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An integrative memory model of recollection and familiarity to understand memory deficits

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Abstract

Humans can recollect past events in details (recollection) and/or know that an object, person, or place has been encountered before (familiarity). During the last two decades, there has been intense debate about how recollection and familiarity are organized in the brain. Here, we propose an integrative memory model which describes the distributed and interactive neurocognitive architecture of representations and operations underlying recollection and familiarity. In this architecture, the subjective experience of recollection and familiarity arises from the interaction between core systems (storing particular kinds of representations shaped by specific computational mechanisms) and an attribution system. By integrating principles from current theoretical views about memory functioning, we provide a testable framework to refine the prediction of deficient versus preserved mechanisms in memory-impaired populations. The case of Alzheimer's disease (AD) is considered as an example because it entails progressive lesions starting with limited damage to core systems before invading step-by-step most parts of the model-related network. We suggest a chronological scheme of cognitive impairments along the course of AD, where the inaugurating deficit would relate early neurodegeneration of the perirhinal/anterolateral entorhinal cortex to impaired familiarity for items that need to be discriminated as viewpoint-invariant conjunctive entities. The integrative memory model can guide future neuropsychological and neuroimaging studies aiming to understand how such a network allows humans to remember past events, to project into the future, and possibly also to share experiences.

1. Introduction

Episodic memory allows us to remember objects and people that we have encountered as well as details about events that we have personally experienced. It gives us awareness of our past experience, it is crucial to a smooth functioning in our daily life, and it permits that we mentally project what might subsequently happen on the basis of our past memories (Tulving 1999). Unfortunately, episodic memory is fragile and can be disrupted by certain conditions. Some people experience memory impairments (amnesia) suddenly after an acute brain damage. Others experience a progressive memory decline because of a neurodegenerative pathology such as Alzheimer's disease (AD).

The understanding of episodic memory mechanisms and how they are implemented in the brain has progressed extensively thanks to research in neuropsychology and neuroimaging. Current theories posit that episodic memories can be retrieved via two processes: *recollection*, which designates the recall of the specific details from the initial experience of the events, including details about the spatiotemporal context, and *familiarity*, which refers to knowing that one has experienced something in the past without recalling details about the encoding episode (Mandler 1980; Tulving 1985; Yonelinas 1994).

In the following sections of this target article, we first define the processes of recollection and familiarity in psychological terms (sect. 2). Then, we summarize the current most influential frameworks that describe their neural substrates. The existing frameworks differ by their focus on cognitive operations versus type of representations, by the emphasis on a

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specific brain region versus neural systems, and by the assumption that recollection and familiarity processes are either localized to a brain region or not localized (section 2). Next, we consider how a more complete understanding of recollection and familiarity would benefit from combining different accounts into a unified framework that bridges several cognitive and neural mechanisms (sect. 3). Therefore, we propose an integration of principles, currently pertaining to separate theories, in a neurocognitive architecture of interacting operations and representations within large-scale cerebral networks that allow familiarity and recollection (sects. 4 and 5). Such an integrative perspective allows us to generate new hypotheses about the nature of memory deficits in brain-lesioned populations and neurodegenerative diseases. Section 6 thus presents predictions about recollection and familiarity deficits in memory-impaired populations, with a detailed illustration on AD.

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2. Recollection and familiarity

In psychological terms, recollection is defined as a retrieval process whereby individuals recall detailed qualitative information about studied events (Montaldi & Mayes 2010; Yonelinas et al. 2010). Some authors consider that there is recollection as soon as one retrieves at least one detail that is not currently perceived, inducing moderate to high confidence that the event actually occurred (Higham & Vokey 2004; Yonelinas et al. 2010), but the amount of details may vary from one trial to the other (Higham & Vokey 2004; Parks & Yonelinas 2007; Wixted & Mickes 2010). These associated details typically represent the context in which an event took place (i.e., place, time, environmental or internal details) (Ranganath 2010). Recollection can be accompanied by a subjective experience of mentally reliving the prior experience with the event, as if one were mentally traveling back in time to re-experience it (Tulving 1985).

In contrast, familiarity is a feeling of oldness indicating that something has been previously experienced. It is thought to support predominantly recognition of single pieces of information (i.e., items such as objects and people; Ranganath 2010), but associations between similar types of information could also be recognized as familiar (Mayes et al. 2007). Subjectively, feelings of familiarity are more or less strong feelings that one knows that something has already been encountered, leading to varying degrees of confidence (Tulving 1985; Yonelinas et al. 2010). According to some theories, the feeling of familiarity arises when one interprets enhanced processing fluency of a stimulus as a sign that it was previously encountered (Jacoby et al. 1989; Whittlesea et al. 1990). Fluency is typically defined as the speed and ease with which a stimulus is processed and may arise from many sources (e.g., mere repetition, perceptual clarity, rhyme, predictive context, oral-motor sequence), including past occurrences (Oppenheimer 2008; Reber et al. 2004a; Topolinski 2012; Unkelbach & Greifeneder 2013). Because people intuitively know from their earliest years that fluently processed items are more likely to have been encountered previously, a feeling of fluency during a memory task will be likely interpreted as related to prior exposure (Schwarz 2004). However, several conditions have to be fulfilled for fluency to be used to guide memory. First, fluency has to be judged as a diagnostic cue for memory (Westerman et al. 2002). Second, the experienced fluency has to be greater than expected in a given context (i.e., individuals have to be surprised by the ease with which they are able to process an item) and should not be attributed to a more plausible source (e.g., the intrinsic perceptual quality of the stimulus) than past occurrence. Thus, if people appraise past encounter as an improbable source of fluency or if a more plausible source is detected, individuals will disregard fluency as a relevant cue for recognition decisions (Kelley & Rhodes 2002; Miller et al. 2008; Willems & Van der Linden 2006). This disqualification will prevent fluency to give rise to a feeling of familiarity.

2.1. Existing models of recollection and familiarity

Neuropsychological investigation of recollection and familiarity in memory-impaired populations (e.g., those with normal aging, amnesia, epilepsy, neurodegenerative diseases) as well as neuroimaging studies examining the neural correlates of recall and recognition memory tasks (using mainly functional magnetic resonance imaging [fMRI]) have provided a huge corpus of data that have led to the development of neurocognitive models of episodic memory functioning. Most memory models focus on the role of the medial temporal lobe (MTL) in recollection and familiarity, since seminal neuropsychological work has shown that amnesia arises following MTL damage (Scoville & Milner 1957). Much controversy still surrounds the precise contributions of the different MTL subregions, most notably the hippocampus and the adjacent perirhinal and entorhinal cortices. With the exception of unitary models suggesting that MTL structures contribute to both recollection and familiarity as a function of memory strength (Squire et al. 2007; Wixted & Squire 2011), the majority of models suggest that there is fractionation of memory processes in the MTL by reference to recollection and familiarity. These MTL models can be distinguished as a function of whether they define the role of the hippocampus and adjacent MTL cortices in terms of putative cognitive operations or according to the nature of representations. Most frameworks target the role of anatomical regions (and their functional network), but a few speak at the scale of individual neurons or populations of neurons within a brain region.

2.1.1. MTL process models

These models propose that the different MTL regions have distinct computational properties (Montaldi & Mayes 2010; Norman & O'Reilly 2003). In particular, only the hippocampus is capable of pattern separation (to create distinct memory representations for similar inputs) and pattern completion (once the hippocampus has bound the elements of an episode into a memory trace, subsequent experience of a subset of the elements causes the remaining elements to be reactivated by association). Thanks to these properties, the hippocampus is specialized for recollection of details. In contrast, the perirhinal and parahippocampal cortices extract statistical regularities in repeated inputs by creating sharper patterns. By contrast with novel inputs that activate weakly a large pattern of units, the sharpness of MTL cortical patterns indexes familiarity (Norman & O'Reilly 2003). The perirhinal cortex would thus encode similarities between events (LaRocque et al. 2013) and support familiarity. At the scale of neurons, some models describe familiarity signals as resulting from decreased firing of perirhinal neurons for repeated stimuli (Bogacz & Brown 2003; Bogacz et al. 2001; Sohal & Hasselmo 2000). This would arise because the number of active neurons that responded to a novel stimulus reduces as the stimulus becomes familiar.

2.1.2. MTL representational models

These models emphasize the different kinds of information incorporated in representations formed in the hippocampus versus the parahippocampal region (Aggleton & Brown 1999; Davachi 2006; Eichenbaum et al. 2007; Ranganath 2010). Whereas the perirhinal and parahippocampal cortices encode specific constituent elements of an event (e.g., objects, spatial layout), the hippocampus encodes representations of the relationships between the elements. According to the binding of item and context model (Diana et al. 2007; Ranganath 2010), the perirhinal cortex and parahippocampal cortex encode, respectively, item and context information, and the hippocampus encodes representations of item-context associations. Retrieval of item representations in the perirhinal cortex can support familiarity, while context representations and item-context bindings support recollection. As in MTL process models, the hippocampus is important for recollection, but these views consider that the parahippocampal cortex is also important for recollection because it represents contextual information.

2.1.3. The representational-hierarchical models

Recently, there has been accumulating evidence that the MTL mediates processes beyond long-term episodic memory. It is also involved in perception and short-term memory. In this view, the role of the MTL would be best described in terms of how each region represents information rather than in terms of a specific process (Cowell et al. 2006; Graham et al. 2010; Saksida & Bussey 2010). Actually, the MTL is considered an extension of the representational hierarchy of object processing within the ventral visual stream. The complexity of representations increases from posterior occipital areas to the anterior lateral and medial temporal regions. The perirhinal cortex represents the culmination of this object processing pathway, performing the most complex feature computations required to discriminate objects with a high degree of visual feature overlap. In a memory task, the perirhinal cortex can differentiate between objects that share features. Most recent suggestions also posit that the capacity of the perirhinal cortex to distinguish between overlapping item representations makes it a critical region to disambiguate conceptual entities with shared properties, such as living objects (Clarke & Tyler 2015; Inhoff & Ranganath 2015), in various tasks such as naming or recognition memory. As for the hippocampus, its function goes beyond object processing, as it represents relational configurations and scenes that can support performance in a variety of tasks, such as perceptual discrimination of scenes, navigation, imagination, source memory, and so forth (Clark & Maguire 2016; Cowell et al. 2010). So, this theoretical approach does not map recollection and familiarity onto specific regions. The role of MTL subregions are rather defined in terms of the type and complexity of representations they contain and all could generate familiarity and recollection (Cowell et al. 2010).

In all these models, the role of another region of the MTL, the entorhinal cortex, is poorly specified. The entorhinal cortex receives the inputs and outputs of other MTL regions, but its anterolateral and posteromedial parts appear to belong to different systems. Indeed, it has been suggested that the anterolateral entorhinal cortex may have functional specialization similar to the perirhinal cortex, whereas the posteromedial entorhinal cortex would support the same function as the parahippocampal cortex (Keene et al. 2016; Maass et al. 2015; Schultz et al. 2012). Moreover, investigation of connection pathways in the MTL suggests that the hippocampus should not be treated as a unitary region, but has distinct connectivity preference along its anterior-posterior portions and as a function of its subfields (Aggleton 2012; Libby et al. 2012). The perirhinal cortex has preferential connection with anterior CA1 and subiculum, whereas the parahippocampal cortex connects more with the posterior CA1/CA2/CA3/dentate gyrus and subiculum.

2.1.4. Whole-brain network models

However, the MTL is not the only region that contribute to recollection and familiarity. As notably evidenced by neuroimaging studies, recollection also involves the posterior cingulate cortex, the retrosplenial cortex, the inferior parietal cortex, the medial prefrontal cortex, anterior nuclei of the thalamus and mammillary bodies (Aggleton & Brown 1999; Ranganath & Ritchey 2012). This network has been labeled the general recollection network (Rugg & Vilberg 2013). The extended cerebral network for familiarity involves, besides the perirhinal cortex, the ventral temporal pole, the dorsolateral prefrontal cortex, the dorsomedial nuclei of the thalamus, and the intraparietal sulcus (Johnson et al. 2013; Kim 2010; Ranganath & Ritchey 2012). Currently, very few theoretical models of recollection and familiarity have integrated these large-scale cerebral memory networks. Recently, however, Ranganath and colleagues (Ranganath & Ritchey 2012; Ritchey et al. 2015) revised the binding of item and context model to suggest that the MTL regions are actually part of two broad memory systems. The perirhinal cortex is considered as a core component of an extended anterior temporal system that also includes the ventral temporopolar cortex, lateral orbitofrontal cortex, and amygdala. This system may be essential for processing entities (that is, people and things), and would be involved in item familiarity. In contrast, the parahippocampal cortex is considered as core component of an extended posterior medial network that includes the mammillary bodies and anterior thalamic nuclei, presubiculum, the retrosplenial cortex, and the default network (comprising the posterior cingulate cortex, precuneus, lateral parietal cortex, and medial prefrontal cortex). It would be involved in tasks that require a mental representation of the relationships between entities, actions, and outcomes, such as recollection-based memory tasks. Such models considering the whole-brain network architecture of memory processes are critical, given the fundamentally interconnected nature of brain structures.

Currently, yet, some aspects of recollection and familiarity have not been fully integrated in memory models. In particular, current models do not encompass the notion that explicit memory judgments and experiences, such as feelings of remembering and familiarity, arise from attribution mechanisms that interpret memory signals, such as fluency cues (Voss et al. 2012; Whittlesea 2002), and take into account expectations in a particular context (Bodner & Lindsay 2003; McCabe & Balota 2007; Westerman et al. 2002). A line of research considers how feelings of familiarity emerge when previous exposure to some information induces a sense of facilitated processing (i.e., fluency feeling) that is attributed to past occurrence of the information (Westerman et al. 2002; Whittlesea & Williams 2001a; 2001b). Similarly, both fluency signals and attribution mechanisms may also contribute to the experience of recollection (Brown & Bodner 2011; Li et al. 2017; McCabe & Balota 2007).

Here, we propose to integrate the current state of knowledge about the neurocognitive bases of recollection and familiarity by incorporating, into a single model, separate lines of research, namely neural models of recollection and familiarity and attributional models of memory experiences. This integrative memory model builds on currently most influential dual-process views of the cognitive and neural bases of recollection and familiarity, and takes into account the highly interconnected nature of the human brain in order to propose a distributed and interactive neurocognitive architecture of representations and operations underlying recollection or familiarity.

3. The integrative memory model: A neurocognitive architecture of recollection and familiarity

The notion of recollection and familiarity has been used to refer to processes and subjective experiences, leading sometimes to confusion between these aspects. In the integrative memory model (see our Figure 1), we describe recollection and familiarity as the interaction between *core systems* that store specific types of representations uniquely shaped by specific computational

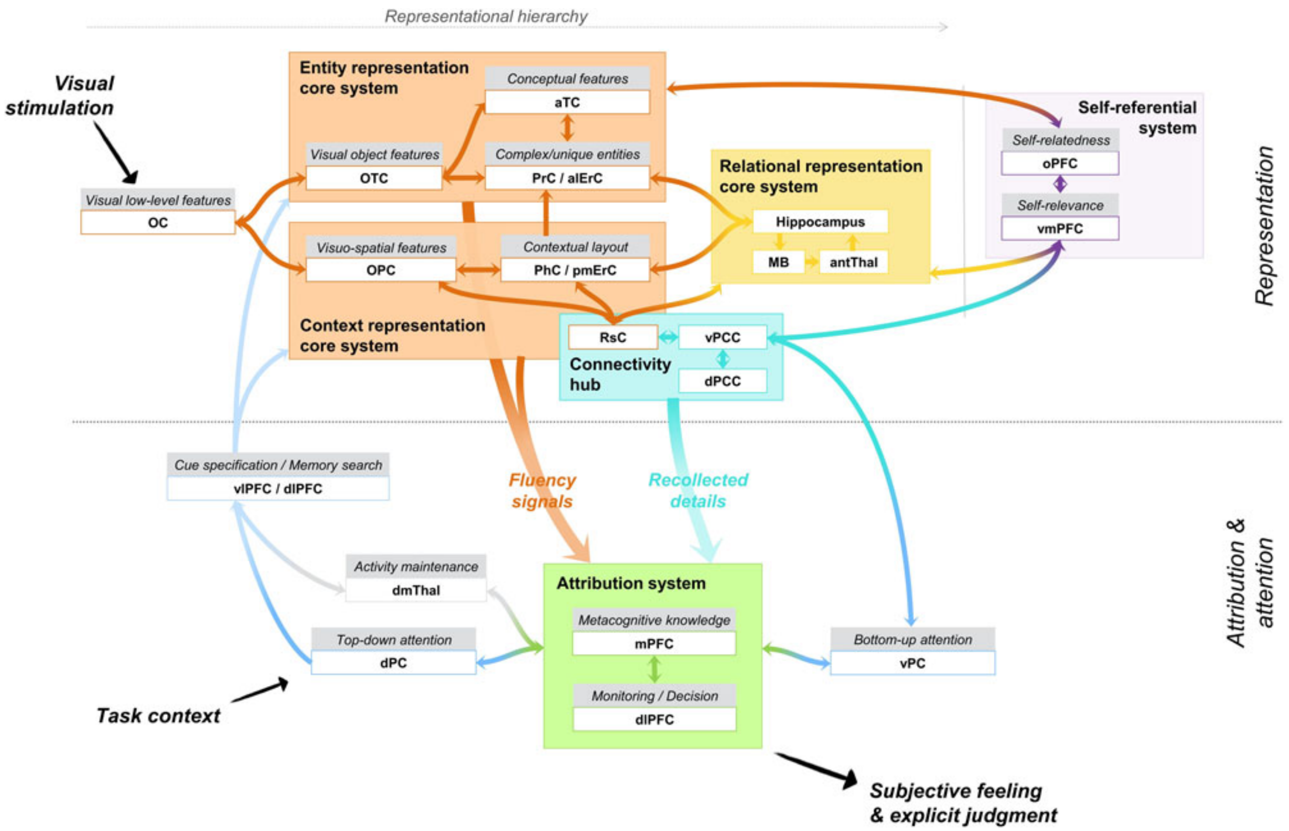

Figure 1. Integrative memory model. *Key*: OC: occipital cortex; OTC: occipito-temporal cortex; PrC: perirhinal cortex; aTC: anterior temporal cortex; alERC: anterolateral entorhinal cortex; PhC: parahippocampal cortex; OPC: occipito-parietal cortex; pmERC: posteromedial entorhinal cortex; antThal: anterior nuclei of the thalamus; MB: mamillary bodies; RsC: restrosplenial cortex; vPCC: ventral posterior cingulate cortex; dPCC: dorsal posterior cingulate cortex; oPFC: orbital prefrontal cortex; (v)mPFC: (ventro)medial prefrontal cortex; vPC: ventral parietal cortex; dlPFC: dorsolateral prefrontal cortex; dPC: dorsal parietal cortex; vlPFC: ventrolateral prefrontal cortex; dmThal: dorsomedial nuclei of the thalamus.

operations and make up the content of the memory and an *attribution system* framed by the task context that translates content reactivation into a subjective experience. Recollection emerges preferentially from reactivation of traces from a *relational representation core system*, whereas familiarity emerges mainly from reactivation of traces from the *entity representation core system*.

