvinick, Cohen, & Carter, 2004; Botvinick, Nystrom, Fissell,
Carter, & Cohen, 1999) and potential role of this region in supporting episodic memory for incongruous stimulus relationships.

**Neural mechanisms underlying conceptual-and-perceptual components of visual recall**

Given our behavioral results revealed a consistent schema-congruency enhancement effect for both the conceptual and perceptual recognition tests, we wanted to identify brain regions that reflected conceptual-and-perceptual components of visual recall. As such, we constructed four trial types: MM, MH, HM, and HH, which characterized performance on the conceptual and perceptual recognition tests for schema-congruent and schema-incongruent conditions respectively. By employing such a setup, we identified regions supporting overall conceptual recognition (MM + MH < HM + HH) and overall perceptual recognition (MM + HM < MH + HH) and subsequent interactions. Of chief interest was the interaction of conceptual/perceptual recognition and stimulus congruency. Given our behavioral results revealed a consistent, significant schema-congruency enhancement effect, we predicted that the medial PFC would support conceptual-and-perceptual components of schema-congruent information. This prediction was also informed by findings that the medial PFC showed a congruency x conceptual recognition interaction (Table 5).

Indeed, an interaction between stimulus congruency and joint conceptual/perceptual components of visual recall revealed a ventral region in the
medial PFC (Figure 13A) whose activity was greater for conceptual/perceptual recognition for the schema-congruent condition compared with schema-incongruent condition (Figure 13B). Interestingly, we found medial PFC activity for conceptual components of visual recall specific to schema-congruent conditions regardless if perceptual components were retrieved (i.e. HH trial type) or not (i.e. HM trial type). A reverse interaction revealed no regions neither did similar analyses emphasizing perceptual recognition performance (i.e. MH and HH trials).

Medial PFC sensitivity to the conceptual relationships of existing schemas adds to a set of findings from the neuropsychological literature finding that patients with lesions to the ventral medial PFC present with difficulties in judging whether information is congruent/incongruent to a schema (Ghosh, Moscovitch, Melo Colella, & Gilboa, 2014) and commit fewer false alarms (relative to healthy controls) to related, unstudied items in a traditional false-memory paradigm (Spalding et al., 2015).

Complementary evidence from neuroimaging studies employing similar false-memory paradigms find greater activity in the medial PFC for conceptual false recognition (Garoff-Eaton, Kensinger, & Schacter, 2007) further suggestive of this regions role in the semantic processing and retrieval of congruous stimulus associations.

Finally, findings from another literature are in support of the medial PFC’s role in the evaluation of well-established stimulus associations characteristics of the schema-congruent encoding condition. Specifically, the medial PFC is proposed to support
evaluation of stimuli associated with rich environmental contexts, or stimuli associated with well-learned ‘context frames’ (Bar et al., 2007; Bar, 2004, 2007). In addition, while findings from the context frames literature provide little discussion regarding the mnemonic contributions of the medial PFC, they do suggest this region’s role in evaluating the context with which stimuli co-occur in our environment.

4.5 Study conclusion

Recent years have witnessed an increase in the number of neuroimaging and neuropsychological investigations of schema processing and memory. Chiefly implicated in supporting memory for schemas have been the medial PFC. Existing studies however have employed paradigms that have poor correspondence to the rodent studies of schema or to human neuroimaging studies of episodic memory. To address this, we employed an imaging paradigm with a cued-recall component to examine the neural correlates underlying visual recall for schema-congruent and schema-incongruent information. We report three findings. (1) Behaviorally, robust schema-congruency enhancements were found for tests of visual recall, conceptual, and perceptual associative recognition. (2) Medial PFC and MTL activity tracked increases in visual recall for schema-congruent pairs whereas MTL activity alone tracked increases in visual recall for schema-incongruent pairs. (3) Activity in the medial PFC, not the MTL, subserved conceptual recognition components of visual recall. Collectively, this finding
confirms a role for the medial PFC in recall of schema-congruent information and specifies its support of conceptual components of schema-related content.

5. General Discussion

If we revisited the thought experiment described at the opening of this document and subsequently re-administered the straw poll, it is the authors contention that the mini-review provided of the medial PFC contributions to human cognition along with findings presented from two empirical neuroimaging studies would convince researchers of a mnemonic role of the medial PFC. Specifically, what is becoming evident is an emerging role for the medial PFC in associative information processing and more recently, a role in associative recognition memory. The studies presented above confirm and extend this growing body of evidence. In the sections that follow, I proceed to discussing these findings as it relates to the existing literature, discuss the limitations of the presented studies and finally, propose some interesting avenues for future research inquiry.