The distinction between core systems and an attribution system has two implications. First, the core systems build the memory trace and damage to these systems induces severe degradation of the content of the memory. In contrast, the attribution system modulates the use of memory traces as a function of expectancies, task context, and goals, leading to subjective experiences and explicit judgments. Lesion of the attribution system affects mainly the quality and adequation of the memory output to the task at hand. Second, although most memory situations generate an explicit output that matches the content of the memory (e.g., recollection follows reactivation of a relational representation), this might not always be the case. This means that the qualitative and subjective experience that one has in a given memory task may dissociate from the memory reconstructed by a core system. For instance, even if the relational representation core system reactivates specific item-context details, one may experience a feeling of familiarity. This is because explicit outputs during a memory task (i.e., old/new decisions, confidence judgments, and subjective experiences of remembering or knowing) follow from processing the outputs of the relational or entity representation core system in an *attribution system*. We assume that the attribution mechanisms are common down-stream mechanisms that serve both recollection and familiarity. In this framework, recollection and familiarity are considered as independent processes, in the sense that the underlying memory representation can be retrieved via the entity representation core system only, the relational representation core system only, or via both concomitantly (Jacoby et al. 1997).

4. Detailed description of the integrative memory model

4.1. Encoding

Core systems are specialized for encoding and storing specific kinds of representations. The nature of the information that is processed in each core system is determined by the computational operations and level of associativity that characterize its constituent brain regions. Although each core system must be viewed as a representation system rather than as harboring recollection or familiarity processes, we suggest that recollection and familiarity are preferentially associated with specific types of representations: relational representations (centered on the hippocampus) for recollection, and entity representations (centered on the perirhinal cortex) for familiarity. Consistently, fMRI studies examining encoding-related activities observed that hippocampal activity is predictive of subsequent source recollection but uncorrelated with item recognition, and that perirhinal activity predicts item familiarity–based recognition, but not subsequent recollection (Davachi et al. 2003; Kensinger & Schacter 2006; Ranganath et al. 2004). Recollection of details from the initial experience of an event also usually relies on contextual information that is stored in a *context representation core system*, but, as detailed below, some contextual tagging of entities occurs and elements of context (e.g., a building) may be subsequently recognized as familiar. Finally, the notion that these objects, people, and events have been personally experienced is recorded by the interaction between representation core systems and a *self-referential system*.

In the *entity representation core system*, encountered entities pertaining to experienced events are encoded. An entity is defined as an exemplar item (i.e., token) from a category (i.e., type) that distinguishes itself from other similar items thanks to its unique configuration of perceptivo-conceptual features. The *entity representation core system* comprises the perirhinal cortex, anterolateral enthorinal cortex, occipitotemporal cortex, and anterior temporal cortex. Of note, even if the entorhinal cortex has a hierarchically higher level of associativity than the perirhinal cortex (Lavenex & Amaral 2000) and recent data speak for a specific role of the anterolateral entorhinal cortex in object-in-context processing (Yeung et al. 2019), there are currently not sufficient data to clearly distinguish the role of the perirhinal cortex and the anterolateral entorhinal cortex. Based on studies showing a role for the anterolateral entorhinal cortex in disambiguation of similar objects (Yeung et al. 2017), we will consider here that the perirhinal cortex and anterolateral entorhinal cortex together form a system specialized for entity representation. This system is dedicated to the processing and encoding of single entities (Ranganath & Ritchey 2012), with preferential represention of objects and faces (Kafkas et al. 2017; Martin et al. 2016), unified associations (Haskins et al. 2008), and pairings of similar entities (e.g., two faces) (Hirabayashi et al. 2013; Mayes et al. 2007). It has been suggested to additionally represent the association of a written concrete word with its corresponding object concept (Bruffaerts et al. 2013; Liuzzi et al. 2015).

Critically, the *entity representation core system* is defined by the nature and complexity of the representations it can process and encode for long-term memory after a single exposure to the stimulus. More specifically, in line with the representational-hierarchial view (Cowell et al. 2010; Graham et al. 2010; Saksida & Bussey 2010), there is a hierarchy in terms of the complexity of the representation in the *entity representation core system*. Consider here the example of object processing (Fig. 1). While individual features (e.g., shape, texture, color) are processed in ventral occipitotemporal areas (*visual object features*), integration of these features into more and more complex entities are achieved as one moves anteriorly along the ventral visual stream. It is at the level of the perirhinal cortex and anterolateral entorhinal that all visual features are integrated in a single complex representation of the object that can be discriminated from other objects with overlapping features. Moreover, the perirhinal cortex may also act as a conceptual binding site. Whereas defining conceptual features such as the category are represented in the anterior temporal areas, the integration of the meaning to object representations will occur in the perirhinal cortex via its interaction with the anterior temporal area (*conceptual features*) (Martin et al. 2018; Price et al. 2017; Taylor et al. 2011). Indeed, the perirhinal cortex is notably recruited when concepts with confusable features must be distinguished (Clarke & Tyler 2015). For instance, the perirhinal cortex is needed to distinguish between living things during naming (and recognition memory tasks), as living things share a lot of common features and are more easily confusable than non-living things (Kivisaari et al. 2012; Wright et al. 2015). By incorporating features from various sensory and conceptual areas, the perirhinal/anterolateral entorhinal cortex forms unique conjunctive representations of entities allowing the resolution of ambiguity in the face of objects with overlapping features and the identification of objects in a viewpoint-invariant manner (Erez et al. 2016). These representations rely on a computational property of the perirhinal/anterolateral entorhinal cortex that can be referred to as *entity pattern separation,* by which similar objects are given separate representations based on specific conjunctions of features, even after a single exposure (Kent et al. 2016). This property allows humans to quickly recognize familiar objects in the stream of resembling objects from the environment.

Given that entities are typically experienced as part of an event, the perirhinal/anterolateral entorhinal cortex also encodes the significance of entities in a context-dependent manner (Inhoff & Ranganath 2015; Ranganath & Ritchey 2012; Yeung et al. 2019). This is possible thanks to the connections between the perirhinal cortex and the parahippocampal/posteromedial entorhinal cortex, which is part of the *context representation core system* together with the occipitoparietal cortex and retrosplenial cortex. The parahippocampal cortex represents, preferentially, buildings and scenes, which often constitute the contextual setting for an event (Bar et al. 2008; Kafkas et al. 2017; Martin et al. 2013; Preston et al. 2010), and the posteromedial entorhinal cortex encodes an internally generated grid of the spatial environment (Doeller et al. 2010). The *context representation core system* would provide a contextual tagging of the entity, which allows us to take into account the background in which the entity occurred and give distinct meanings and values to the entity. In their article, Inhoff and Ranganath (2015) give the example of a ticket purchased at a county fair to buy food and rides, whose significance changes beyond the fairgrounds because that same ticket would have little value outside the fair. In addition, we recognize entities that we have personally experienced. Self-reference is also important to define the significance of entities. Via connections of the perirhinal cortex to the orbital prefrontal cortex (Lavenex et al. 2002), the entity representation may also record the self-relatedness of the entity (D'Argembeau et al. 2005; Northoff et al. 2006). Like the contextual significance, self-relatedness of entities may modulate our behavior with regard to the entities. For example, a piece of clothing should lead to different behaviors depending on whether it belongs to me or somebody else.

In brief, entities encountered as part of experienced events are stored in long-term memory in a distributed and hierarchical manner in the entity representation core system. While simple perceptual and conceptual features are represented in occipitotemporal and anterior temporal areas, the conjunctions of multimodal features are represented as pattern-separated entities in the perirhinal cortex and the anterolateral entorhinal cortex. Some contextual and self-related tagging via interactions between the entity representation core system and the context representation core system and self-reference system will modulate the significance of entities. The concept of unification is close to the notion of conjunction, with the difference that unification can sometimes be an active encoding strategy whereas conjunction refers to the configurational nature of stimuli. Indeed, unification consists in encoding different pieces of information in a way that integrates them into a single entity (Parks & Yonelinas 2015). Previous fMRI studies have shown that processing object-color associations by mentally integrating color as an object feature activates the perirhinal cortex (Diana et al. 2010), as does the encoding of word pairs as new compound words (Haskins et al. 2008).

The *relational representation core system* involves the hippocampus, subiculum, mamillary bodies, and the anterior nuclei of the thalamus. It rapidly encodes a detailed representation of the item bound to associated contextual information (Montaldi & Mayes 2010; Ranganath & Ritchey 2012) or more generally complex high-resolution bindings (Yonelinas 2013). In the case of item-context binding, inputs consist in the entity representations from the perirhinal/anterolateral entorhinal cortex entering the hippocampus anteriorly, and context representations (e.g., spatial layout) from the parahippocampal/posteromedial entorhinal cortex entering the hippocampus posteriorly (Ranganath & Ritchey 2012; Staresina et al. 2011). The context representation in the parahippocampal cortex is itself fed by inputs from neocortical regions that represent the specific contents of the context in which the item is embedded (e.g., sounds, visual details, and spatial layout), stored in occipitoparietal sites (*visuospatial processing*; Rissman & Wagner 2012), and brought to the parahippocampal cortex via the retrosplenial cortex. The self-referential nature of the experienced episodes is also embedded in the memory trace thanks to connection of the hippocampus and retrosplenial cortex with the ventromedial prefrontal cortex (Andrews-Hanna et al. 2010). The binding of multimodal and qualitatively different pieces of information occurs in the hippocampus (CA3 via the dentate gyrus) where each unique episode is encoded as a separate represention via *relational pattern separation* (Berron et al. 2016; Leal & Yassa 2018; Montaldi & Mayes 2010; Norman & O'Reilly 2003), so that two very similar events will have two distinct memory traces. For instance, if we attend two concerts based on the same album of our favorite band, we will still be able to remember the details of each concert as a unique episode.

This pattern-separated representation in the hippocampus constitutes a summary, or an index, of the distributed neocortical representations of the specific details of the episodes (Teyler & Rudy 2007). Contrary to the conjunctive representations in the entity representation core system where components are fused in a frozen integrated trace, the hippocampal representation keeps components separate and flexibly bound (Eichenbaum 2017c). This allows the learning of inferences between items that are indirectly related, and subsequent flexible use of representations (Eichenbaum & Cohen 2014). So, relational binding and pattern separation are the core computational properties of the relational representation core system.

While the nature of the representations in the entity representation core system makes it specialized for rapidly signaling that objects, faces, and simple combinations of those are known (i.e., familiarity judgments), the bound representations in the relational representation core system makes it specialized for reactivating the specific details of experienced events (i.e., recollection). In other words, familiarity and recollection are processes that emerge naturally from the ways in which different brain regions represent the experienced world. But, as will be detailed next, the final explicit memory output will depend on the attribution system.

4.2. Retrieval

4.2.1. Familiarity-based retrieval

As illustrated in Figure 2, the typical sequence of operations leading to familiarity starts with the repetition of an encoded entity (Montaldi & Mayes 2010; Ranganath 2010; Voss et al. 2012). For instance, during a recognition memory test, target items are the replication of previously studied items. In our example of the processing of an object item, the repetition of the perceptual and/or conceptual features of the item triggers enhanced *processing fluency* (and reduced activity) in the occipitotemporal and anterior temporal areas where these features were first processed (Reber 2013). Several fMRI studies also showed that enhanced processing fluency of items induces a reduction of activity in the perirhinal cortex that predicts familiarity-based memory (Dew & Cabeza 2013; Gonsalves et al. 2005; Meyer et al. 2010). Here, we make the novel hypothesis that the perirhinal and

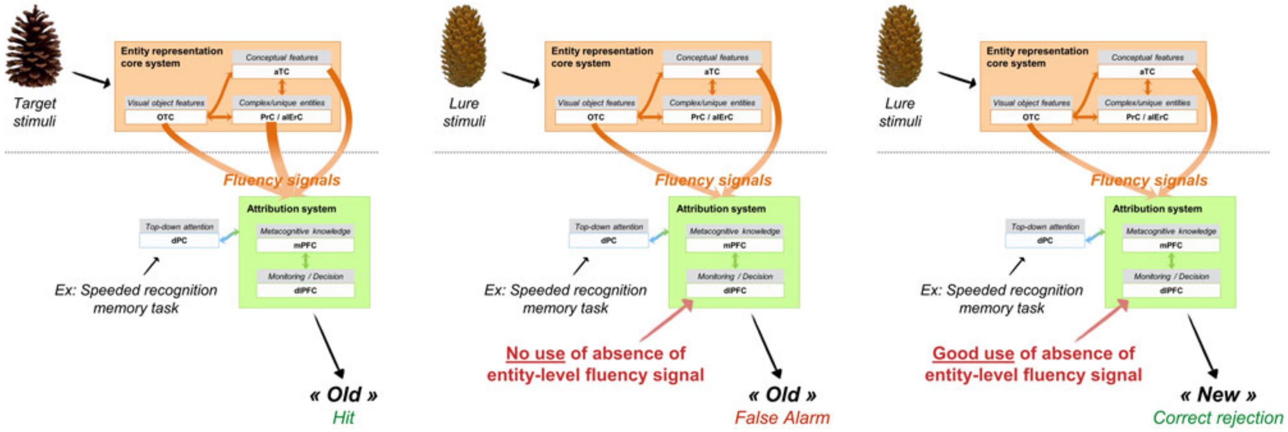

Figure 2. Main mechanisms supporting familiarity-based retrieval in the example of a lab-based object recognition memory task with resembling targets and lures.

anterolateral entorhinal cortices are sensitive to the repetition of the actual conjunction of features that makes up the specific and viewpoint-invariant representation of the item, associated with a specific meaning, and thus generates enhanced *entity-level processing fluency* and can lead to familiarity for this entity. In addition, any region representing features of the previously encountered object can reactivate these specific features when re-exposed to them and thus generates familiarity-based memory through fluency. So, perceptual and conceptual fluency for features arising in occipitotemporal and anterior temporal cortices can also generate familiarity for these features. The dominant type of signal that will contribute to familiarity depends on the characteristics of the memory task (Lanska et al. 2014; Lucas & Paller 2013; Taylor & Henson 2012b). For instance, in a task where participants have to rapidly discriminate between old pictures of objects and new pictures of completely different objects (e.g., Besson et al. 2015), reactivation of simple perceptual features (e.g., a small grey fluffy object for the picture of a grey kitten) or conceptual features (e.g., a feline) is sufficient to successfully identify the studied stimuli. In contrast, if old objects are mixed with very similar objects from the same category (e.g., Yeung et al. 2013), accurate familiarity-based discrimination will rely on the reactivation of the studied conjunctions of features. This implies that familiarity may arise from different regions, depending on the materials (e.g., Kafkas et al. 2017) and demands of the task, and that lesions to the perirhinal cortex will not necessarily affect all forms of familiarity.

Besides fluency signals, other signals may also operate in recognition memory tasks. We focus here on fluency signals because we wish to model recognition memory decisions that allow the brain to identify a specific stimuli as previously encountered. Item-specific discrimination is a key property of familiarity in everyday life, as we adapt our behavior to familiar unique entities. For instance, we will speak to people we know, we will take our own cup to fetch some coffee, we will pick up our coat among others in a cloakroom, and so forth. For all these situations, we propose that fluency-based familiarity is central. However, feelings of familiarity can arise from many other sources. Some of them are non-memory, such as affective information (Duke et al. 2014) or proprioceptive information (Fiacconi et al. 2016) that have been shown to generate a subjective sense of familiarity if manipulated in memory situations. Others are from the memory domain, but support global matching or similarity judgments when a presented stimulus globally maps onto a stored representation (Norman & O'Reilly 2003). But even then, the involvement of fluency in the emergence of a feeling of familiarity through affective information, proprioceptive information, or global matching cannot be ruled out (Duke et al. 2014).

Still, whatever its source, enhanced processing fluency in itself is not sufficient to produce familiarity. It has been suggested that fluency only minimally contributes to memory decisions because some patients with amnesia demonstrate chance-level recognition memory (hence, no sign of familiarity), despite successfully completing priming tasks conducted on the same set of stimuli (priming being also driven by fluency) (e.g., Levy et al. 2004). In the same vein, enhancing the processing fluency of some stimuli had only a small influence on amnesic patients' memory performance in some studies (Conroy et al. 2005; Verfaellie & Cermak 1999), while other studies found reliable improvement of recognition memory performance in amnesia following manipulation that enhanced processing fluency (Keane et al. 2006). Such findings can be explained if one considers that the transformation of fluency signals into familiarity-based decisions involves complex cognitive and metacognitive mechanisms (Whittlesea & Williams 2000; Willems et al. 2007). Accordingly, our integrative memory model argues that one cannot explain familiarity-based memory decisions without considering the role of the *attribution system*.

Therefore, explicit familiarity judgments and the subjective feeling of familiarity result from attribution of fluency to the prior occurrence of the stimulus (via the *attribution system*) (Whittlesea & Williams 2000). The fluency heuristic relies on signal flow from the entity representation core system regions to the attribution system, via connections between the perirhinal cortex and the prefrontal cortex (mainly, orbitofrontal, medial, and dorsolateral prefrontal areas; see Aggleton & Brown 1999; Lavenex et al. 2002; Libby et al. 2012). The mechanisms thought to intervene in the attribution system, such as metacognitive and monitoring operations, have been notably associated with the prefrontal cortex in the context of memory tasks (Chua et al. 2014; Henson et al. 1999). Direct involvement in the fluency heuristic comes from electrophysiological studies (i.e., event-related potentials) (Kurilla & Gonsalves 2012; Wolk et al. 2004), notably showing that the attribution of fluency to the past versus the disqualification of fluency as a memory cue was associated with late frontal potentials.

The fluency heuristic involves sophisticated *monitoring and metacognitive* mechanisms. First, the *metacognitive knowledge* (supported by medial prefrontal areas) that fluent processing is a sign of prior occurrence exists since childhood (Geurten et al.

2017; Olds & Westerman 2012; Oppenheimer 2008); but this metacognitive heuristic can be unlearned through regular encounter with memory errors, as this might be the case for patients with severe memory problems (Geurten & Willems 2017). Second, the characteristics of the specific task at hand will determine the relevance of using fluency signals. This is determined via several *monitoring* mechanisms, supported by dorsolateral prefrontal cortex and that may happen at a non-conscious level. Fluency cues will be used if they are expected as diagnostic cues for recognition decisions (Westerman et al. 2002) and if the experienced fluency is salient relative to the context (Jacoby & Dallas 1981; Westerman 2008). People set an internal criterion along the varying dimension of memory strength depending on the task specificities. A feeling of surprise is experienced when the intensity of the fluency signal exceeds this criterion (Yonelinas et al. 2010). If no alternative source is detected to explain the intensity of this signal, fluency will be attributed to past occurrence and will give rise to a feeling of familiarity. If not so attributed, fluency will be disregarded and no feeling of familiarity will arise.

Such an explicit judgment of familiarity occurs when *top-down attention*, supported by the dorsal parietal cortex, is focused on recognition memory decisions. According to the attention-to-memory model (Cabeza et al. 2008; Ciaramelli et al. 2008), the dorsal parietal cortex allocates attentional resources to memory retrieval according to the goals of the person who remembers, and is often involved in familiarity-based decisions because familiarity may induce low confidence. This is the case in recognition memory paradigms where participants must judge how familiar stimuli are, but this can also occur in daily life (e.g., judging the most familiar brand of an article at the supermarket in order to choose the one usually bought). Yet, this explicit expression of familiarity may be distinguished from the *subjective feeling* of familiarity. Although both often co-occur in memory tasks – so that a participant can gauge how strong is his or her feeling of familiarity during confidence judgments, for example – a strong feeling of familiarity may sometimes arise outside of any memory task and capture attention in a bottom-up fashion. One typical example is the butcher-on-the-bus phenomenon where one is surprised by the involuntary strong feeling of knowing the person, albeit in the absence of any recollection.

To come back to the cases where amnesic patients failed to use fluency cues in recognition memory tasks despite preserved perceptual or conceptual fluency, a likely interpretation in the framework of the attribution system considers that this is due to changes in metacognitive knowledge and monitoring in amnesic patients compared to controls (Geurten & Willems 2017). More specifically, because of their continued experience of memory errors in everyday life, amnesic patients may have modified their metacognitive knowledge so as to unlearn the fluency heuristic (Geurten & Willems 2017; Ozubko & Yonelinas 2014). Additionally, their expectations relative to the origin of fluency feelings may have adapted in a way that makes them readier to detect alternative sources to fluency (Geurten & Willems 2017). Altogether, this will lead them to disqualify fluency as a cue for memory decisions (Conroy et al. 2005; Ozubko & Yonelinas 2014; Verfaellie & Cermak 1999), unless other fluency sources are very difficult to detect (Keane et al. 2006).

In initial network models (Aggleton & Brown 1999), the dorsomedial nucleus of the thalamus has been considered as a node within the familiarity system. However, its critical involvement remains unclear because of the divergence of findings relative to a selective impairment of familiarity following lesion to the dorsomedial thalamus (Danet et al. 2017; Edelstyn et al. 2016). Theoretical positions about the role of this region currently diverge. On the one hand, the dorsomedial thalamus could support familiarity, but the loss of inputs to the prefrontal cortex following damage to this region would have wider consequences on cognition, with possible impact on recollection (Aggleton et al. 2011). On the other hand, it could have a general role in several cognitive domains by virtue of its regulatory function over the prefrontal cortex, allowing the maintenance of frontal activity over delays necessary to perform complex reflections and decisions (Pergola et al. 2018). In a recognition memory task, the dorsomedial thalamus was found to become critical when interference between stimuli increased (Newsome et al. 2018). Following on this latter view (Pergola et al. 2018), in the integrative memory model we have positioned the dorsomedial thalamus as a modulator of prefrontal activity, such that it would support the maintenance of prefrontal activities during tasks that are demanding in terms of attribution processes (e.g., discrimination between similar interfering stimuli).

4.2.2. Recollection-based retrieval

Figure 3 illustrates the mechanisms involved in recollection-based retrieval. Typically, recollection-based retrieval starts with exposition to partial information from a past episode (either an entity or elements of the context). The partial information cue triggers the reactivation of the complete pattern via *pattern completion* within the hippocampus (CA3/CA1) (Norman & O'Reilly 2003; Staresina et al. 2013). As the pattern stored in the hippocampus is an index of distributed contents in the neocortex, its reactivation induces the reinstatement of stimulus-specific neocortical representations (Rissman & Wagner 2012; Staresina et al. 2013) in such a way that the contents that were processed when the event was initially experienced and encoded are reactivated at retrieval. Thus, the sensory-perceptual and visuo-spatial details of the memory (e.g., object features, persons' characteristics, spatial configuration, sounds) stored in posterior cerebral areas are brought back. The signal from the hippocampal index is transferred to distributed neocortical sites via the mammillary bodies (connected to the hippocampus by the fornix), the anterior nuclei of the thalamus, and the retrosplenial cortex (Brodmann areas BA29 and BA30). In other words, Papez's circuit is the core pathway for recollecting the content of past experienced episodes (Aggleton & Brown 1999).

In addition to strong connections with the hippocampus and anterior thalamus, the retrosplenial cortex is linked to the parahippocampal cortex, occipital areas, and adjacent posterior cingulate cortex (BA23 and BA31) (Kobayashi & Amaral 2003; Parvizi et al. 2006; Suzuki & Amaral 1994; Vogt & Pandya 1987; Vogt et al. 1987). The posterior cingulate cortex and the retrosplenial cortex appear to play a pivotal role as interfaces between the hippocampus and the neocortex, thanks to their highly connected nature. Indeed, they have been identified as hubs of connectivity (Hagmann et al. 2008; van den Heuvel & Sporns 2013). However, the different patterns of connection of the retrosplenial cortex and posterior cingulate cortex suggest different contributions (Greicius et al. 2009). As a gateway between the hippocampus and regions storing the sensory-perceptual details of the memory (especially, visuo-spatial information in the parahippocampal cortex and occipitoparietal cortex), the retrosplenial is a key region for enabling cortical reinstatement of the content of memories. It is part of the *context representation core system*, and its damage will likely prevent content reactivation and lead to amnesia (Aggleton 2010; Valenstein et al. 1987; Vann et al. 2009a).

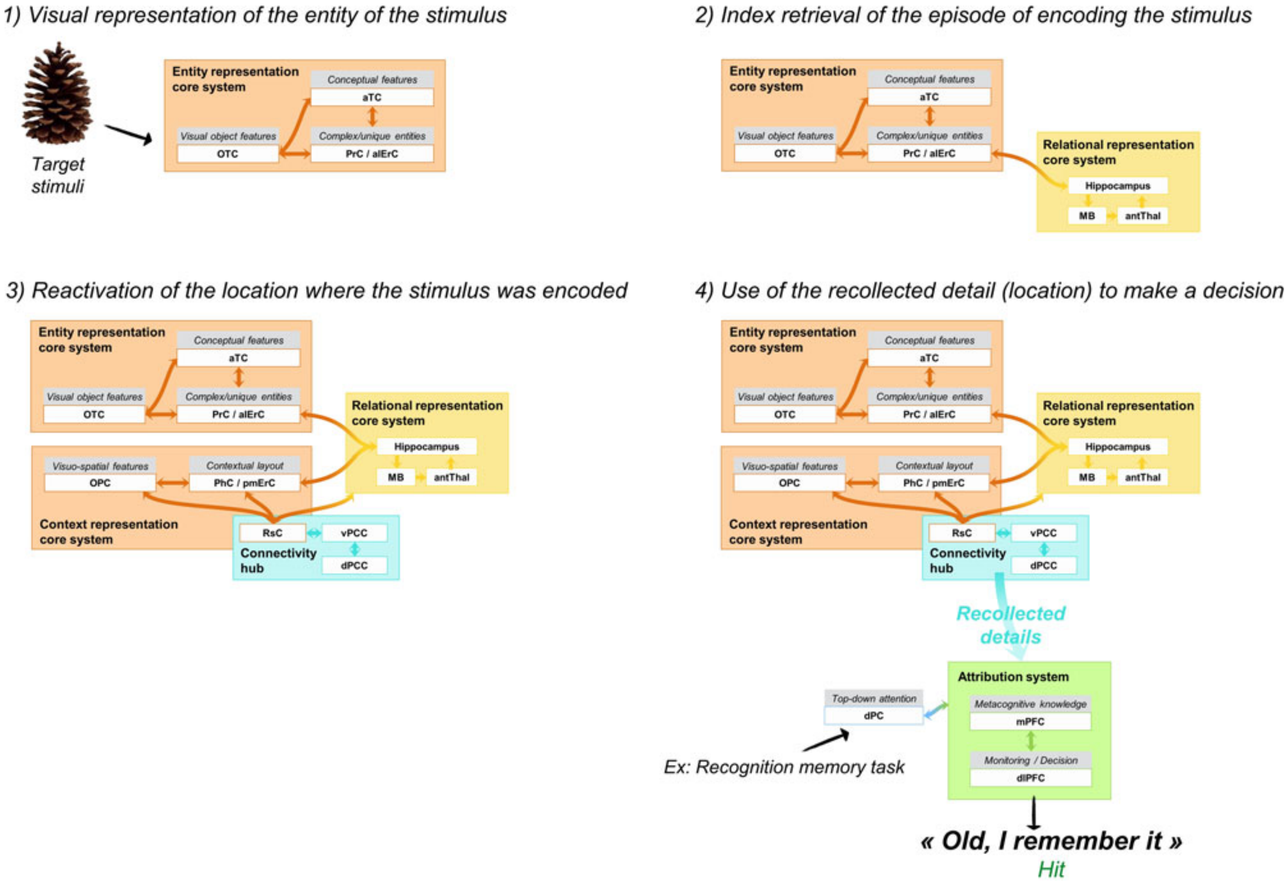

Figure 3. Illustration of the main steps for a recollection-based memory judgment in the example of an object recognition memory task (following encoding of objects in various spatial locations).

In contrast, the posterior cingulate cortex sits outside the context and relational representation core systems because it does not contribute to recollecting the content of episodes like the retrosplenial cortex does. Intracranial recordings from posterior cingulate sites in epileptic patients show enhanced gamma band activity specific to autobiographical remembering (Foster et al. 2012), but perturbation of posterior cingulate neurons by electric brain stimulation in the intracranial electrodes do not produce any observable behavioral responses, nor any subjective experience in the participants (Foster & Parvizi 2017). By contrast, electrical stimulation of the MTL evokes a subjective experience of déjà vu/déjà vécu, reminiscence of scenes or of visual details of known objects (Barbeau et al. 2005; Bartolomei et al. 2004). This suggests that the posterior cingulate cortex does not store any content related to experienced memories, but rather plays a supportive role during recollection. More specifically, the posterior cingulate cortex contributes to the quality of recollection and the subjective experience of remembering due to its central position as hub of connectivity. A distinction is made between the ventral and dorsal posterior cingulate cortex (Vogt et al. 2006). While the ventral posterior cingulate cortex connects notably with the inferior parietal cortex and ventromedial prefrontal cortex, the dorsal posterior cingulate cortex has main connections with the superior parietal cortex and the dorsolateral prefrontal cortex (Bzdok et al. 2015; Leech et al. 2011; Parvizi et al. 2006; Vogt et al. 2006).

The ventral posterior cingulate cortex is part of the default mode network (Leech & Sharp 2014; Margulies et al. 2009), which has been associated with various internally-directed cognitive functions, such as episodic memory retrieval, self-referential processing, and mentalizing (Buckner et al. 2008). During recollection, the ventral posterior cingulate cortex will support pattern completion by allowing the reactivation of the *self-referential* character of memories for personally experienced events via its connection to the ventromedial prefrontal cortex (D'Argembeau 2013). It should be noted that recollection can occur in the absense of self-referential feeling, as illustrated by the case of a patient who remembered personally experienced events with contextual details, but who had the feeling that these events did not belong to him (Klein & Nichols 2012). However, the lack of self-referential character in recollected memories would prevent them from inducing the subjective feeling of travelling back in time to re-experience one's past (Tulving 1985). Then, the sudden recovery of the whole memory trace on the basis of a simple cue (i.e., ecphory) captures *bottom-up attention* and engages the ventral attention network, more specifically the ventral parietal cortex (supramarginal gyrus and angular gyrus [attention-to-memory model, Cabeza et al. 2012]), via the ventral posterior cingulate cortex connection.

As for the dorsal posterior cingulate cortex, it is thought to be a transitional zone of connectivity, linking the default mode network and a frontoparietal network involved in executive control (Leech & Sharp 2014). In our integrative memory model, this frontoparietal network corresponds to the attribution system interacting with attention. Of note, the retrosplenial cortex also has direct connections with the dorsolateral prefrontal cortex (Kobayashi & Amaral 2003; Vann et al. 2009a), suggesting that the posterior cingulate gyrus as a whole acts as a gateway between the hippocampally centered relational representation core system and the frontoparietal attribution and attention system. Therefore, we propose that the posterior cingulate gyrus hub of connectivity, comprising the retrosplenial cortex and posterior cingulate cortex, has a pivotal role in the integration of all the recollection-related operations and contents. It would act as a relay node allowing activation to spread from the relational representation core system throughout the entity representation core system, context representation core system, self-referential system, and the attribution system. Dysfunction of this node would disintegrate the network, preventing the full reinstatement of the memory. Consistently, Bird et al. (2015) have shown that the posterior cingulate gyrus allows the reinstatement of episodic details and the strength of the posterior cingulate reinstatement activity correlated with the amount of details that the participants could subsequently recall.

Finally, in order for the individual to report an "old" judgment based on a recollective experience, *attribution* mechanisms should come into play, taking into account the task context and memorability expectations (*metacognitive knowledge and monitoring*; McCabe & Balota 2007). We assume that the fundamental cognitive operations are the same as in the case of familiarity, but the nature of representations on which this applies differs. Here, the attribution system will assess, notably, the amount of recollected details (Johnson et al. 2009) and their relevance (Bodner & Lindsay 2003). This implies that, even if an individual recollects qualitative details about an event, he or she may report a familiarity-based recognition decision if the retrieved information is judged irrelevant or insufficient to succeed at the task and to be qualified as recollection (e.g., "Remember" response; Bodner & Lindsay 2003). In addition, the criterion for recollection will depend on task context. For instance, in McCabe and Balota's (2007) study, medium-frequency words were intermixed with high-frequency or low-frequency words at test. Remember responses were greater for medium-frequency targets when they were tested among high-frequency, as compared with low-frequency words. This suggests that participants are more likely to experience recollection when targets exceed an expected level of memorability in the context of words that were relatively less distinctive.

In line with the hypothesis that the posterior cingulate gyrus contributes to consciousness (Vogt & Laureys 2005), an additional hypothesis of the integrative memory model is that the spread of activation throughout distributed brain regions via the posterior cingulate gyrus hub, the catching-up of attention related to ecphory, and the high diagnosticity of such signal in terms of evidence of past experience is equivalent to a mobilisation of a global neuronal workspace (Dehaene & Naccache 2001; Vatansever et al. 2015) that conveys consciousness of remembering and a feeling of re-experiencing (i.e., autonoetic consciousness). In this view, autoneotic consciousness would thus be an emerging property of integrated reactivation of the representation core systems together with the attribution system, where the posterior cingulate gyrus plays a central role.

Table 1 summarizes the key computational operations and the corresponding types of content that can be represented thanks to these properties, according to the integrative memory model. We distinguish the core systems that create the memory trace, that will become available for familiarity- and recollection-based memory decisions (as well as other cognitive functions, as described in sect. 5.3 below), and the subjective experience of remembering and knowing which are emerging psychological phenomena arising from the interaction between the core systems representations and the cognitive operations of the attribution system.

5. Further characteristics of the integrative memory model

5.1. Interactions within the integrative memory model

Although the core systems that represent the memory traces generating recollection and familiarity are independent, it is important to consider how these systems interact. Interaction will occur when the representations from the entity and context representation core systems are used to create relational associations in the relational representation core system, which are subsequently reinstated during pattern completion. For instance, fMRI studies have shown that covert retrieval of the context previously associated with an item activated the parahippocampal cortex when probed with the item alone, whereas perirhinal-related representations of the item were activated by presenting the associated context, with

Table 1. Main computational/cognitive operations and associated representations/psychological consequences in the integrative memory model.