5.1 A look back at our central questions

To elucidate the precise mnemonic contributions of the medial PFC, focus was placed on its potential role in supporting associative recognition memory. The decision to focus on associative recognition memory processes as opposed to item recognition memory was a consequence of choosing a memory form that we rely on a daily basis. As
agents navigating an increasingly complex environment, we do not regularly interact with other members of our species in isolation or in a controlled laboratory setting but rather engage with them in a stimulating environment, often across time and space dimensions. Hence, interrogating the brain regions supporting associative recognition memory would provide a study of the memory processes that we undergo in our daily social interactions. Underscoring this point, the mini-review provided above of medial PFC contributions to human cognition revealed a common role of this region in associative information processing. Findings from the domains of social cognition (Amodio & Frith, 2006), episodic memory (Johnson & Rugg, 2007; Rugg & Vilberg, 2013), and visual perception (Bar et al., 2007; Bar, 2004) commonly report increased medial PFC engagement during experimental conditions imposing demands on the evaluation of stimulus associations.

To address our broader goals, two studies were conducted and described in detail above in preceding sections. More specifically, Study 1 examined the following questions: (a) does the role of the medial PFC extend beyond its established role in supporting subsequent episodic item encoding and if so, (b) does its mnemonic support reflect memory quality characteristic of recollection-based recognition memory or familiarity-based recognition memory. Addressing these questions, medial PFC was found as a primary region supporting associative recognition memory for personal beliefs (presented as face-belief statement pairs) that in particular, strongly resonated
with participant belief systems and furthermore, this recognition memory was associated with very high confidence ratings typical of recollection-based recognition memory. In short, this study provided evidence that medial PFC can indeed support associative recognition memory of stimuli embedded in our daily interactions.

Study 1 provided evidence of medial PFC support of associative recognition during encoding. Additionally, this study used rich, ecologically valid stimuli and experimental instructions that mirrored participant’s interactions in everyday life. Study 2 attempted to extend these findings by employing stimuli more amenable to laboratory conditions, determining the mnemonic role of the medial PFC during retrieval memorial phases, and finally for a different kind of associative stimulus processing. To this end, Study 2 addressed the following questions: (a) What are the neural correlates underlying successful memories for schema-congruent and schema-incongruent information, (b) Does the use of a cued-recall memory test corroborate previous findings using recognition memory tests, and (c) whether medial PFC activity supported specific forms of associative recognition mainly conceptual versus perceptual. Addressing these questions, we found medial PFC activity supporting memory for schema-congruent but not schema-incongruent content, we corroborated existing evidence of schema-congruent memory support in a cued-recall paradigm, which paralleled paradigms commonly used in the rodent and human neuroimaging literatures and finally, provided evidence that the medial PFC supports conceptual associative recognition.
Collectively these findings have helped advance our understanding of medial PFC function but there were some limitations to the experimental paradigms addressed in the following section.

### 5.2 Limitations of the presented studies

Although study 1 and study 2 contribute to the literature in meaningful ways, I acknowledge limitations to the experimental designs employed by both studies. It is the belief of the author that if future investigations address these limitations, they will consequently enhance the contributions of the findings (reviewed above) to the literature linking episodic memory and the medial PFC.

Concerning study 1, one of the biggest design limitations is the absence of a control experimental condition consisting of stimuli non-social (e.g. objects, abstract/meaningless shapes) in nature. *First*, having a condition of non-social stimuli while requiring participants to making judgments complementary to strong agree/strong disagree (e.g. aesthetically pleasing/displeasing) would allow for analyses determine whether the medial PFC is preferentially supports associative recognition of stimuli of social-relevance. Similar design conditions have been used elsewhere (Mitchell, Banaji, et al., 2005; Mitchell et al., 2005) in studies of social cognition and self-referential processing. *Second*, another design feature we could have incorporated would be to present conditions requiring a perceptual judgment (e.g. judging font type). Such a design feature, incorporated by other neuroimaging studies (Gozzi et al., 2010; Krueger
et al., 2007), would serve as a baseline control task and allow us to first identify regions critical for evaluation of social stimuli and then search within these regions for associative recognition memory interactions. I note here, however, that belief-statements were presented that endorsed neither liberal-nor-conservative political stances nor thus serving as controls. 

*Third*, given activity in the default-mode network tends to increase during task-irrelevant conditions (Buckner et al., 2008) such as baseline phases of a task, employing an active baseline task may prevent below-baseline activity in these regions. Additionally, by using an active baseline task (arrows/even-odd) may have inhibited inter-trial rehearsal of face-belief statement pairs during the encoding phase of the task. 