Entity representation core system		Relational representation core system	
Computational operations	*Representations*	*Computational operations*	*Representations*
Hierarchical integration	From features to conjunctions of features	Relational binding	Item-context associations
Entity pattern separation	Unique conjunctive representations of objects, people, and simple associations	Relational pattern separation	Unique representations of complex associations (index)
Fluency due to prior exposure	Reactivated features/conjunctions	Pattern completion	Reactivation of distributed representations of components
Feeling of familiarity		Remembering	
Cognitive operations	*Psychological phenomenon*	*Cognitive operations*	*Psychological phenomenon*
Fluency heuristic (i.e., attribution)	Feeling of familiarity	Attribution	Recollective experience
Metacognitive knowledge & monitoring	Modulation of use of the fluency heuristic	Metacognitive knowledge & monitoring	Modulation of attribution
Top-down attention	Explicit judgment of familiarity	Global neuronal workspace	Autonoetic consciousness

the hippocampus coordinating the reinstatement (Diana et al. 2013; Staresina et al. 2012; Wang et al. 2013).

Moreover, at the level of memory outputs from the attribution system, familiarity and recollection can interact (Kurilla & Westerman 2008; 2010; Mandler et al. 1969; Whittlesea 1997). Notably, a feeling of familiarity can trigger an active search in memory to recollect specific details about some event. For instance, when seeing a familiar face in the crowd, one often wishes to remember one's past interactions with that person. Typically, we will elaborate retrieval cues, with the support of the ventrolateral prefrontal cortex (i.e., *cue specification*, Figure 1), trying to specify contextual information associated with the face until we find an appropriate cue that will trigger pattern completion in the hippocampus (Ciaramelli et al. 2008). Alternatively, recollection acts as a control over familiarity. For instance, when some aspects of a stimulus feels familiar, remembering that they were actually part of another memory allows us to correctly reject the current stimulus (e.g., recombined pairs in associative memory tasks, exclusion trials in the Process Dissociation Procedure).

Also, expectancies induced by the task characteristics can shift the balance between recollection and familiarity as outputs. For instance, some materials such as pictures induce high expectations in terms of memorability compared to other kinds of materials (i.e., the distinctiveness heuristic). In this case, participants think that they will recollect many perceptual details. If they do not for a given stimulus, they will consider it is new even if they experience fluency feelings. As recollection was anticipated but not familiarity, fluency cues are disregarded because of the absence of recollection (Dodson & Schacter 2001; Ghetti 2003).

Finally, the individual may set specific goals for a given memory situation, that will generate a retrieval mode orientating attention towards the search for particular types of information. This will rely on the interaction between the dorsolateral prefrontal cortex and dorsal parietal cortex (Cabeza et al. 2008; Lepage et al. 2000). For instance, an individual may favor global processing of information leading to familiarity versus analytic processing leading to recollection of details (Whittlesea & Price 2001; Willems et al. 2008), or may even search for specific types of details (Bodner & Lindsay 2003; Bodner & Richardson-Champion 2007).

5.2. Beyond recollection and familiarity

In the integrative memory model, similarly to models emphasizing the nature of representations used for memory, core systems store specific contents that serve in memory tasks to retrieve the objects, people, actions, settings, and so forth, that have been experienced. But the same representations can also be used to perform other tasks. Indeed, perceptual discrimination between entities with overlapping features and their maintenance in short-term memory have been found to involve the perirhinal/anterolateral entorhinal cortex (Barense et al. 2016; Graham et al. 2010). Naming and conceptual discrimination of such entities also rely on perirhinal integrity (Clarke & Tyler 2015). Similarly, the hippocampus uses relational representations in navigation, short-term memory, perceptual discrimination, imagination, and so forth (Clark & Maguire 2016; Lee et al. 2012; Yonelinas 2013). Hence, even if recollection and familiarity recruit relational and entity representations, they are not the only functions to do so. This has implications for the pattern of deficits arising from damage to these core systems (see sect. 6.1).

Actually, the whole architecture described in the integrative memory model may not be uniquely mnemonic in nature. For instance, the interaction between fluent processing of repeated items in the entity representation core system and the attribution system may lead to affective judgments. This is well illustrated by the mere repetition effect in which repeated items are judged more pleasant and prefered over non-repeated items (Willems et al. 2007). Moreover, the default network, that overlaps partly with the relational representation core system, self-reference system, posterior cingulate gyrus hub of connectivity, ventral parietal cortex, and regions from the attribution system involved in metacognition, is also recruited during imagination of future events, mind wandering, and reflection about one's and others' mental states (Andrews-Hanna et al. 2010). This network may have an adaptive role by which the brain uses past experiences to simulate possible future scenarios in order to prepare humans to react to upcoming events (Buckner et al. 2008). Additionally, the combined use of the default network and the frontoparietal network (corresponding to interacting core and attribution systems here) supports creative thinking (Madore et al. 2019). Thus, the core systems provide the building blocks that are reconstructed and recombined, depending on the individual's goals, with the help of the attribution system.

The very facts that consistent impairments are observed following brain damage and that the same brain regions are activated when different individuals perform a given task, suggest that the neural networks underlying cognitive functions are common to all individuals. The purpose of theoretical models, like the integrative memory model and others, is precisely to reveal the universal neurocognitive architecture of memory. Beyond anatomical similarity of memory functioning, one may wonder about the social role of such organization. Regarding memory, it appears that, when individuals recall a given event (e.g., a TV show episode) with their own words, the pattern of cerebral activation is more similar between people recalling the same event than between recall and actual perception (Chen et al. 2017). This suggests that perceived events are transformed when entering memory in a systematic way that is shared across humans. If true, this would mean that the main purpose of our memory-related neurocognitive scafolding is not only to allow each individual to remember the events that he or she experienced, but more widely to communicate and share beliefs about the past with other people (Mahr & Csibra 2018) and to facilitate the creation of collective memories that build the social identity of human groups (Halbwachs 1980; Hirst et al. 2018).

5.3. Novelty of the integrative memory model compared to other current models of recollection and familiarity

As indicated by its name, the integrative memory model does not have the ambition to propose a novel framework, but rather to integrate some principles from currently most-influential theories. There are therefore a lot of similarities with existing models, although some differences exist. The integrative memory model borrows from representational models the idea that memory processes arise from the use of particular types of representations. The entity representation core system relies on hypotheses from the representational hierarchical view (Cowell et al. 2006; 2010; Saksida & Bussey 2010) and the emergent memory account (Graham et al. 2010). Like the emergent memory account, we consider that memory emerges from hierarchically organized representations distributed throughout the brain. The consequence of this is that familiarity can arise from the reactivation of any of these representations (including outside the MTL). In turn, the relational representation core system builds on relational theories about the role of the hippocampus, by suggesting that the hippocampus flexibly binds disparate pieces of information (Aggleton & Brown 1999; Eichenbaum & Cohen 2014; Eichenbaum et al. 2007). However, our view departs slightly from another representation-based model, Binding of Item and Context (Diana et al. 2007; Ranganath 2010), which posits that the perirhinal cortex supports familiarity for items in general, whereas recollection will rely on context representation in the parahippocampal cortex and item-context binding in the hippocampus. We instead propose that the perirhinal cortex is specifically tuned for the representation of complex conjunctive entities, but not items of lower levels of complexity. Moreover, the context representation core system can support familiarity for scene and buildings.

Contrary to process-based models, the integrative memory model does not localize the recollection and familiarity processes themselves to certain regions, but conceptualizes them as processes emerging from the interaction between specific kinds of representation and attribution mechanisms. However, in line with process models like the convergence, recollection, and familiarity theory and the complementary learning systems (Montaldi & Mayes 2010; Norman & O'Reilly 2003), we consider that the core systems have unique computational properties (e.g., entity versus relational pattern separation) that contribute to shaping the content of stored information. The combination of computational properties and the associated representations makes the relational and entity representation core systems more tuned to recollection and familiarity, respectively. But the ultimate memory output will depend on attribution mechanisms.

The network organization of the integrative memory model clearly resonates with the posterior medial anterior temporal (PMAT) framework (Ranganath & Ritchey 2012; Ritchey et al. 2015), but here we separate the network into several subsystems rather than in two systems. The two views share the idea that this neurocognitive architecture not only supports episodic memory, but also other functions like perception, navigation, and semantic processing. In the PMAT framework, the ventromedial prefrontal cortex is a site of convergence between prefrontal and MTL components of the anterior temporal and posterior medial systems. This region would provide the value of item and bound representations, and exercise some control over the representations – notably, to select the relevant content as a function of the situation, and to help with the integration of new information within existing representations. Similar ideas figure in the integrative memory model, notably by suggesting that the self-representation system (involving the orbitofrontal and ventromedial prefrontal cortex) interacts with the core systems to provide some self-referential tagging, thus modulating the value of the representations in core systems. Close to the idea of control over mnemonic traces, we also include the prefrontal cortex in the attribution system. Although both the PMAT framework and the integrative memory model include the retrospenial cortex and posterior cingulate cortex, their role is conceived slightly differently. In the PMAT framework, both the retrosplenial cortex and the posterior cingulate cortex form parts of the posterior medial system that allows individuals to orient in time, space, and situation. In our model, we suggest that the retrosplenial cortex is an integral part of a core system dedicated to storing visuo-spatial and contextual information. In contrast, the posterior cingulate cortex acts as a relay node during cortical reinstatement of the memory trace and, by connecting all systems within the network, including the attribution system, it would contribute to the subjective experience of mentally reliving the episode. This is an original hypothesis of the integrative memory model suggesting a key role of the posterior cingulate gyrus in autonoetic consciousness.

Finally, the articulation of the model around the interaction between core systems and the attribution system is probably the most novel aspect of the integrative memory model. Currently, no recollection/familiarity neurocognitive framework has taken into account the principles from attribution theories. A first proposal relating the fluency heuristic to the perirhinal cortex has however been formulated by Dew and Cabeza (2013). We expand it by suggesting that reactivation of any component of the hierarchically represented item (i.e., object, face, building, word, simple association) will generate a fluency signal which is interpreted by the attribution system in the light of metacognitive knowledge. Similarly, reactivated patterns of complex representations via the hippocampus are also evaluated through the glasses of metacognitive knowledge before being attributed to the past. Because the mapping of attribution processes with cerebral regions is still to be confirmed, a lot remains to be learned about the exact neurocognitive mechanisms involved in the attribution system. For now, we have integrated theories about control mechanisms over memory to propose a mechanistic account of the attribution system. Notably, the attention-to-memory model (Cabeza et al. 2008; 2012; Ciaramelli et al. 2008) is key in describing the role of the parietal and prefrontal regions in attention and monitoring mechanisms.

6. The integrative memory model to understand recollection and familiarity deficits

6.1. Damage to core systems versus attribution system

According to the integrative memory model, the dissociation of recollection and familiarity in patients with lesions selective to the hippocampus or perirhinal/entorhinal cortex (Barbeau et al. 2011; Bowles et al. 2010; Brandt et al. 2016) would arise because the core representations are damaged. Hippocampal lesions prevent the encoding and retrieval of relational representations, and so hamper the possibility to re-experience all details from a past episode. In contrast, perirhinal/entorhinal lesions affect the creation of entity representations that cannot be subsequently felt as familiar. However, in the latter case, our model predicts that not all forms of familiarity will be impaired following perirhinal/entorhinal damage, but, more specifically, familiarity-based *discrimination* between stimuli that share features and require a conjunctive trace. This should be tested by directly manipulating the level of confusability of targets and distractors in recognition memory tests. Moreover, if the same representations support episodic recognition memory, short-term memory, and perception, a patient with a selective hippocampal lesion should present with impaired use of relational representations in a variety of tasks, beyond the episodic memory domain. For example, K.A., a patient with developmental amnesia and atrophy of the hippocampus, fornix, mammillary bodies, and anterior thalamic nuclei (i.e., the relational representation core system) shows both impaired source memory and impaired relational binding in short-term memory, with preserved conjunctive binding in short-term memory (Jonin et al. 2018; 2019). In contrast, a patient with a selective perirhinal/entorhinal lesion should be impaired in the processing of entities across recognition memory, perception, and short-term memory. Recently, Lacot et al. (2017) reported that J.M.G., who had damage to the MTL cortices preserving the right hippocampus, failed on a variety of recognition memory tasks involving objects and abstract pictures, but had good visual recall for spatial patterns and geometric figures and good scene-recognition performance. Interestingly, recollection as well as familiarity for objects and abstract pictures were affected, emphasizing the idea that the nature of representations carried by the perirhinal/entorhinal cortex versus the hippocampus matters more than the memory processes to explain J.M.G.'s profile.

With regard to the context representation core system, severe anterograde amnesia associated with mild retrograde amnesia has been described following lesion to the retrosplenial cortex (for reviews, see Aggleton 2010; Vann et al. 2009a). As the retrosplenial cortex connects the hippocampus to regions storing the sensory-perceptual details of memories, patients with retrosplenial amnesia should present with a recollection deficit (Aggleton 2010), as well as poor scene recognition and perceptual discrimination. The paucity of retrosplenial amnesia cases has not allowed researchers to test this prediction yet. However, Valenstein et al. (1987) described a case that showed impaired recall of paired associates and complex figures, but relatively preserved recognition memory for faces. This finding could speak for intact familiarity-based memory for entities contrasting with deficient relational memory.

Finally, frontal lesions should affect the adequacy of the explicit output with regard to the characteristics of the task or the quality of the subjective experience because of disruption of the attribution system. Some studies described impairment of monitoring of memory output following lateral prefrontal cortex lesions, leading notably to false recognitions (Schacter 1997). Moreover, metamemory abilities are negatively affected by frontal lesions, especially in medial prefrontal cortex (Pannu & Kaszniak 2005). If such monitoring and metacognitive mechanisms are common to recollection and familiarity processes, as we suggest, both should be impacted by prefrontal lesions. A few studies have assessed the consequences of frontal lesions on recollection and familiarity. Their results were inconclusive, with some studies reporting deficits only in recollection (Anderson et al. 2011; Stamenova et al. 2017; Wheeler & Stuss 2003), others indicating deficits only in familiarity (Aly et al. 2011; MacPherson et al. 2008), and a few studies describing deficits in both recollection and familiarity (Duarte et al. 2005; Kishiyama et al. 2009). This inconsistency is perhaps not surprising if one takes into account the fact that prefrontal areas are not supporting recollection and familiarity processes per se, but rather, are dealing with expectations, and with selection and monitoring processes operating on the reactivated content in answer to the specificities of the task at hand. In this view, a prefrontal lesion could reduce the expression of recollection/familiarity-based memory outputs in some conditions, but not others. We believe that the effect of frontal lesions on recollection and familiarity would be best apprehended by examining variation in memory outputs as a consequence of manipulations affecting expectations and criterion setting.

6.2. Recollection and familiarity in the course of Alzheimer's disease

The case of Alzheimer's disease (AD) is interesting to consider in the light of the integrative memory model for at least two reasons. First, this is a progressive disease in which the trajectory of cognitive decline is related to the spreading of neurofibrillary tangles and neuronal loss (Jack et al. 2013) starting in the anterolateral entorhinal and perirhinal cortices (Braak & Braak 1995; Braak & Del Tredici 2015), corresponding to Braak's Stage 1. As hippocampal pathology comes later (Braak's Stage 3), Braak's Stage 1 represents a unique model of selective MTL lesions targeting the entity representation core system, which is very rarely encountered in other neuropsychological populations (Barbeau et al. 2011; Bowles et al. 2007). Moreover, in amnestic mild cognitive impairment (aMCI), a diagnostic entity at high risk of developing AD (Albert et al. 2011), dysfunction of the posterior cingulate gyrus appears as a prominent feature (Chetelat et al. 2003; Dunn et al. 2014; Salmon et al. 2008). More specifically, although both the ventral and dorsal posterior cingulate cortex show hypometabolic activity in aMCI (Mutlu et al. 2016), the retrosplenial cortex demonstrates the most consistent reduction in metabolism (Nestor et al. 2003). Two mechanisms may contribute to such retrosplenial hypometabolism in aMCI: atrophy of the region (Pengas et al. 2010; Scahill et al. 2002), and distant consequence of the pathology affecting the hippocampus and anterior nuclei of the thalamus (Braak & Braak 1991; Villain et al. 2008). This loss of inputs is aggravated by disruption of the cingulum bundle that connects the hippocampus to the retrosplenial cortex (Villain et al. 2008). Patients with aMCI would therefore be a target population to link changes in recollection-based memory to the pathology of regions within the relational and context representation core systems.

Second, even if several studies have investigated the integrity of recollection and familiarity in aMCI and AD, the exact profile of deficits is still unclear. Most puzzling is the lack of any consensus regarding the fate of familiarity in aMCI and AD. Whereas a number of studies have reported preserved familiarity in these populations, an almost equal number of studies have shown that familiarity is deficient (for reviews, see Koen & Yonelinas 2014; Schoemaker et al. 2014). Of course, this divergence across studies can be partly explained by differences in terms of methods (i.e., paradigm used to assess recollection and familiarity, nature of the materials, etc.) and characteristics of the patients (i.e., severity of cognitive decline, cognitive domains affected beyond memory, heterogeneity of the aMCI population, and so forth). A systematic evaluation of these factors that modulate familiarity performance in aMCI and AD would actually be warranted. Beyond these methodological issues, we propose that considering the complex multifaceted nature of familiarity may shed some light on these divergent findings.

One factor that could help explain why it is difficult to get a clear picture of the exact profile of impairment of recollection and familiarity from current findings in aMCI and AD is the progressive nature of the pathology. Because key regions within the cerebral architecture of the integrative memory model are affected at different stages of the disease, we hereby propose a hypothetical scheme for the chronological pattern of deficits in the course of AD (see Figure 4). More specifically, some dimensions of recollection and familiarity processes may become dysfunctional at a specific stage of the disease depending on the brain regions most affected at that time. Progression stages will mainly refer to Braak's neuropathological stages (Braak & Braak 1991; 1995), in association with hypometabolism and atrophy. Amyloid burden does not appear to correlate with cognitive decline, but provides the background that defines Alzheimer's pathological changes (Jack et al. 2018). Figure 4 indicates when a deficit starts to appear, assuming that already existing impairments are still present and exacerbated by increased pathological burden.

In Stage 1, neurofibrillary tangles and neuropil threads are limited to the transentorhinal cortex, corresponding to the medial portion of the perirhinal cortex and the anterolateral entorhinal cortex (BA 35) (Taylor & Probst 2008). Even if individuals in that stage have amyloid pathology, they are asymptomatic and

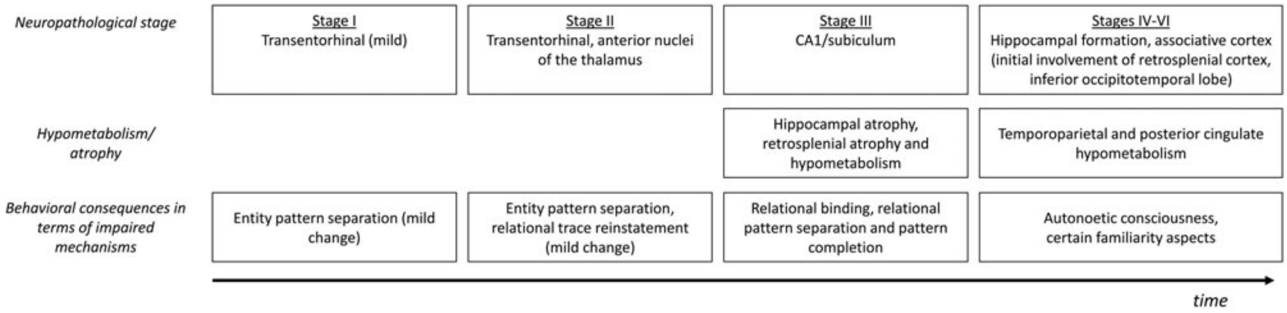

Figure 4. Chronological unfolding of deficits to specific mechanisms as a function of neuropathological changes in the course of Alzheimer's disease.

cognitively healthy. Nevertheless, we predict that the presence of neuropathology in the perirhinal/anterolateral entorhinal cortex would affect the ability of Stage 1 individuals to create complex conjunctive representations (i.e., entity pattern separation). This may not impact everyday life functioning, as the difficulty would be limited to specific cases requiring fine-grained entity-level discrimination, but could be seen in tasks that particularly probe rapid familiarity-based recognition of entities among very similar stimuli (Besson et al. 2017). Familiarity for non-conjunctive information and recollection should remain intact.

Stage 2 is still called a "transentorhinal stage" because it is characterized mainly by an aggravation of transentorhinal pathology. While most individuals in Stage 2 are asymptomatic, a few aMCI patients may harbor Stage 2 neuropathology (Petersen et al. 2006). Whereas impaired familiarity for entity should be relatively modest in Stage 1, it would be more clearly established in Stage 2, proportionally to neuropathology in the perirhinal/anterolateral entorhinal cortex. Of note, Braak and Braak (1991) reported mild changes to the anterior nuclei of the thalamus. As an important relay node in the Papez's circuit (Aggleton & Brown 1999), the anterior thalamic nuclei participate in the recollection of the content of past experienced episodes (i.e., relational representation core system). Therefore, slightly impoverished recollection should accompany these early pathological changes in the anterior thalamus. Still, poor familiarity for entities should dominate.

Stage 3 corresponds to invasion of neurofibrillary tangles in the hippocampus, initially affecting CA1 and the subiculum. Individuals in Stage 3 present significant memory decline compared to Stage 2, but no general cognitive decline (Grober et al. 1999). Most aMCI patients are indeed in this stage (Petersen et al. 2006). Moreover, in aMCI, hippocampal atrophy is typically found, especially in CA2 and CA3 (Hanseeuw et al. 2011), and a consistent hypometabolism is observed in the retrosplenial cortex (Nestor et al. 2003). Altogether, this would lead to dysfunction of the relational and context representation core systems, affecting the ability to bind item and context information in pattern-separated representations. Reinstatement of encoded patterns should also be impaired. Thus, recollection deficits are expected to occur, together with familiarity for entities as in earlier stages. Familiarity for non-conjunctive information still remains intact and poor recollection may dominate the memory profile in Stage 3/aMCI patients.

Stage 4 starts to include demented AD patients, with more and more severe cognitive impairment as one moves towards Stages 5 to 6 (Braak & Braak 1991; Grober et al. 1999; Petersen et al. 2006). In Stage 4, in addition to pathology affecting most parts of the hippocampal formation, mild changes to the isocortex can be seen. From Stage 5 onwards, the isocortex becomes more and more severely and widely affected, with a spreading of tau pathology to connected regions (Brettschneider et al. 2015). Initial isocortical pathology is notably present in the retrosplenial cortex and inferior occipitotemporal cortex (Braak & Braak 1991), and then transmits progressively to connected regions. On FDG-PET (i.e., fluorodeoxyglucose-positron emission tomography), one can see a typical pattern of temporoparietal, ventromedial prefrontal, and posterior cingulate hypometabolism from the mild AD stage (Herholz et al. 2002). Frontal atrophy also emerges, although later (Salat et al. 2001).

In Stage 4 and early Stage 5, impaired recollection should dominate as more and more regions contributing to the creation and reinstatement of complex relational representations are lesioned, notably the retrosplenial cortex. Consistently, an fMRI study indicated that, when AD patients used residual recollection capacities, they activated the posterior cingulate gyrus as healthy controls did, but showed impaired functional connectivity between the posterior cingulate gyrus and the hippocampus, inferior parietal cortex, and dorsolateral prefrontal cortex (Genon et al. 2013). Moreover, decreased self-reference memory effects suggest that the connection between the content of the memory trace and the self-reference system is reduced in early AD (Genon et al. 2014), in relation to atrophy in the medial prefrontal cortex and posterior cingulate gyrus (Wong et al. 2017). In addition, the difficulty to process entities, in memory tasks as well as in others such as perceptual tasks, would still correlate with the degree of pathology in perirhinal/anterolateral entorhinal cortex, as suggested by recent data in mild AD (Bastin et al. 2014; Delhaye et al. 2019; Kivisaari et al. 2013; Yeung et al. 2017). Finally, creation and reactivation of traces for simple items and associations associated with feelings of familiarity should remain possible, but mild pathology in the inferior occipitotemporal area could disturb processing of certain categories of stimuli that depend on this area, such as faces.

However, when attribution still functions relatively well (likely Stages 3 and 4, and maybe early Stage 5), in the context of objective (recollection) memory difficulties in everyday life, we predict that fluctuant familiarity may be observed because of metacognitive changes. Indeed, studies in amnesia have suggested that awareness of memory deficits in everyday life may modify the metacognitive assessment of fluency cues and lead to increased disqualification of such cues (Geurten & Willems 2017; Ozubko & Yonelinas 2014). Along those lines, for early stages of AD, the interaction between anosognosia and reliance on fluency cues would be a promising avenue for research. In aMCI and AD, awareness of memory difficulties is variable among patients (Starkstein 2014). It is possible that patients who acknowledge their memory deficits may be less prone to rely on fluency-based feeling of familiarity and would discard them more readily, whereas anosognosic patients would not and may even demonstrate an over-reliance on fluency-based familiarity.

When the disease starts to impact regions belonging to the attribution system (late Stage 5 and Stage 6), the interaction between (already degraded) contents and attribution becomes severely compromised, and both recollection and familiarity are likely to appear impaired in recognition memory tasks. In particular, patients will lose the ability to subjectively relive past events (i.e., autonoetic consciousness) and this deficit would correlate with decreased functional connectivity between the posterior cingulate hub and the rest of the network. Moreover, less efficient attribution processes could modify the transformation of reactivated content into subjective judgments and feelings. For example, in AD, despite the deficit in their recollection abilities, patients show increased false recollections (Gallo et al. 2010) and have a continued willingness to adopt retrieval strategies oriented towards recollection (Willems et al. 2008). To explain false recollections, it can be hypothesized that patients relax their criterion for experiencing recollection and even very partial recollection may trigger a feeling of remembering.

This hypothetical scheme of chronological changes in key mechanisms within the integrative memory model suggests that cross-sectional comparisons of groups of aMCI or AD patients on general measures of recollection and familiarity would provide divergent results because of variability in the pathological status (in terms of Braak's staging) of patients and in the type of mechanisms that tasks preferentially assessed. An ideal approach to test the unfolding of memory impairments would be longitudinal assessments of individuals from the asymptomatic stages of AD, with tasks designed to measure specific mechanisms such as entity pattern separation, relational pattern separation, pattern completion, and so forth, and with a possibility to relate these cognitive changes to the progressive topography of neurodegeneration, using, for example, tau-PET tracers (Schwarz et al. 2016).

7. Conclusions

The integrative memory model presents a framework of the computational mechanisms and their cerebral bases which support the encoding and retrieval of events in interacting core systems and attribution system. This model is not opposed to existing influential neurocognitive models of memory, but rather complements them by integrating many of their principles into a single view. This integration allows us to generate novel hypotheses. For instance, we have proposed that disruption of the posterior cingulate connectivity hub, where the retrosplenial cortex and ventral and dorsal posterior cingulate cortex play distinct but complementary roles, will alter cortical reinstatement of encoded details and autonoetic consciousness. Another novel prediction is that reactivation of traces in core systems does not necessarily lead to the subjective experience of recollection and familiarity. Subjective feelings and final explicit recognition judgments involve late attribution mechanisms. The intervention of such attribution processes could explain why apparently impaired use of familiarity may result from a strategic disqualification of fluency cues in people with memory problems.

We propose the integrative memory model with the aim to move forward research on the nature of the memory deficits in brain-damaged populations, as we believe that future studies should be framed in accordance with the latest advances in the knowledge about memory functioning. In particular, we consider the course of AD as a good example for applying our framework, by suggesting a scheme of chronological dysfunction of specific mechanisms depending on the topographical progression of neuropathological changes. Such a scheme suggests that the predominant impairment in terms of recollection and familiarity will shift during the course of the disease, with very early neurodegeneration of the perirhinal cortex associated with deficits in tasks that rely on the representation of items as viewpoint-invariant conjunctive wholes (e.g., familiarity for entities), and with increasingly dominant impairment of recollection when pathology invades several regions from the relational representation core system.

Our model could also serve as the basis to understand memory impairments in various conditions, ranging from healthy aging to disorders such as amnesia, temporal lobe epilepsy, and frontotemporal dementia. Further studies on brain damage that affects specific regions related to recollection and familiarity might provide important tests of the neurocognitive architecture of memory, and these could lead to a reconsideration of the proposed model – for example, if some hypothesized region-mechanism links were falsified by experiments. The proposed neurocognitive architecture is certainly not comprehensive and should evolve to incorporate other mechanisms. For instance, the notion of time, which is critical in episodic memory (Eichenbaum 2013), is not considered here.

Finally, a broader avenue for research would be to examine the role of the proposed neurocognitive architecture *beyond* memory: the role it plays in allowing humans to prepare for future events and to share the past.

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Open Peer Commentary

Refining the bigger picture: On the integrative memory model

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Abstract

The integrative memory model contains multiple subsystems. In this commentary, the processes within these subsystems are questioned. First, the assumption that familiarity largely reflects perceptual fluency is examined. Next, the distinction between "process" and "representational" models of temporal lobe function is challenged. Finally, the "relational representation core system" (or "extended hippocampal system"), which is central to the model, is especially sketchy. Here, I highlight key questions to be addressed in order to understand this system's role in trace formation.

Bastin et al. attempt to reconcile a plethora of different models concerning brain networks for the encoding, consolidation, and retrieval of episodic memory. There is much to admire, especially as a voice is given to many different ideas that have evolved over the past 20 years. The emphasis is on picking out common themes and bringing them together. A related theme is to look beyond the temporal lobe, to integrate parietal and frontal areas, as well as the medial diencephalon. These represent significant achievements, not least because they create bridges between the memory network models largely derived from classic neuropsychology, for example, the study of amnesic patients with confirmed brain pathology (which highlights the "relational representational core system") and wider network models, largely derived from functional magnetic resonance imaging (fMRI). An almost inevitable cost of this amalgamation is that elements of the current model remain underspecified, leaving them difficult to test.

The integrative memory model is embedded within dual-process models, which distinguish recollection from familiarity. It is presumed that the principal signal for familiarity comes from perceptual fluency, the change in threshold for information that has been previously experienced. This is an odd choice for several reasons. First, as stated, some amnesics can show seemingly intact repetition priming yet catastrophic recognition memory. Second, experiments showing that perceptual fluency can contribute to recognition often require special constraints. Third, electrophysiological studies, starting from the pioneering work of Malcolm Brown, reveal that for visual information, at least, some neurons in the rhinal cortex reduce their firing following stimulus repetition. This attenuated activity is not only seen in single-cell recordings in animals but is also present in fMRI studies (Aggleton & Brown 2006). The reduced activity in these neurons, thought to reflect long-term depression (Griffiths et al. 2008), would be sufficient to solve both familiarity and recency judgments. At the same time, it would be odd to categorise this signal reduction as perceptual fluency, as the latter would be expected to increase activity on stimulus repetition, given the fall in threshold. While it is the case that some perirhinal neurons may increase their firing gradually after hundreds of stimulus repetitions in test conditions associated with reinforcement (Holscher et al. 2003), this methodology is a far cry from cognitive tests of recognition memory. Although I agree with the authors' statement that "lesions to the perirhinal cortex will not necessarily affect all forms of familiarity" (target article, section 4.2.1, para. 1), their model places undue emphasis on what is probably a subsidiary process (perceptual fluency).

The authors also discuss distinctions between "process" and "representational" models within the medial temporal lobe. Process models emphasise the computational properties of a structure (e.g., pattern separation by the hippocampus) whereas representational models emphasise the different kinds of information available in different brain sites (e.g., context-rich information in the hippocampus versus context-sparse information in perirhinal cortex). This distinction has been previously made, but represents a false dichotomy. Those espousing "representational" models surely do not presume that changes in representation happen by magic, they arise from the novel connections and architecture that permit different computations in different areas. At the same time, the dense, reciprocal interconnections between different medial temporal lobe sites result in the shared ownership of some representations (and processes).

Central to the integrative memory model is the "relational representation core system" (see sect. 3). The key components of this system are the hippocampus, mammillary bodies, anterior thalamic nuclei, and their interconnections – the "extended hippocampal system" (Aggleton & Brown 1999). These medial diencephalic interconnections are presumed to help build the memory trace, in which item and context are bound. Recollection then emerges preferentially from reactivation of traces within this system. Surprisingly little evidence is provided by Bastin et al. for this core system, yet animal models and the analysis of patients with colloid cysts have proved most insightful. To take the latter, it has been repeatedly shown that interruption of the fornix (which provides hippocampal inputs to both the anterior thalamus and mammillary bodies, among other sites) is sufficient to cause an anterograde amnesia that preferentially impairs recollection (Vann et al. 2009b). The resulting losses in recollection, but not familiarity, correlate closely with the extent of mammillary body atrophy (Tsivilis et al. 2008). Renewed interest in the mammillary body–anterior thalamic axis has provided novel insights into the memory loss in conditions such as developmental amnesia (Dzieciol et al. 2017), Korsakoff's syndrome (Segobin et al. 2019), thalamic vascular damage (Carlesimo et al. 2011), and Alzheimer's disease (Aggleton et al. 2016).

Even less consideration is given in the integrative memory model for why these two medial diencephalic structures are so critical. It appears that these particular structures provide key information for memory encoding that otherwise would not reach the hippocampus (Aggleton et al. 2010). If we just focus on the anterior thalamic nuclei, we can see that afferents potentially matching the above criteria arise from the mammillary bodies, parts of the frontal lobe (especially more dorsal areas), the reticular thalamic nucleus, and Gudden's tegmental nuclei (via the mammillary bodies). These inputs can interact with hippocampal processing via projections from the anterior thalamic nuclei to hippocampal and parahippocampal areas. A related possibility is that anterior thalamic and hippocampal efferents converge on a third site, for example, retrosplenial cortex, where their combined interaction is critical for memory. The discovery of spatial cells in the rat anterior thalamus (Jankowski et al. 2015) adds weight to the idea that these diencephalic processes involve individual mnemonic representations, as suggested by the integrative memory model. Key questions remain as to why there is an apparent duplication of information across medial diencephalic and temporal structures, allied to the need to test their independence and interdependence.

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Representational formats in medial temporal lobe and neocortex also determine subjective memory features

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Abstract

Episodic memories are shaped by the representational format of their contents. These formats are not only determined by medial temporal lobe areas, but essentially also by the neocortical regions which these areas control. The representational formats of medial temporal lobe and neocortex are sufficient to determine both, memory contents and subjective memory qualities, without the further need for an attribution system.

Bastin et al. propose an integrative framework for episodic memory based on interactions between two representational subsystems and an attribution system. They suggest that an "entity representation core system" supports familiarity, a "relational representation core system" is recruited for recollection, and an "attribution system" determines subjective memory qualities (target article, sect. 3). I agree with many aspects of their proposal. Describing memory in terms of the representational formats in which prior experiences are reinstated, and linking these formats to specific brain structures and distinct subjective qualities, is a fruitful and innovative approach. The authors nicely describe that the common distinction between representational and process-based memory theories is not as clear-cut as it may seem, since specific types of representations lend themselves more naturally to specific computational processes.