*Fourth*, given the political demography of our participant pool, the majority of our scanned participants were self-described liberals. As such, we could not conduct a similar analysis of Mitchell and colleagues (2006) (Mitchell, Macrae, & Banaji, 2006) in finding differential medial PFC activity as a consequence of political similarity/dissimilarity. 

Turning to study 2, *first*, the primary design limitation was the inability to examine the neural correlates underlying memorial advantages from schema-incongruent information. Failure to find a memorial advantage for schema-incongruent information is however commonplace in neuroimaging studies of schemas (e.g., van Kesteren, Fernández, et al., 2010b; van Kesteren et al., 2013). Some have posited enhancements from schema-incongruent encoding when testing recognition memory for
information irrelevant to a preexisting schema (pg. 216, van Kesteren et al., 2012). To test this postulation, we tested memory for information (picture associative recognition and source memory for object location placements) unbound to a schema. With respect to perceptual recognition, we did not find schema-incongruent enhancements (Figure 9A) and with respect to source memory for object locations, we found on average, below chance performance in scanned participants (mean location source-memory performance: 23.3%) inhibiting analysis of this memory type. Thus, we could not test schema-incongruent memory enhancements and there instantiation in the brain. Second, we did not collect eye movements during the object-assignment task (Figure 5A) of the study. Eye movements have been found to be an objective measure of episodic memory (Hannula & Ranganath, 2009; Hannula et al., 2010). Additionally, we could examine encoding-retrieval relationships as indexed by recorded eye movements. Third, another design limitation contributing to an inability to examine schema-incongruent memory enhancements could have arisen from the short delay between encoding and retrieval memory phases. Available behavioral evidence suggests that the differences between schema-congruent and schema-incongruent conditions for associative recognition memory performance decreases with increasing time between encoding and retrieval phases (van Kesteren, Rijpkema, et al., 2013). As such, imposing a greater delay may have permitted us to examine the neural bases of schema-incongruent memory enhancements.
5.3 **Putting the current findings in ‘context’**

In the sections below, we provide a discussion of how the study findings presented above fit specifically into the cognitive neuroscience of episodic memory literature. Focus is placed on this literature given the study goals.

5.3.1 **Expanding the scope of the canonical medial temporal lobe memory system**

Hitherto, the lion’s share of neuroimaging studies on episodic memory processes have focused on contributions made by MTL sub-regions (e.g. hippocampus along with rhinal and parahippocampal cortices). This is not without merit given the wealth of lesion and neuropsychological consistently implicating these MTL sub-regions in supporting recognition memory. In fact, the preponderance of evidence have led some researchers to boldly postulate that these MTL sub-regions form a “medial temporal lobe memory system”, working in concert to uniformly support recognition memory processes (Squire et al., 2004; Squire & Zola-Morgan, 1991). Other researchers have taken issue with this proposal and have argued that the MTL is not a monolithic set of regions but are divided based on differential contributions made towards recollection (i.e. contextual/associative) and familiarity (i.e. acontextual/item) recognition memory (Eichenbaum et al., 2007).

While debate persists as to the precise role of the MTL in supporting recognition memory, regions outside the MTL are found to support recognition memory. For
example, within the parietal cortex, the ventral parietal cortices are shown to support episodic recollection whereas dorsal parietal cortices support episodic familiarity (Cabeza, 2008). Another brain area with an increasingly acknowledged role in episodic memory has been the medial PFC. Despite large-scale meta-analyses reporting this region in episodic memory studies (Cabeza & Nyberg, 2000; Spaniol et al., 2009), its role is rarely-if-ever discussed in these articles. This is potentially due to few studies at the time these meta-analyses were published that reported medial PFC activity corresponding to either episodic recollection and/or familiarity. The landscape however has transformed, with proposals that the medial PFC is a component of a recollection network (Rugg & Vilberg, 2013), engaged in autobiographical memory retrieval (Cabeza & St Jacques, 2007), in recollection of stimuli evaluated in a self-referential manner (Leshikar & Duarte, 2012), in contextual processing of schema-related content (Bar, 2004; Ghosh et al., 2014), and in memory for schema-related content (van Kesteren et al., 2012).

The studies presented in this document add to this body of evidence by showing medial PFC engagement in support of associative recognition memory for two sets of associations: face-belief statement pairs and object-scene-picture pairs. These two associations differ in their elemental composition, the extent to which they mirror everyday social interactions, and the phases with which these associations were retrieved. Interestingly, across studies we found medial PFC engagement during subsequent memory and successful recall of associations confirming its contributions to
successful episodic memory during two different memorial phases. Signaling an increasing role of the medial PFC in supporting episodic memory, recent reviews have begun to specifically address the type and quality of memories supported by this region (Moscovitch et al., 2016).