Despite my overall agreement, I would like to make two critical comments. First, I believe the proposed framework could emphasize more the impact of memory representations in neocortical areas beyond the medial temporal lobe. Second, I am not convinced that representational systems only determine the content of memories whereas an attribution system defines their subjective quality. Instead, I suggest that the subjective qualities of memory can also be explained by specific representational formats, rather than by a separate system for metacognitive judgments.

With regard to the first aspect, Bastin et al. strongly focus their proposal on the contribution of the hippocampus and the perirhinal cortex. As demonstrated by decades of neuropsychological research, these structures are indeed central and indispensable for memory functioning. Nevertheless, the representational features of memories as well as their subjective properties (see also my second point below) are determined not only by properties of medial temporal areas, but crucially also by the representational formats in specific neocortical areas which they control during retrieval. The authors do acknowledge the role of neocortical regions such as the occipitotemporal and posterior parietal cortex for the entity representation core system and for integrative functions; however, they do not attempt to explain properties of memory representations by the representational features of these neocortical areas. In fact, it is unlikely that the full content of memories resides in the distribution of synaptic weights in medial temporal areas. Instead, as acknowledged by the authors, these regions act as "pointers" to neocortical areas (Pacheco et al. 2019; Teyler & Rudy 2007).

I would like to give four examples where neocortical areas are relevant for understanding memory representations. First, episodic memories are characterized by either an egocentric or an allocentric visual perspective (Conway & Pleydell-Pearce 2000; Nigro & Neisser 1983). These perspectives are putatively determined by egocentric representations in posterior parietal cortex (e.g., Byrne et al. 2007) versus perspective-invariant (allocentric) representations in the temporal neocortex. Second, memory representations contain varying degrees of perceptual detail versus general semantic information, and in extreme cases may only consist of schematic event knowledge. The perceptual versus conceptual representational format of a memory likely maps onto neocortical processing steps (with schema representations depending strongly on prefrontal regions). Third, episodic memories rely on the construction of mental scenarios (Barry & Maguire 2019; Cheng et al. 2016) whose level of detail can be flexibly adapted to fit situational demands. Their different degrees of representational detail may reflect the different processing steps in sensory areas as well as contributions from semantic expectations and schemas, which all rely on neocortical areas. Finally, autobiographical episodic memories in healthy subjects can, if they are sufficiently relevant, become central constituents of personal narratives, that is, of the stories that people tell about themselves (e.g., Renoult et al. 2012). By contrast, intrusions and flashbacks in posttraumatic stress disorder patients are characterized by a lack of semantic processing and narrative integration; therapeutic concepts such as narrative exposure therapy attempt to transform these pathological representational formats into more context-dependent and semantically integrated ones (Schauer et al. 2011).

Now, egocentric versus allocentric visual perspectives, perceptual versus conceptual representations, flexible representations, and the amount of narrative integration are just some examples for those representational features of memories which can only be understood by taking into account the representational properties of neocortical areas – in particular, in ventral and dorsal visual streams and in the corresponding networks in other sensory modalities. This is emphasized in conceptual frameworks such as Brewin's "dual representation theory" (Brewin et al. 1996). These frameworks still assume a central role of medial temporal lobe structures (including the amygdala, which is not mentioned in the Bastin et al.'s proposal) for controlling these representations, whose properties are nevertheless essentially determined by the specific computations in neocortical areas.

With regard to my second point, I believe the authors underestimate the influence of representational properties on the subjective features of memories. Although I agree that fluency signals and context-dependent expectations may shape how we subjectively experience a reinstated memory representation, the subjective, or phenomenological, features of episodic memory are primarily determined by the specific representational formats of the memorized events. In addition to the examples described above, feelings of familiarity and recollection can also be best explained by the representational properties of an event – that is, whether individual items or relational information is being remembered. In fact, Bastin et al. acknowledge that these types of representations are predominantly associated with feelings of familiarity or recollections; however, as there are some cases where these feelings dissociate from their typical contents, they propose to explain the feelings by metacognitive mechanisms rather than representational features. I would actually find it more parsimonious to embrace the general heuristic value of representational formats for explaining subjective memory experiences and conceptualize possible dissociations as atypical effects of representations for which the overall system was not designed. In fact, it is not even clear whether feelings of familiarity that occur in atypical conditions – and in particular in patients with neurological disorders – are the same as those under common circumstances. In other words, if feelings of familiarity or recollection do not match with the typical representational format of the corresponding memories, are these feelings really the same as in more common cases?

The integrative memory model is detailed, but skimps on false memories and development

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Abstract

The integrative memory model combines five core memory systems with an attributional system. We agree with Bastin et al. that this melding is the most novel aspect of the model. But we await further evidence that the model's substantial complexity informs our understanding of false memories or of the development of recollection and familiarity.

The integrative memory model is comprised of six interacting memory systems. There is a relational representation core system central to recollection, and an entity representation core system central to familiarity. These connect to a context representation core system, a self-referential system, and a connectivity hub. The productions of these systems interface with a unitary attribution system reminiscent of the evaluation process in Whittlesea's (1997) Selective Construction and Preservation of Experiences (SCAPE) account of memory. SCAPE's attribution system is where cued memory traces, stimulus structure, task, and context interact in what Leboe-McGowan (2019) dubbed the "hokey pokey" (in reference to the popular children's participation dance) to yield subjective experiences and reports of recollection or familiarity.

We are thrilled to see a neurocognitive model that incorporates an attributional process informed by Whittlesea's work. And we agree with Bastin et al. that the melding of the core and attributional systems is the most novel aspect of the integrative memory model. However, the "hokey pokey" of multiple systems in the integrative memory model, particularly the inclusion of separate systems for recollection and familiarity, is antithetical to Whittlesea's unitary memory system approach. In Whittlesea's (1997) words, "Memory is fundamentally very simple. Human performance derives its complexity not from the architecture or processing of memory but from the variety of tasks, stimulus structures, and contexts to which memory is exposed" (p. 260). Here, we side with Whittlesea, and suggest that a drawback of the integrative memory model's complexity is that it may be difficult to determine whether recollection or familiarity arise from productions within the model's core systems or evaluations within the attribution system. Given the alignment of integrative memory model systems with distinct brain architectures, perhaps researchers can leverage brain imaging and connectivity analyses to justify this complexity. Regardless of whether the integrative memory model's complexity proves justifiable, however, we suggest that it currently has at least two major blind-spots: false memories and development. We consider each in turn.

False memories

Memory is a fundamentally reconstructive process; therefore, a truly integrative model of memory must explain how false memories arise. Rates of false memory phenomena, including the misinformation effect, can exceed 50% of participants (e.g., Loftus et al. 1978). Similarly, high levels of false memories occur in the Deese–Roediger–McDermott effect, in which people falsely recollect a nonstudied word (e.g., sleep) that is the top semantic associate of a list of presented words (e.g., bed, rest, tired, etc.) (Deese 1959; Roediger & McDermott 1995). Finally, rates of rich false memories, in which people come to believe entire events that never happened, can reach 50% of participants (e.g., Scoboria et al. 2017). Some of these false memories merely feel familiar. The integrative memory model describes how familiarity-based retrieval can produce correct or false recognition (see Bastin et al.'s Fig. 2). However, a sizable proportion of these and other types of false memories are experienced as recollected. Although the integrative memory model provides a detailed description of recollection-based true memories (see their Fig. 3), it does not currently address the processes underlying recollection-based false memories.

From both theoretical and applied perspectives, it is important to understand how and when false recollection versus false familiarity arise, and how true and false memories differ (Bernstein & Loftus 2009). Instead of tackling false memories, Bastin et al. focus on the model's ability to explain memory impairments, including amnesia, frontal lesions, and especially the various stages of Alzheimer's disease. Damage to the integrative memory model systems may explain deficits in recollection or familiarity, but how does it explain whether someone experiences false memories as recollected versus familiar? Do false recollections arise within the core systems or the attribution system? How could we tell? Perhaps the aforementioned brain imaging and connectivity analyses can be used to answer these questions. We suggest that studying the conditions that predict whether individuals with amnesia, frontal lesions, and Alzheimer's disease will experience a false memory as recollected versus familiar would enhance the model's contribution.

Development

Bastin et al. thoroughly review the neuro-atypical memory literature, and detail how lesions and other neural insults impair recollection and/or familiarity. They suggest that longitudinal study of memory impairments would have great utility. We agree. However, we suggest that the authors have overlooked an important complementary approach – namely, the study of how recollection and familiarity develop and shift across the lifespan. Childhood and old age involve dramatic structural and functional changes to brain and behavior. Therefore, we believe that it would be informative to consider developmental patterns in recollection and familiarity across the lifespan. In the case of false memory, the integrative memory model might be informed by considering how the likelihood of different memory errors shifts in childhood and adulthood. In memory implantation studies, experimenters use suggestive techniques to lead participants to remember having experienced certain event details or entire events that never occurred (see Loftus 2018). From our reading of the lifespan developmental literature on false memory, misinformation-based and rich false memories tend to follow a U-shaped development: These false memories are more frequent in childhood and older adulthood than in younger adulthood (see also Brainerd & Reyna

2005; Frenda et al. 2011). Conversely, the Deese–Roediger–McDermott illusion increases linearly from childhood to older adulthood (e.g., Brainerd et al. 2008; Gallo 2010). How might these different data patterns relate to the core versus attributional systems in the integrative memory model? We welcome Bastin et al.'s insights on how developmental patterns in false memory illusions might constrain or validate their model. Indeed, we feel it would be informative to consider the development of recollection and familiarity processes for both true and false memories.

In sum, Bastin et al. should justify the integrative memory model's substantial complexity by addressing how that complexity contributes to our understanding of (1) different types of false memory phenomena (particularly false recollection), and (2) the development of recollection and familiarity for true and false memories across the lifespan. By incorporating these missing elements, we feel the integrative memory model would be more integrative and thus better live up to its name.

Entities also require relational coding and binding

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Abstract

Although Bastin et al. propose a useful model for thinking about the structure of memory and memory deficits, their distinction between entities and relational encoding is incompatible with data showing that even individual objects – prototypical "entities" – are made up of distinct features which require binding. Thus, "entity" and "relational" brain regions may need to solve fundamentally the same problems.

A fundamental tenet of the integrative memory model proposed by Bastin et al. is the distinction between entity representation and relational representations. This distinction is based on the premise that there is a meaningful sense of an "entity" that is holistic and unitized and can be stored and retrieved without recollection or binding; for example, Bastin et al.'s claim that at the "level of the perirhinal cortex and anterolateral entorhinal all visual features are integrated in a single complex representation of the object that can be discriminated from other objects with overlapping features."

It is natural to think that meaningful visual objects might be unitized entities for visual memory, and indeed many memory researchers take this claim for granted. However, we believe this view of unitized, fully bound representation of objects is inconsistent with the cognitive data on object memory. In particular, supposed "entities" such as visual objects are not unitized representations, but themselves are stored as separate features requiring binding in the same fundamental way that objects need to be bound to contexts. This calls into question the core distinction between entities and relations proposed by the integrative memory model and other similar models: If even single objects are stored in a way consistent with the "relational system" – where the "representation keeps components separate and flexibly bound" (target article, sect. 4.1, para. 7) – then it is not clear what an entity would be or whether the fundamental nature of the brain regions subserving object memory are really distinct from those subserving item-context integration.

Work from our labs shows that visual object features are stored and accessed independently in long-term memory: Different features of single individual objects are forgotten at different rates (Brady et al. 2013); and people remember particular features but don't remember which objects these features belonged to (Utochkin & Brady 2019). For example, if people are shown a blue open backpack and then asked to choose among sets of four backpacks that are blue/open, blue/closed, or red/open, red/closed, people can forget the color but still can remember its "open-ness" (Brady et al. 2013). Or, if people are shown one mug (mug A) full of coffee and another mug (mug B) empty, they are well above chance reporting that they saw one full mug and one empty mug, and that they saw mug A and mug B, but they are at chance at ascribing the "fullness" and "emptiness" to the particular mugs A and B (Utochkin & Brady 2019).

Indeed, the idea that some items might be stored in a fully unitized representation (in an "entity" system) seems incompatible with the cognitive problem that object representations are designed to solve. One of the central requirements of a visual memory system is robustness to variation (Schurgin & Flombaum 2018). If object representations were totally integrated entities in memory, their recognition in the real world would be extremely problematic, given the infinite number of poses and states these objects can take, as well as variations in orientation, lighting, and more. One might argue that this invariant recognition is possible if a unitized "concept" of a particular object is formed during multiple episodes – connecting across multiple experiences when an object is presented in different states and viewpoints. But this claim immediately implies an independence of the features forming the core of this concept and those representing the way it changes across contexts.

In contrast to any view based on unitized object memories, we have demonstrated that people's memories are extremely robust to variation even at the level of individual objects, suggesting that representations even at the level of objects are based on separate features that are flexibly bound together rather than unitized. For example, imagine you saw an open-doored cabinet, and then later we asked which cabinet you had seen – but now the "old" item was shown in a new state (the same cabinet now has its doors closed, changing a huge number of visual features). We have shown that people are nearly perfect at generalizing in this way, and can do so even if the "foil" presented at test is a new open-doored cabinet, designed to maximally mislead participants (Utochkin & Brady 2019). Therefore, we believe the flexible nature of binding attributed by the integrative memory model only to item-context distinctions and recollection situations, need to be extended to nearly every level of representation of objects as well as contexts.

Similar evidence for independence and structured representation rather than unitized objects is present in the visual working memory literature, where it is frequently found that both objects and separate features can be stored and objects are not stored as single integrated units (see Brady et al. 2011 for review). Since working memory is critical for consolidation into long-term memory, this may be the beginning of the non-unitized, non-integral storage of items in memory.

Overall, we believe that entities are stored in a way that is not holistic or unitized – and thus, at nearly every level of representation, there is a need for flexible, relational encoding. If this is a common property of memories for individual objects (which is associated with "entities") and complex episodes (requiring the involvement of "relational representations"), then is there a fundamental difference in the representation of these two kinds of information, as proposed by the authors? If there is, then how does one know where an entity ends and a relational representation begins? We believe our work and that of the rest of the visual memory community is more consistent with the idea that there is a *hierarchy* of representations, each requiring the storage of relational information and each allowing for the possibility of misbinding and other retrieval failures. Thus, rather than a strong dichotomy between entities and relational storage, the benefits of flexible, independent storage, and the resulting problem of binding features together, occur at every level of the hierarchy – from the simplest visual feature conjunctions to the binding of objects into contexts and into events.

Improving the integrative memory model by integrating the temporal dynamics of memory

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Abstract

Despite highlighting the role of the attribution system and proposing a coherent large-scale architecture of declarative memory, the integrative memory model would be more "integrative" if the temporal dynamics of the interactions between its components was clarified. This is necessary to make predictions in patients with brain injury and hypothesize dissociations.

"Integrative" is a major asset and is highly relevant to qualify the model presented by Bastin et al. in the target article. *Integration* is inseparable from *multimodality* and *multidimensionality*: the integrative memory model postulates that the systems processing representations, relations, and attributions are linked inside a coherent "architecture" allowing emergent properties. Within this context, one of the major advances proposed by the integrative memory model is the integration and the clarification of the role of the attribution system, which is thought to depend mostly on the prefrontal cortex. In contrast, most previous models of memory were centered on the temporal lobes and Papez circuit.

Some of the aspects of the temporal dynamics of memory that are currently not fully described in the model are: time perception during memory (Eichenbaum 2017a); time sequences that distinguish temporally distinct episodes and stimuli (Ekstrom & Ranganath 2018; Ranganath & Hsieh 2016); projection in the future (Addis & Schacter 2012); and the time scale for building memories at the cellular level (Kukushkin & Carew 2017). However, in this commentary we want to focus on another aspect of temporal dynamics that is essential to clarify the architecture of the integrative memory model. Because the integrative memory model, as its name implies, integrates different components, it is crucial to specify what kind of relation they entertain. This information is missing from the present model. The authors have devoted a large portion of the target article to describing the general architecture of the components, leaving little space to discuss exactly how they relate. (We think that their model could have been dubbed the interaction memory model just as well as the integrative memory model.)

Yet, although not fully specified, the integrative memory model is already based on a few assumptions regarding its temporal dynamics. For example, in line with many previous studies, familiarity is supposed to be rapid. The model also assumes that memory "emerges from *hierarchically* organized representations distributed throughout the brain" (target article, sect. 5.3, para. 1; emphasis added), which suggests a precise order in which the different components are activated. In contrast, most arrows connecting the different components of the model are bidirectional, perhaps due to the lack of knowledge about the connectivity between the components. However, the very presence of these arrows suggests structural and functional connections that have to be characterized.

Using behavioral reaction times for various memory tasks, it is possible to get an idea of the latency of the activation of some of these systems and such latencies can be used as upper time constraints. For example, behavioral paradigms based on time constraints can be used to precisely assess the speed of familiarity (Besson et al. 2012). Recording brain activity using surface EEG (electroencephalography) or MEG (magnetoencephalography), possibly with source reconstruction, or combined EEG-fMRI (functional magnetic resonance imaging) recordings (Hoppstädter et al. 2015) provides a more refined idea of the activation latencies of each component of the model. Intracranial EEG is spatially more precise and reveals, for example, a striking delay between the activity of the perirhinal cortex and the hippocampus that should be taken into account in models of memory (Barbeau et al. 2008; Trautner et al. 2004). Methodological advances even allow comparison of the neuronal activity of different medial temporal lobe regions involved in memory (Mormann et al. 2008). Moreover, it is also possible to calculate the strength of functional interactions between brain regions, as well as causality and synchrony indices, using various approaches such as fMRI (Staresina et al. 2013), intracranial EEG (Krieg et al. 2017; Kubota et al. 2013; Steinvorth et al. 2010), and thorough analyses of neuronal activity (Staresina et al. 2019).