5.3.2 Is there a domain-general cognitive function of the medial PFC?

Consistent across many of the experimental paradigms reviewed above is reports of medial PFC activity during conditions which demand associative information processing. For example, within self-referential paradigms, evaluating the associations of elements comprising the self (e.g. personal experiences, thoughts, and feelings) is critical to accurately judging traits as either self-relevant or self-irrelevant. Within judgment and decision-making paradigms, across studies, medial PFC activity tracks increases between associations of stimulus value and subsequent reward (O’Doherty, 2004). Turning to the visual-perception domain, ventral areas of the medial PFC are recruited during perception of objects associated with highly co-occurring environmental contexts compared with objects associated with infrequently co-occurring environmental contexts (Bar, 2004). Though little time was devoted to discussing future-thinking and/or imagining the future, the medial PFC is thought to support the ability to imagine the future (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007). Specifically, events that are yet to occur are thought to rely on an association of similar sets of previously experienced events to compute an expectation of
the yet to be encountered event. The neuroimaging studies discussed in this document build on these separate literatures. By finding medial PFC recruitment for conditions (across both studies) linked to a strong previously learned context or conditions where beliefs strongly resonated with personal belief systems, we confirm a potentially domain-general role of the medial PFC in associative information processing. Indeed, similar ideas has been echoed by others who have postulated that ventral areas of the medial PFC serve as a ‘convergence zone’ for these associations (Damasio, 1996).

5.4 Areas for future research inquiry

Given the medial PFC resides at the nexus of social cognition and episodic memory, we sit at a particularly ripe time for future research investigations examining its role in human cognition. This is evident in theoretical proposals unifying medial PFC findings from domains of memory and decision-making tasks (Euston, Gruber, & McNaughton, 2012), domains of future planning and memory (Schacter et al., 2012), and domains of episodic memory and conceptual knowledge (van Kesteren et al., 2012). Common to these theoretical proposals are attempts to identify a domain-general role of the medial PFC. While an increasing number of researchers are acknowledging a role for the medial PFC in episodic memory, much work is required to determine the conditions under which the medial PFC is preferentially engaged in the service of memory. In the sections that follow, a few interesting lines of future research inquiry are provided.
5.4.1 Does the medial PFC ‘care’ about non-social stimuli or non-social orienting tasks?

The findings discussed in the mini-review of medial PFC make it evident that experimental paradigms emphasizing stimulus evaluation along social reliably engage the medial PFC. More specifically; a social aspect of medial PFC function is supported by neuroimaging studies comparing activity evoked by the same encoding task but for social and non-social stimuli (Mitchell, Heatherton, & Macrae, 2002) or when comparing activity for social (e.g. impression formation) versus non-social (e.g. sequence order) encoding tasks (Mitchell, 2004).

Recent evidence in the self-referential literature has found medial PFC activity supporting associative recognition memory for objects when assigned to the participant as opposed to an unfamiliar, other individual (Kim & Johnson, 2012). Astonishingly, simply informing that a presented object belonged to the participants (as opposed to another) evoked medial PFC activity and in-turn led to both item and associative recognition memory enhancements in the self-own condition. Within the schema-processing domain, a recent neuroimaging study presenting abstract, fribble-like stimuli found medial PFC recruitment during the memory of schema-congruent pairs relative to schema-incongruent pairs (Brod, Lindenberger, Werkle-Bergner, & Shing, 2015).

Together, this preliminary set of studies provide initial clues as to a potential role of the medial PFC engagement in tasks that extend beyond the traditionally used social
stimuli and social orienting tasks. Future studies will have to examine how the medial
PFC supports associative information processing and memory for non-social stimuli.

5.4.2 Differential functional contributions of ventral-and-dorsal medial
PFC

Thus far, little discussion has been devoted to the differential functional
contributions of medial PFC sub-regions primarily ventral versus dorsal medial PFC. A
ventral/dorsal functional divide is evident when examining the anatomical/functional
connectivity of the medial PFC in addition to examining findings from the domains of
self-referential processing and autobiographical memory retrieval.

Anatomical connectivity as indexed by white matter fiber pathways reveal a
traditional fiber system, the uncinate fasciculus, connecting regions in the ventral medial
PFC with MTL sub-regions (Schmahmann et al., 2007). This is paralleled in functional
connectivity studies finding ventral medial PFC connectivity with MTL sub-regions
comprising an MTL memory subsystem whereas the dorsal medial PFC is connected to
regions including the temporoparietal junction and lateral temporal regions (Andrews-
Hanna et al., 2010).

Functional neuroimaging findings provide support for a ventral/dorsal
functional division. In the self-referential processing domain, the ventral medial PFC
supports stimulus processing that is self-relevant whereas the dorsal medial PFC
supports stimulus processing that is other-relevant. This is mirrored in the
autobiographical memory literature with findings of the ventral medial PFC engaged
more for self-versus-other memory retrieval. Additionally, the imaging studies presented in this document find ventral areas of the medial PFC supporting associative recognition of personal beliefs and for recall and associative recognition of schema-congruent information. Both studies emphasized self-relevant stimulus processing to arrive at decisions and thus findings across both studies of ventral medial PFC activity supporting memory fits well with previous evidence finding ventral/dorsal medial PFC functional divisions.

Given the dorsal medial PFC is activated for inferring the beliefs of others, future research can determine its potential role in schema processing by crossing self-referential processing with stimulus congruency. Specifically they can instruct participants to judge whether other persons from other cultures would find certain stimuli congruent/incongruent and assess whether the dorsal medial PFC can support schema-congruent information when evaluated in reference to another individual.

5.4.3 Age-related influences on processing and memory of schema-related content

The extent to which the healthy aging process affects the medial PFC support of associative recognition memory for schema-congruent information is an interesting and yet unexplored research problem.

On one hand, there is evidence that semantic memory (i.e. knowledge of the real world) is well-preserved across the lifespan (Hedden & Gabrieli, 2004). This is supported by behavioral studies in older adults showing an increased reliance on...
schema-related information when compared with younger adults (e.g. Hess & Slaughter, 1990; Hess, 1985). Moreover, studies of episodic memory with younger and older adult participants have reported the ability of older adults to perform as well as younger adult participants on episodic memory tasks when encoding conditions encourage elaborative encoding (e.g. stimulus judging whether stimuli are pleasant/unpleasant) relative to ‘impoverished’ encoding strategies (e.g. judging whether stimuli are bigger/smaller than shoebox) (e.g. Kirchhoff, Anderson, Barch, & Jacoby, 2012; Kuo, Liu, Ting, & Chan, 2014).

While evidence is scant, previous findings have reported minimal differences in medial PFC activity between younger and older adults for item recognition of information encoded in a ‘self-referential’ manner compared with information encoded in an ‘other-referential’ manner (Gutchess, Kensinger, & Schacter, 2007). Interestingly, another study employing the same paradigm found a similar pattern of findings when testing for associative recognition memory (Leshikar, Duarte, 2014). Furthermore, this pattern extends to a non-mnemonic task wherein older and younger adults made either social or non-social judgments (Cassidy, Shih, Joanne, Gutchess, 2012). These findings are also supported by volumetric studies of cortical thickness showing little-to-no age-related thinning of the medial PFC in comparison to either the lateral or parietal cortical areas (Salat, 2004).
While evidence reviewed thus far would predict no age-related differences in medial PFC activity for associative recognition of schema-congruent information, studies have found age-related differences in medial PFC activity during self-referential tasks (Gutchess, Kensinger, & Schacter, 2010) and overall age-related declines in medial PFC contribution to social judgments made during mentalizing tasks (Moran, Jolly, & Mitchell, 2012). Given inconsistent evidence exists in the neuroimaging of cognitive aging literature of either a similar or dissimilar role of the medial PFC in supporting associative recognition memory, future studies are required to adjudicate between these two conflicting sets of evidence. Whether an over-reliance on schema-congruent information will lead to increases in medial PFC activity (as compared to younger adults) is an interesting question.

5.4.4 Encoding-retrieval similarity in the medial prefrontal cortex

Neuroimaging studies of episodic memory have begun to examine the relationships between the initial encoding experience and retrieval of previously encountered events. This is achieved by examining the patterns of neural similarity between these two memorial phases. Taking advantage of novel techniques primarily representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008), studies have identified brain regions tracking retrieval of previously encoded material at the trial-level (Staresina et al., 2012; Wing et al., 2015) by measuring the neural similarity between encoding retrieval (i.e. ERS: encoding-retrieval similarity). Employing such an ERS
analysis for the medial PFC would provide definitive proof of its role in episodic memory processes.

Study 2, which uses a cued recall paradigm similar to the investigations using ERS (Staresina et al., 2012; Wing et al., 2015) and thus provides an opportunity to identify whether regions within the medial PFC would index the neural similarity between encoding and retrieval as it relates to successful recall of for schema-congruent contents. An ERS analysis would also help adjudicate whether the medial PFC is critical for remote versus recent memories. In the schema framework, recent memories would correspond to schema-incongruent content whereas remote memories would correspond to schema-congruent content. In showing medial PFC can support remote memories, it would complement a study using multivariate pattern analysis that found ventral areas of the medial PFC support remote memory retrieval (Bonnici et al., 2012) and additionally confirm the multiple trace theory of consolidation (Moscovitch et al., 2016; Nadel et al., 2000; Nadel & Moscovitch, 1997). A recent study using representational similarity analysis comparing whether the medial PFC codes for the social or valence dimensions of picture stimuli found greater similarity in the social dimension (Chavez & Heatherton, 2014) providing an opening to understanding how the medial PFC can support memory via evaluation of the social stimulus dimensions.
General Conclusions

Although the medial PFC is canonically linked to processes undergirding social cognition, emerging evidence indicates its role extends to other cognitive domains including episodic memory.