In parallel, validating these dynamics in clinical situations is necessary. Alzheimer's disease – inducing slowly increasing damages to many brain areas involved in both the representation and attribution systems of the integrative memory model – is a pertinent example chosen by the authors. However, it is insufficient to test the model's dynamics. Experiential memory phenomena such as déjà-vu (an erroneous feeling of familiarity) or reminiscences (memories including a mental content and recollection) allow testing of the model on another time scale (Curot et al. 2017). These phenomena are highly transient – hundreds of milliseconds to a few seconds. This is the real-time scale of familiarity feelings, recollection, ecphory, and mental imagery. They become all the more valuable when they are induced by electrical brain stimulations, since these stimulations also allow inferring the directionality and latency of connectivity (David et al. 2013; Trebaul et al. 2018). For example, the absence of any subjective experience after electrical brain stimulations of the posterior cingulate cortex is mentioned in the target article, suggesting that the posterior cingulate cortex is not involved in representations (Balestrini et al. 2015; Foster & Parvizi 2017). In fact, it also suggests that the posterior cingulate cortex cannot be an entry point in the integrative memory model.

Using such approaches, it would be possible to get an idea of how the model may work effectively. It would also be possible to start making precise predictions about the consequences of injury to specific components of the integrative memory model in neuropsychological populations. Dissociations could be hypothesized and tested. As an important novel aspect of the integrative memory model is the attribution system, it appears particularly relevant to assess more specifically the relations between this system and the entity and context core systems. It is likely that clarifying the dynamics of these relationships will help to reveal novel findings regarding a variety of neuropsychological syndromes. A positive aspect of new neurocognitive models is that their details can be refined, compared to observations, and tested in new experiments, thereby opening new avenues for research. Let's go.

What face familiarity feelings say about the lateralization of specific entities within the core system

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Abstract

The target article carefully describes the memory system, centered on the temporal lobe that builds specific memory traces. It does not, however, mention the laterality effects that exist within this system. This commentary briefly surveys evidence showing that clear asymmetries exist within the temporal lobe structures subserving the core system and that the right temporal structures mainly underpin face familiarity feelings.

In their integrative memory model, Bastin et al. describe recollection and familiarity as the interaction between core systems, which store specific types of representations, and an attribution system that translates content reactivation into a subjective experience. According to the authors, within these systems, specific types of representations (such as people and things) are uniquely shaped by specific computational operations and are involved in item familiarity. Therefore, these systems build specific memory traces, and damage to them induces severe degradation of these memory traces.

Bastin et al. distinguish the function of various structures included in these systems (i.e., perirhinal cortex, ventral temporopolar cortex, lateral orbitofrontal cortex, and amygdala) but do not mention the difference that, according to some authors (e.g., Gainotti 2012; Woollams & Patterson 2018), could exist between left and right anterior temporal lobes in the processing of verbal and non-verbal representations. However, there is convincing evidence that this lateralization of verbal and non-verbal representations of people and things is reflected in the lateralization of the corresponding familiarity feelings that can be observed in both normal and pathological conditions. This is particularly clear for face familiarity feelings, which are very important in personal interaction, because of the social relevance of distinguishing well-known from unfamiliar people.

A relationship between the right hemisphere and face familiarity feelings has, indeed, been repeatedly demonstrated in healthy subjects, by asking them to make familiarity judgments about faces presented separately to the right and left visual fields, and by studying the lateralization of event-related potentials or of magnetoencephalographic (MEG) waveforms evoked by face familiarity. For instance, Stone and Valentine (2005) showed that, when faces were unilaterally presented so briefly that they could not be consciously perceived, the right hemisphere differentiated famous from unfamiliar faces more rapidly than the left hemisphere; and Kloth et al. (2006) suggested that the mechanisms underlying the right hemisphere involvement in face familiarity feelings might primarily concern the early stages of visual processing. Analogously, a selective defect of face familiarity feelings was documented by Gainotti and Marra (2011) in patients with unilateral lesions of the anterior or the posterior parts of the right temporal lobes, who showed a familiar people recognition disorder.

Although a general review of these investigations can be found in Gainotti (2007), I more recently expanded the study of the different hemispheric specialization that might concern the representation of different verbal (name) and non-verbal (face and voice) modalities of person identification (Gainotti 2013). With this aim in mind, I took into account investigations that had evaluated laterality effects in recognition of familiar names, faces, and voices in normal subjects, by means of behavioral, neurophysiological, and neuroimaging techniques. Results of this survey indicated that: (a) recognition of familiar faces and voices shows a prevalent right lateralization, whereas recognition of familiar names is lateralized to the left hemisphere; (b) the right hemisphere prevalence is greater in tasks involving familiar than unfamiliar faces and voices, and the left hemisphere superiority is greater for the recognition of familiar rather than unfamiliar names. Taken together, these data suggest that hemispheric asymmetries in the recognition of faces, voices, and names are not limited to their perceptual processing, but also extend to the domain of their cortical representations.

Also consistent with these general views, but more specifically relevant to the problem of the relations between loss of face familiarity feelings and disruption of the right anterior temporal lobe are the results obtained recently by Borghesani et al. (2019), who studied, in a large sample of patients with neurodegenerative disorders, the neuroanatomical substrates of three different steps of famous-face processing. Using voxel-based morphology, these authors correlated whole-brain gray matter volumes with scores on three experimental tasks that targeted, respectively: (a) familiarity judgment, (b) semantic/biographical information retrieval, and (c) naming. Although performance in naming and semantic information retrieval correlated significantly with gray matter volume in the left anterior temporal lobe, familiarity judgment correlated with the integrity of the right anterior middle temporal gyrus.

Taken together, these findings suggest that computational operations linked to the different formats of representations subsumed by the right and left anterior temporal lobes should be taken into account in a general model which aims to describe the neurocognitive architecture of representations and operations underlying recollection and familiarity.

It could be objected that the integrative memory model aims to understand the organization of episodic memory, whereas the above-surveyed data are more relevant to the organization of semantic rather than episodic memory. However, even leaving apart the interdependence between episodic and semantic memory (e.g., Greenberg & Verfaellie 2010), the specific subject of this commentary concerns familiarity for faces that, due to its relevance in social interactions, lies at the border between the episodic and semantic memory systems.

How do memory modules differentially contribute to familiarity and recollection?

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Abstract

We fully support dissociating the subjective experience from the memory contents in recognition memory, as Bastin et al. posit in the target article. However, having two generic memory modules with qualitatively different functions is not mandatory and is in fact inconsistent with experimental evidence. We propose that quantitative differences in the properties of the memory modules can account for the apparent dissociation of recollection and familiarity along anatomical lines.

Bastin et al.'s integrative memory model of recognition memory conceptually separates the subjective experience, which is created in an attribution system, from the memory contents, which are stored in and retrieved from core memory modules. Basing recognition memory on *generic* perceptual-mnemonic systems seems more appropriate to us than postulating two dedicated memory systems based on differences in phenomenology (Brown & Aggleton 2001). Since phenomenology is private to the individual, it cannot confer an evolutionary benefit and, therefore, evolution cannot select for memory systems based on subjective experiences (Cheng et al. 2016; Suddendorf & Corballis 1997). In the integrative memory model, the memory modules have qualitatively different functions: The entity representation core system processes single items and the relational representation core system processes the relationships between the items. The integrative memory model postulates that retrieval from the former is always associated with familiarity, but familiarity can also arise from the latter, when certain types of stimuli, for example, images of scenes, are used. By contrast, recollection arises only based on the relational representation core system. However, memory retrieval from a particular system by itself is not sufficient to account for the phenomenology, according to the integrative memory model. Instead, subjective experiences of familiarity and recollection are generated by a separate attribution system that evaluates the retrieved memory.

Although we embrace the diversity of memory systems (Werning & Cheng 2017), we argue that memory modules might differ in ways other than those considered by Bastin et al., and that other differences are potentially more consistent with the available evidence on recognition memory. Memory modules can (1) have qualitatively different functional properties, (2) receive different inputs, and (3) have different quantitative properties. The integrative memory model considers the first two cases. Here, we present the confounds of their assumptions and discuss the third possibility.

The integrative memory model predicts that the perirhinal and entorhinal cortices are part of the entity representation core system, which performs entity pattern separation, that is, distinguishing between similar stimuli based on conjunctive representations. The authors suggest that experiments manipulating the similarity between targets and lures can test the role of the perirhinal/entorhinal damage on recognition performance. Such studies exist. When lures were highly similar to targets, recognition performance of aged individuals with mild cognitive impairment (MCI) and Alzheimer's disease (AD) is indeed impaired, compared to age-matched controls (Westerberg et al. 2006). However, the deficits might arise from comorbid hippocampal damage in the early stages of AD and in MCI (Du et al. 2001) rather than from perirhinal damage, or from hippocampal impairment due to aging (Raz et al. 2005), resulting in difficulty in distinguishing similar items (Stark et al. 2013).

Moreover, evidence suggests that it is the hippocampus that is important for distinguishing highly correlated items. In the Westerberg et al. (2006) paradigm, patients with selective hippocampal lesions rejected highly related lures less frequently than healthy controls (Bayley et al. 2008; Holdstock et al. 2002), whereas recognition performance with unrelated lures is often preserved. In agreement with these findings, theoretical work concludes that representational overlap in cortex is higher than in the hippocampus (Greve et al. 2010; Norman & O'Reilly 2003). These experimental and theoretical results seem to oppose the predictions of the integrative memory model.

The second possibility is that memory modules differ in their inputs. According to the dual stream model (Mishkin et al. 1983), perirhinal cortex processes object information ("what" stream), while parahippocampal cortex receives spatial inputs ("where" stream). Information from both streams converges in the hippocampus (Beer et al. 2018). Because, both perirhinal cortex and hippocampus receive object information and almost all recognition memory experiments employ visual stimuli in the same physical location, difference in inputs cannot account for possible differences in phenomenology in recognition memory task. In contrast to Bastin et al., we regard images of scenes as "what" information, which is quite different from information about the animal's current location ("where" information) (Azizi et al. 2014; Neher et al. 2017).

Finally, memory modules can differ in their quantitative properties. The phenomenology of familiarity and recollection, in principle, could be generated within a single type of memory module, for example, in a memory retrieval process with attractor dynamics (Greve et al. 2010). Specifically, after the presentation of a retrieval cue, the state of the memory network is updated until it converges to an attractor state. The success of retrieval depends on the attractor landscape. If the attractor state is veridical, it contains indices to neocortical representations providing additional details in the spirit of the hippocampal indexing theory (Fang et al. 2018a; 2018b; Teyler & DiScenna 1986; Teyler & Rudy 2007). If these keys lead to the retrieval of meaningful information, the retrieved details are assigned higher weights and lead to high-confidence recollective experiences. However, if the attractor state is spurious, then either no details are retrieved or the retrieved information seems improbable. So, a familiarity response is generated with a strength depending on the depth of the attractor state. Therefore, high- and low-confidence responses can rely on familiarity and recollection (Ingram et al. 2012) depending on the attractor depth, the amount of recollective details, and the consistency of the details. This suggestion is akin to the one in the integrative memory model that the attribution system assesses the amount of mnemonic information and leads to recognition phenomenology based on the relevance and strength of retrieved details.

In conclusion, we suggest that the perirhinal cortex gives rise to familiarity more often, because the attractors are shallower due to weaker plasticity, and the network is more prone to generating spurious attractors due to higher noise or less robust representations. By contrast, the hippocampus has stronger plasticity and is less prone to generate spurious attractors, consistent with its specialization for one-shot encoding of episodic memories (Cheng 2013; Cheng & Werning 2016).

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Priming recognition memory test cues: No evidence for an attributional basis of recollection

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Abstract

We argue that while the proposed memory model by Bastin et al. can explain familiarity-based memory judgements through the interaction of a core representation system and an attribution system, recollection-based memory judgements are not based on non-mnemonic signals being attributed to memory.

Bastin et al.'s integrative memory model proposes that subjective memory experiences result from the interaction between core representational systems and an attribution system. The relevant core representational system in the case of familiarity concerns "entity" processing, the implementation of which involves perirhinal cortex, a region regarded to be at the apex of visual object processing. The core representation system for recollection concerns "relational" processing, and includes hippocampus, posterior cingulate, and retrosplenial cortex, which together are believed to coordinate the reactivation of stimulus- and context-specific representations distributed through cortex. So far, this picture is broadly consistent with our impressions of the cognitive, neuropsychological, and neuroimaging literatures on recollection and familiarity.

The "attribution system" is more nebulous, and perhaps more controversial. The term "attribution" implies that in addition to mnemonic signals, *non-mnemonic* signals are sometimes interpreted as having arisen due to prior exposure to the test item. In general, this could be a sensible heuristic, since many non-mnemonic effects, be they perceptual, emotional, aesthetic, and so forth, are known to result from prior exposure to an item, even sometimes in the absence of explicit memory for that prior exposure (e.g., Hamann & Squire 1997; Oppenheimer 2008; Schwarz & Winkielman 2004), so the attribution of such signals to memory is effectively a reverse inference.

In the case of familiarity, it is well established that the fluency with which a test item is processed can be (mis-)attributed to familiarity due to past exposure to the item. By experimentally manipulating the fluency with which a test item is processed (e.g., via masked repetition priming), researchers can induce a familiarity-like feeling which is then attributed to memory. This so-called Jacoby–Whitehouse illusion (Jacoby & Whitehouse 1989) has further been found to be specific to familiarity (Rajaram 1993); a finding that has been replicated many times, including in several studies by one of the present authors (Li et al. 2017; Taylor & Henson 2012a; Taylor et al. 2013; Woollams et al. 2008). We therefore agree that familiarity judgements can be based on the attribution of a non-mnemonic signal (i.e., processing fluency) to memory, as stated in the model.

The integrative memory model further proposes that recollection-based memory judgements are also made based on the interaction between its core system and an attribution system. It is implied that the participant will experience a subjective feeling of recollection if the attribution system assesses the memory trace reactivated to be relevant and sufficient (in terms of amount of information retrieved). However, by the authors' description of the core representational system subserving recollection, the relevant signals for recollection judgements are all memory signals, and therefore, we do not see why an attribution system needs to be posited to intervene between the core representational system and the decision module.

In several studies, we have found that masked *conceptual* primes (rather than repetition or lexically associated primes) presented before items in a recognition memory test increase *correct* recollection responses (Li et al. 2017; Taylor & Henson 2012a; Taylor et al. 2013). However, we do not agree that this constitutes evidence for an attribution system mediating recollection decisions. This is because one hallmark of the attribution framework is that it sometimes misfires, resulting in increased false alarms (*primed unstudied* items being endorsed as old more often than *unprimed unstudied* items). But in our studies, only *correct* recollection responses are increased by conceptual primes; false alarm recollection responses are not increased, and therefore, *mis*-attribution does not reliably occur. Instead, conceptual priming appears to facilitate veridical retrieval of the encoding event.

This is consistent with the notion that the decision module that subserves a recollection judgement relies only on *mnemonic* signals and therefore, contrary to the target model, it does not require mediation by an attribution system.

It is noteworthy that the evidence for the attribution system comes exclusively from studies using single words as stimuli, whereas much of the rest of the model is mainly based on studies that use objects, pairs of objects, pairs of words, and/or visually rich scenes or environments. One crucial difference between these types of stimuli is that the very same word stimuli are commonly encountered outside of the laboratory, whereas object and scene images and their relations are often (though admittedly not always) unique to the experiment. A second crucial difference is that, at least in the priming and recognition memory studies discussed above, words are often presented in visually impoverished encoding conditions (e.g., one at a time on a blank screen), whereas in studies investigating relational memory, object images are often presented in trial-unique contexts, in pairs, or in well-defined locations in an environment. Thus, it is likely that recollection decisions in word-list memory experiments rely heavily on retrieval of contextual elements from the encoding episode (since the stimuli themselves are not distinctive), and these contextual elements are likely to be *internal* (e.g., what the participant thought of when they read the word in the study phase) rather than *external* (e.g., where in the environment, or with which other object or context the target object was presented).

We suggest that the mechanism by which conceptual primes increase correct recollection is related to a (partial) reactivation of the internal context participants activate during the encoding stage, and not to an attribution of a non-mnemonic signal to memory. Crucially, in the present model, when creating a memory trace during encoding, an item is bound to its *external* context (e.g., object-scene), and *internal* context (e.g., conceptual associations/personal experiences with a target word) is not accounted for. Perhaps the neural networks subserving the core representational system for recollection could be expanded to include regions supporting semantic associations (e.g., anterior temporal lobes).

In summary, we agree that familiarity judgements can be based on the attribution of a non-mnemonic signal to memory, as described in the proposed model, but we do not see evidence for an attributional basis of recollection judgements. In addition, we suggest expansion of the core representational system for recollection to include internal context.

The subjective experience of recollection and familiarity in Alzheimer's disease

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Abstract

Although the integrative memory model proposed by Bastin et al. is interesting, particularly for Alzheimer's disease, it may benefit from incorporating the subjective experience of recollection. We therefore offer complementary lines of interpretation to explain how recollection and familiarity in Alzheimer's disease can be dissociated based not only on accounts of their neural correlates but, critically, on the subjective experience of memory in patients.

The integrative memory model proposed by Bastin et al. is theoretically and clinically relevant as it provides a framework for the chronological pattern of recollection and familiarity processes in Alzheimer's disease (AD), depending on the brain regions most affected at each stage of the disease. That being said, the framework can be extended to include the subjective experience of both recollection and familiarity and their abnormalities in patients with AD. Recollection and familiarity have been associated with distinct subjective experiences: Recollection is typically associated with a subjective experience of "mental time travel," in which we experience the conscious sensation of traveling back in time to relive the original event and to see it in our mind's eye, whereas familiarity is typically associated with a feeling of knowing characterized by a vague and unspecific experience of remembering (Tulving 2002). Regarding Alzheimer's disease, patients typically demonstrate a shift from the ability to mentally relive past events (i.e., a shift from recollection) to a general sense of familiarity that may be expressed by the patients as a sense of "having experienced this before" (El Haj et al. 2015).