To examine this emergent role, over two studies, behavioral and neuroimaging measures revealed a role of the medial PFC in supporting associative recognition memory processes. This generalized for evaluation and later retention of stimulus associations that are omni-present in our daily social lives and for stimulus associations that characterize our knowledge of the real-world concepts. Interestingly, medial PFC activity was preferentially activated during experimental conditions that were deemed too strongly resonate with personal belief systems or subjective conceptions of the world. This strong resonance led to memorial benefits mediated by the medial PFC suggestive of a potential downstream benefit this region may have in supporting memory for stimulus associations.

Collectively, these findings add to a growing body of evidence from the self-referential and emerging schema literatures that the medial PFC can support associative recognition memory. Furthermore, the medial PFC was found to support concept associative recognition adding to neuroimaging and neuropsychological evidence suggesting its sensitivity to the conceptual relationships between stimuli. Moreover, these findings suggest a potential role for the medial PFC in supporting associative
information processing that is potentially deployed in the service of task demands that are mnemonic in nature.

Ultimately, the studies described above should provoke future research inquiry of the mnemonic roles of the medial PFC that extend beyond its role in social cognition.
### Appendix A

<table>
<thead>
<tr>
<th>Original viewpoint socio-political belief statements</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Believes the government should provide housing for everyone in need.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks marijuana should be legalized for recreational use.</td>
<td>L</td>
</tr>
<tr>
<td>Believes everybody should pay high taxes for extensive social welfare.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks all U.S. forces should be removed from Afghanistan.</td>
<td>L</td>
</tr>
<tr>
<td>Believes Obama is doing a great job as president.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks pornography should be legal for the adult population.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the U.S. should advance human rights in other countries.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks the government should invest more in scientific research.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks America has become too conservative.</td>
<td>L</td>
</tr>
<tr>
<td>Believes social security should be protected at all costs.</td>
<td>L</td>
</tr>
<tr>
<td>Supports reform to introduce universal healthcare in the U.S.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks corporations cannot be trusted to voluntarily protect the environment.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the U.S. should elect a woman president.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks Hispanic Americans should get jobs without discrimination.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks the Muslim faith is misunderstood in America.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks we should encourage communal ownership of property.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks our civil liberties are being violated in the name of counter-terrorism.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks U.S. should increase taxes for rich people.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes the government should invest more in education.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks African American children should get more scholarships.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes that same sex couples should be allowed to adopt children.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the U.S. should welcome immigrants from around the world.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks gays and lesbians should be able to get legally married.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes we should penalize businesses that mislead the public.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes the decision to go to war is never justified.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks Jews should have more influence on American politics</td>
<td>Z</td>
</tr>
<tr>
<td>Supports the building of an Islamic community center at Ground Zero.</td>
<td>L</td>
</tr>
<tr>
<td>Believes the U.S. should prohibit the death penalty.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks America is still a very racist nation.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks African Americans should have more influence on American politics</td>
<td>Z</td>
</tr>
<tr>
<td>Believes politicians should speak out against homosexuality.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks religious leaders should influence people’s votes.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks good parents sometimes need to spank their children.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes all Americans should be permitted to carry guns.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks the U.S. has too many immigrants.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks people are too open about sex these days.</td>
<td>PC</td>
</tr>
<tr>
<td>Belief</td>
<td>Group</td>
</tr>
<tr>
<td>----------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>Thinks that reports about global warming have been exaggerated.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks citizens should support candidates of the same race.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes our government must maintain strong military forces.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks everyone needs to accept his or her place within society.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes that no one is born gay.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes the law should strictly control immigration.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks government employees are overpaid.</td>
<td>L</td>
</tr>
<tr>
<td>Believes abortion should only be performed when a woman's life is threatened.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes the government should invest more in defense.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks tax dollars should not be used to support the arts.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks everybody should oppose teaching evolutionary theory.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports the Tea Party movement.</td>
<td>L</td>
</tr>
<tr>
<td>Believes the lowering the national debt is essential.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks most people on welfare are abusing the system.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks racial profiling is sometimes necessary.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks that mothers may have careers, but their first duty is to be homemakers.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes religious values should be taught in schools.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks Americans should vote based on self-interest.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks Medicaid is a drain on the taxpayers.</td>
<td>L</td>
</tr>
<tr>
<td>Believes the country should fear Muslims.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks that sex outside marriage is usually immoral.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes different sorts of people should keep to their own kind.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the law should limit experiments with human embryos.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports U.S. military interventions in other countries.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks the U.S. should support creation of a Palestinian state.</td>
<td>L</td>
</tr>
<tr>
<td>Believes terminal patients should have the right to die.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes people should have the right to kill in self-defense.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks elected officials are diligent public servants.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks Washington is run by special interests.</td>
<td>L</td>
</tr>
<tr>
<td>Believes astrology accurately explains many things.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes you cannot be moral without being religious.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the use of torture with terror suspects is sometimes justified.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes some races are superior to others.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes we should always support our government, even when it is wrong.</td>
<td>PC</td>
</tr>
<tr>
<td>Supports the U.S. troops in Iraq and Afghanistan.</td>
<td>L</td>
</tr>
<tr>
<td>Believes the U.S. should bring democracy to other nations.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks military action that defies international law is sometimes justified.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks officials in Washington are out of touch with the people.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks the U.S. should support the pro-democracy movement in China.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks nuclear energy is too dangerous to pursue.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes young people should care more about politics.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks Republicans and Democrats can work together effectively.</td>
<td>L</td>
</tr>
<tr>
<td>Supports federally funded school voucher programs.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks the U.S. should use military force in Iran.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks it is a waste of time to try to rehabilitate some criminals.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes people are ultimately divided more by class than by nationality.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the U.S. should use nuclear weapons again.</td>
<td>Z</td>
</tr>
<tr>
<td>Is no longer proud to be called an American.</td>
<td>L</td>
</tr>
<tr>
<td>Believes America is the best country in the world.</td>
<td>L</td>
</tr>
<tr>
<td>Believes all people should have the right to participate in strikes.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks the U.S. is too dependent on foreign oil.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks the U.S. should use military force against Palestinians.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports campaign finance reform.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks the U.S. should support dissidents in dictatorial countries.</td>
<td>Z</td>
</tr>
</tbody>
</table>

**Companion counter-viewpoint socio-political belief statements**

<p>| Thinks homeless people should not receive federal assistance. | Z |
| Thinks that smoking pot is a crime that warrants punishment. | L |
| Thinks tax dollars should not be spent on programs for the poor. | Z |
| Believes we need to increase the number of troops in the Middle East. | L |
| Thinks Obama should not be re-elected for a second term. | L |
| Believes pornographic material should be banned from the internet. | PC |
| Believes the U.S. should avoid involvement in international debates on civil rights. | Z |
| Believes the U.S. spends too much money on research in the sciences. | Z |
| Believes liberal politics are harming America. | L |
| Believes social security should be abolished. | L |
| Thinks that health care reform is not needed. | L |
| Believes most companies support limits on carbon emissions. | PC |
| Believes women should not hold high political offices. | Z |
| Thinks job discrimination based on race is sometimes justifiable. | Z |
| Thinks most American respect the Muslim faith as much as any other religion. | L |
| Thinks protection of private property is essential. | L |
| Believes preservation of national security justifies violations of privacy. | PC |
| Believes tax cuts for the wealthy would jumpstart the economy. | Z |
| Thinks school budgets need to be cut. | Z |
| Believes affirmative action should be abolished. | Z |
| Thinks gays and lesbians do not make good parents. | PC |
| Believes the U.S. should only accept immigrants from select nations. | L |
| Believes marriage is a sacred union between one man and one woman. | Z |</p>
<table>
<thead>
<tr>
<th>Statement</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thinks it is sometimes ok for corporations to lie to protect investors.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks war is sometimes the only option.</td>
<td>L</td>
</tr>
<tr>
<td>Believes all religious faiths have equal influence on politics in the U.S.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks that Islam is to blame for the tragedy on September 11, 2001.</td>
<td>L</td>
</tr>
<tr>
<td>Believes threat of the death penalty helps prevent crime.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes there is very little racial discrimination in the U.S.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks African American sufficiently represented in Washington.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes we need more openly gay political leaders.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes religion should play no part in politics.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes corporal punishment is always wrong.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks more strict gun control laws are needed.</td>
<td>L</td>
</tr>
<tr>
<td>Believes new immigrants contribute greatly to American society.</td>
<td>L</td>
</tr>
<tr>
<td>Believes people should be more comfortable talking about sex.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks global warming is a major concern for our environment.</td>
<td>L</td>
</tr>
<tr>
<td>Believes you should vote for the best candidate, regardless of race or religion.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks the size of the U.S. military should be reduced.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes everyone has the potential to be successful.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks there is probably a genetic basis for homosexuality.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks U.S. immigration laws are too stringent.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes federal employees deserve substantial salaries and benefits.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks is important to support the Pro Choice movement.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks too many tax dollars are spent on defense.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports increased federal funding for the visual and dramatic arts.</td>
<td>L</td>
</tr>
<tr>
<td>Believes all children need to understand the science of evolution.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks Tea Party Republicans are disrupting progress in congress.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks maintaining federal programs is more important than deficit reduction.</td>
<td>L</td>
</tr>
<tr>
<td>Believes most unemployed people would rather work than receive a handout.</td>
<td>L</td>
</tr>
<tr>
<td>Believes a person’s race should never be considered during security screenings.</td>
<td>L</td>
</tr>
<tr>
<td>Believes mothers and fathers should share childcare duties equally.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks it is important that public schools remain secular.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks Americans should vote with their communities in mind.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports federal assistance for people who cannot afford healthcare.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks the U.S. needs to increase support for Muslim Americans.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes there is nothing wrong with casual sex between consenting adults.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks it’s important to interact with people from different cultures.</td>
<td>PC</td>
</tr>
<tr>
<td>Supports increased funding for stem cell research.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks America should not intervene in wars in other nations.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes the U.S. must protect the state of Israel.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks assisting a suicide is a criminal offense.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks killing another human is always wrong.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes many politicians don’t truly care about their constituents.</td>
<td>L</td>
</tr>
<tr>
<td>---------------------------------------------------------------</td>
<td>----</td>
</tr>
<tr>
<td>Believes the presence of industry lobbyists in Washington is appropriate.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks we can only believe in what we can see, hear or touch.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks many religious leaders are corrupt.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes physical abuse during interrogations is never acceptable.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks people of all colors should be treated the same.</td>
<td>PC</td>
</tr>
<tr>
<td>Thinks civil disobedience can be patriotic.</td>
<td>PC</td>
</tr>
<tr>
<td>Opposes the presence American soldiers overseas.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks democracy cannot work in every country.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes the U.S. should always act in compliance with the United Nations.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes most politicians work to improve the daily lives of Americans.</td>
<td>L</td>
</tr>
<tr>
<td>Believes human rights violations in other countries should be overlooked.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes nuclear power may hold the answer to our energy crisis.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks most college students are well informed on international affairs.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes the two party system is doomed to failure.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks charter schools are harming America's public school system.</td>
<td>L</td>
</tr>
<tr>
<td>Believes the U.S. should refrain from additional military involvement in the Middle East.</td>
<td>Z</td>
</tr>
<tr>
<td>Supports education and job training for those in prison.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes people from different countries usually have different fundamental values.</td>
<td>PC</td>
</tr>
<tr>
<td>Believe the use of the atom bomb was a horrible mistake.</td>
<td>Z</td>
</tr>
<tr>
<td>Thinks all U.S. citizens should feel patriotic.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks it would be better to live in another country.</td>
<td>L</td>
</tr>
<tr>
<td>Thinks unions are detrimental to the workforce as a whole.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes the American government controls the world's oil supply.</td>
<td>L</td>
</tr>
<tr>
<td>Supports the Palestinian cause in the Gaza.</td>
<td>Z</td>
</tr>
<tr>
<td>Believes campaign donations do not influence politician’s actions.</td>
<td>PC</td>
</tr>
<tr>
<td>Believes America should try to oust dictators of other nations.</td>
<td>Z</td>
</tr>
</tbody>
</table>
References


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Biography

Vijeth Iyengar was born in Baton Rouge, Louisiana on October 4, 1987. In 2005, he matriculated to Tulane University in New Orleans, Louisiana. His first semester in college however, was spent at Cornell University due to the impact of Hurricane Katrina on the city of New Orleans. During his time at Tulane, he completed summer internships at the National Institute for Neurological Disorders & Stroke and the Louisiana Department of Health and Hospitals. In 2009, he completed his Bachelors of Science degree from Tulane University majoring in Cell and Molecular Biology. In 2010, he joined the psychology and neuroscience department at Duke University. Vijeth obtained his MA in psychology from Duke University in 2013. He is the recipient of a National Science Foundation Graduate Research Fellowship (supporting the first study) and named a 2016 finalist in the Presidential Management Fellows program in the science, technology, engineering, and mathematics track.