The decline of recollection in Alzheimer's disease can be attributed to decline in specific processes of the recollective experience. This decline has been pointed out by research demonstrating decline in the recollective experience during retrieval of past personal events in patients with AD, including decline in subjective processes, such as reliving, travel in time, remembering, realness, rehearsal, and visual imagery (El Haj et al. 2016). Among these subjective processes, decline of visual imagery seems to play a key role in the decline of recollective experience in patients with AD. The decline of visual imagery in AD seems to deprive patients from the ability to retrieve and manipulate mental images during retrieval, and also deprive them from visual cues that mediate and/or accelerate their search through memory stores (El Haj et al. 2019a; 2019b).

The relationship between decline of visual imagery and decline of the recollective experience in AD can be understood by highlighting research using the Field/Observer paradigm, which has been widely used to assess the subjective experience of recollection and familiarity in general populations (Nigro & Neisser 1983; Rice & Rubin 2011). In one study in AD, patients were invited to retrieve past personal events and, subsequently, provide a "Field" response, if they could visualize the event through their own eyes, or an "Observer" response if they could visualize themselves in the scene as a spectator would (El Haj et al. 2019b). Results demonstrated increased "Field" and decreased "Observer" responses in patients, suggesting a diminished ability of patients with AD to construct vivid images when recollecting the past.

In summary, the decline of the recollective experience during retrieval can be associated with declines in several components of the subjective experience, such as reliving, travel in time, remembering, realness, and rehearsal. Critically, decline of visual imagery seems to deprive patients from the ability to construct mental images when recollecting the past. We propose that these processes should be considered by the integrative memory model, as proposed by Bastin et al., to better account for recollection deficits in patients with AD. We believe that a decline in the subjective experience during retrieval in patients with AD leads to a decline of recollection and, consequently, to the emergence of a general sense of familiarity that is typically associated with a sense of "having experienced this before." As pointed out by Bastin et al., the integrative memory model is not comprehensive and should evolve to incorporate other mechanisms. Therefore, we propose that the integrative memory model is sufficiently flexible to include these subjective processes and may be enriched by this inclusion.

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Cognitive control constrains memory attributions

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Abstract

Cognitive control constrains retrieval processing and so restricts what comes to mind as input to the attribution system. We review evidence that older adults, patients with Alzheimer's disease, and people with traumatic brain injury exert less cognitive control during retrieval, and so are susceptible to memory misattributions in the form of dramatic levels of false remembering.

We agree with Bastin et al. that attributional processes play an important role in memory performance, but we argue that attributional processes should be considered in the broader context of issues related to cognitive control. In particular, the authors emphasize the importance of attributions that follow a potential response coming to mind but they make only passing reference to the role of task context as well as goals that are important for bringing a potential response to mind. In contrast, we need to distinguish forms of cognitive control that constrain retrieval processing to restrict what comes to mind (pre-access control) and post-access source monitoring. Burgess and Shallice (1996) used a similar distinction to argue that confabulation stems from a failure to properly constrain retrieval processing, rather than being limited to post-access monitoring. In what follows, we briefly describe data from our studies done with others to show that a difference in ability to constrain retrieval is important for understanding memory misattributions in special populations.

Our early work revealed both correct attributions of fluency (e.g., Jacoby & Dallas 1981) as well as memory misattributions of the sort focused on in the target article (e.g., Jacoby et al. 1989; Kelley & Rhodes 2002). Our more recent work shows the importance of pre-access cognitive control as a means of avoiding memory misattributions. Jacoby et al. (2005a) used a response-priming procedure to reveal dramatic false remembering by older adults. Younger and older participants studied word pairs (e.g., *knee bone*), and their memory was tested by providing the left-hand member of each pair along with a fragment of the right-hand member (e.g., *knee b_n_*) as cues for its recall. Immediately prior to the recall test for each pair, a prime was presented that was either (i) the same as the target word (a congruent prime; e.g., *bone*), (ii) a misleading alternative to the target word (an incongruent prime; e.g., *bend*), or (iii) a neutral, non-word stimulus (a baseline prime; *&&&*). The misleading prime word fit the word-fragment context, making it a plausible response. A decline in cognitive control was revealed in that older adults were much more likely to report the misleading prime as being the word previously studied than were young adults. Further, they were 10 times more likely than were young adults to show dramatic false memory by claiming to "remember" having studied the misleading prime (0.42 vs. 0.04). A multinomial model fit to these data revealed that the poorer performance of older adults largely reflected a deficit in their ability to constrain retrieval. Older adults were more likely to be "captured" by the misleading prime to an extent that prevented any subsequent attempt to recollect.

A subsequent study using the capture procedures (Millar et al. 2018) found that participants in an early stage of Alzheimer's disease (AD) were more likely to be misled by an incongruent prime than were normal older adults. Results from the multinomial model revealed that AD participants were more often captured by the misleading prime (see Balota & Duchek 2015 for a review of evidence that a deficit in cognitive control underlies memory deficits in AD participants.) A parallel study showed that patients with traumatic brain injury (TBI) also are prone to being captured by the misleading prime (Dockree et al. 2006), and have higher rates of false "remembering" of the prime than do normals. These studies show that memory deficits sometimes reflect a deficit in the ability to constrain retrieval processes, rather than reflecting a late occurring, post-access deficit in memory attributions.

Cognitive control problems reflecting capture are general. In a preliminary study, Failes et al. (unpublished manuscript) found a high correlation for older adults between false memory and false hearing. The capture procedure was used to show false memory, whereas the procedure for showing false hearing used a capturing sentence context that misled responding. False hearing can reflect poor cognitive control in the form of an absence of careful listening; instead, people rely on what readily comes to mind. Similarly, false memory can be described as reflecting a deficit in careful remembering (recollection). In a related vein, Dockree et al. (2006) found that correct responding by TBI participants in the misleading prime condition of the capture paradigm was positively correlated with performance on a prospective memory task.

For older adults, Jacoby et al. (2005a; 2005b) found that use of a recognition memory test largely eliminated the effects of a misleading prime, showing that capture effects are largely pre- versus post-access. Although recall tests are likely to be more revealing of deficits in cognitive control, such deficits can be revealed on recognition memory tests. Jacoby et al. (2005b) used a memory-for-foils procedure to reveal such a deficit. During a study phase, words in one condition were "deeply" processed (*judge pleasantness*), whereas those in another condition were "shallowly" processed (*Does the word contain an O or U?*). For both conditions, studied words were intermixed with new words (foils) for a test of recognition memory. Subsequently, a test of memory for the foils was given. Younger adults showed better memory for foils from the prior test of deeply encoded words, compared to memory for foils from the prior test of shallowly encoded words, showing that they had recapitulated the encoding task in an attempt to constrain recognition memory. In contrast, such pre-access cognitive control was not shown by older adults, suggesting that they did not engage in source constrained retrieval during the recognition test. Kelley and Alban (2015) describe results from further experiments using the memory-for-foils procedure to investigate differences in cognitive control.

The above-mentioned studies show the importance of specifying the nature of misattributions, distinguishing between pre-access cognitive control of what comes to mind and post-access monitoring of why a response came to mind after it has done so. Much prior research has focused on post-access attribution processing (source monitoring). Deficits in pre-access cognitive control are likely as or more important. Pre-access constraint on what comes to mind limits the possibility of memory misattributions, whereas a lack of constraint places people at risk.

There is more to memory than recollection and familiarity

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Abstract

Theoretical models of memory retrieval have focused on processes of recollection and familiarity. Research suggests that there are still other processes involved in memory reconstruction, leading to experiences of knowing and inferring the past. Understanding these experiences, and the cognitive processes that give rise to them, seems likely to further expand our understanding of the neural substrates of memory.

Dual-process theories have much to recommend them in the study of memory, as elsewhere in psychology (Anderson & Bower 1972; Jacoby 1991; Mandler 1980; Yonelinas 2002). One particular version of dual-process theory has come to dominate both psychological and neuroscientific thinking: the distinction between recollection and familiarity. Ordinarily, we think of remembering as a full-fledged, conscious recollection, including the time and place at which the event took place and some reference to the person's role as agent, patient, stimulus, or experiencer. But another retrieval process, generally known as "familiarity," lacks all of these accoutrements: there is just the event itself, absent any spatiotemporal or personal context, shimmering in the mind, feeling somehow familiar. In the target article, Bastin et al. have done an excellent job in summarizing the neural substrates of these two recollective experiences, and their integrative model seems both comprehensive and persuasive.

Identifying the neural substrates of mental functions depends critically on the availability of an accurate description of the functions themselves. In that sense, at least, cognitive (and social and affective) neuroscience depends critically on cognitive (and social and affective) psychology. "An analysis at the behavioral level lays the foundation for an analysis at the neural level. Without this foundation, there can be no meaningful contribution from the neural level" (Gallistel 1999, p. 843; see also Coltheart 2006; Hatfield 2000; Kihlstrom 2010). So the question remains whether the dualism of recollection and familiarity exhausts the forms that memory retrieval can take.

This may not be the case. For example, one of the most important contributions to dual-process theories of memory was a paper by Tulving (1985), which distinguished between two forms of memory retrieval: "remembering" that an event occurred, as a full-blown episodic memory, and "knowing" that it happened, somewhat on the order of semantic memory. Rather quickly, "remembering" was relabeled as "recollection," while "knowing" was reinterpreted in terms of familiarity, similar to priming or implicit memory (e.g., Gardiner 1988; Yonelinas 2002); but in both formulations "knowing" was a residual category: any memory not classified as "remembered" was perforce classified as "known." As a consequence, "knowing" may include a variety of distinct recollective experiences, each of which may have its own separate neural substrate.

In fact, evidence from a variant on the "remember/know" paradigm shows that there is more than one alternative to remembering an event (Kihlstrom, in press). We can have abstract knowledge that an event occurred, in the absence of conscious recollection of its environmental and personal context, much as we know where we were born without actually remembering it. Or we can have an intuitive feeling that something is familiar, the way someone's face or voice can "ring a bell" at a cocktail party, even though we cannot remember the person's name or the circumstances under which we might have previously met him or her. In these ways, recognition-by-knowing can be distinguished from recognition-by-feeling in much the same way as, in the traditional remember/know paradigm, recognition-by-remembering can be distinguished from recognition-without-remembering.

Reports of "knowing" are more likely to occur following deep semantic processing, whereas reports of "feeling" are more likely to occur following shallow, phonemic processing. Recognition-by-knowing is associated with higher confidence ratings than recognition-by-feeling, while recognition-by-feeling is increased when subjects are encouraged to adopt a liberal criterion for item recognition. Recognition-by-feeling is associated with longer response latencies than recognition-by-knowing, and increases when subjects are given a long time to think about their responses. False recognition is often accompanied by "feeling," but rarely accompanied by "knowing," so that signal-detection measures of recognition accuracy are higher for knowing than for feeling. Recognition-by-knowing increases with additional study trials, eventually supplanting recognition-by-remembering, while recognition-by-feeling drops essentially to zero. In these and other ways, knowing the past can be distinguished from the feeling of familiarity.

While these experimental findings support a tripartite classification of recollective experience into remembering, knowing, and feeling, there is also "believing" – the inference that an event occurred, in the absence of any recollection at all. Remembering-as-believing is relevant to the controversy over recovered memories and "false memory syndrome," if patients have been inappropriately persuaded by their therapists, friends, or prevailing cultural memes that they were traumatized in the past (Kihlstrom 1998; 2006; McNally 2003). It may also be involved in cases of false confession (Kassin 2008; 2017). "Believing" may also be involved in memory illusions observed under laboratory conditions (Roediger 1996), including the post-event misinformation effect (Loftus 2005; Loftus & Palmer 1974) and the associative and categorical memory illusions (Gallo 2010; Knott et al. 2012; Roediger & McDermott 1995; Smith et al. 2000). Having studied a list of vehicles, for example, subjects may be inclined to incorrectly say "Yes" to items on a recognition test only because they, too, name types of vehicles. This might be an associative priming effect, similar to familiarity, but it might also simply reflect the subject's beliefs about the items that were on the list.

Just as there is more to memory than recollection and familiarity, there is more to memory than the medial temporal lobe (MTL). Long ago, Bartlett (1932) argued that remembering went far beyond mere trace retrieval, and involved problem-solving, inference, and even creativity as the individual reconstructed a mental representation of the past. More recently, Mandler (1980) reminded us that recognition involved the *judgment* of prior occurrence, suggesting that signal-detection analyses should pay as much attention to the bias in the decision process as we do to the sensitivity of the sensory process. The implication is that, in examining the neural substrates of recollection, familiarity, and other memory retrieval processes, we need to move beyond our almost-exclusive focus on the MTL, as Bastin et al. and others (e.g., Ranganath & Ritchey 2012) have begun to do. Considering recollective experiences such as knowing, feeling, and believing may take our understanding of memory retrieval beyond recollection and familiarity, and expand our understanding of the neural bases of memory even further.

The role of anxiety in the integrative memory model

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Abstract

We suggest that the inclusion of anxiety, as one relevant mood factor, could enhance the implementation of the integrative memory model in research and the clinic. The role of anxiety in Alzheimer's disease neuroanatomy, symptomology, and progression is used as an example. Customization of the integrative memory model can establish strong foundations for pathology-specific models of memory deficits, enhancing the development of precision medicine applications.

The integrative memory model presented by Bastin et al. could be augmented to apply more directly to specific memory deficits. Alzheimer's disease (AD) etiology, which is used to describe the application of their model, often involves significant anxiety and comorbid depression (Zhao et al. 2016). The authors note the involvement of affective and subjective factors, and suggest that memory deficit-related anxiety may be due to not meeting cognitive and memory goals, but do not go into great detail. Failure to meet goal-associated stress could interfere with the salience and strength of cues critical to effective recollection and/or familiarity processes. In both symptomology and assessment, anxiety can significantly affect memory task context, adversely interfering at the familiarity stage and with recollection circuit signaling. Anxiety is also likely to disrupt memory through interactions with metacognition.

While the literature related to the impact of anxiety on specific AD-associated memory nuclei discussed by Bastin et al. is not substantial, there is growing evidence of associations between anxiety and AD (Donovan et al. 2018). Anxiety is a predictor for early onset AD (Kaiser et al. 2014) and the conversion of mild cognitive impairment (MCI) to AD (Gallagher et al. 2011). The importance of familiarity in early etiology and the accumulating observations of anxiety during this period suggests that an increased integrative focus on neural mechanisms of anxiety and familiarity, where nuclei involved in both processes are evaluated simultaneously, may provide valuable insight on the specific nature of the role of anxiety in susceptibility to MCI and AD, progression to AD, and the progression of AD symptomology. Bastin et al. note that recollection is critically dependent on the posterior cingulate, which has also been implicated in anxiety as a component of the default mode network (DMN) (Maddock & Buonocore 1997; Zhao et al. 2007). This region could have anxiety-associated effects on recollection due to its strong connections with hippocampal and entorhinal areas, where adverse effects of anxiety exacerbate neurodegenerative changes in the posterior cingulate, disrupting recollection processes there and in related regions. As AD progresses, and as recollection circuits are impaired, the role of anxiety becomes more difficult to assess due to decreased awareness of cognitive and memory deficits. Although the degree to which metacognition is intact in AD is debated (Moulin et al. 2003), it is possible that anxiety has more substantial adverse effects in individuals/populations and/or early stages where metacognition is relatively intact. Focusing research on these individuals and/or stages would more effectively target the role of anxiety in AD-related memory deficits.

One could argue that while an anxiety domain could enhance the application of the integrative memory model, it may not be initially necessary. However, it is also possible that the inclusion of the effects of anxiety on memory processes is critical to an accurate and comprehensive understanding of AD, given the acute impact on memory processes, high comorbidity, and growing evidence of anxiety- and stress-related depression as AD risk factors. Anxiety and associated stress may modify interactions between familiarity and recollection, affecting memory acutely through neuroendocrine mechanisms and chronically through neurodegenerative mechanisms (amyloidopathy, tauopathy, neuroinflammation, and microglial dysfunction). Amyloid β has been specifically associated with symptoms of anxiety and depression in cognitively normal older adults (Donovan et al. 2018), and neuroticism may mediate this association (Snitz et al. 2015). Neuroticism-related anxiety may increase susceptibility for emotional distress and negative affect, and subsequent age-related cognitive decline, MCI, and AD. Anxiety may be more strongly associated with amyloid β and tau levels than depression (Ramakers et al. 2012), and increased consideration of anxiety may lead to greater consistency in mechanistic studies of predisposing factors. Psychosocial stress has been linked to neuroinflammation and microglial dysfunction in AD (Piirainen et al. 2017), and it is postulated that this could involve anxiety-mediated mechanisms. The inclusion of the anxiety domain could be used to identify a key subpopulation of AD patients who would benefit from a targeted intervention, whether it be psychotherapy, pharmacotherapy, or a complimentary intervention, such as mindfulness. Identifying how and when anxiety contributes to memory deficits could also identify key early interventional periods.

The inclusion of anxiety, and potentially other mood factors, in the integrative memory model is not limited to AD, and parallels can be made with the customization of mindfulness-based stress reduction techniques for pathologies ranging from depression and anxiety to hypertension, including dementia (Russell-Williams et al. 2018). Given the heterogeneity of AD etiology, this type of precision medicine approach could substantially improve disease progression and/or quality of life outcomes (Reitz 2016). It is suggested that the integrative memory model can be used as a strong foundation for additional population and pathology-specific models of memory deficits.

Two processes are not necessary to understand memory deficits

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Abstract

Bastin et al. propose a dual-process model to understand memory deficits. However, results from state-trace analysis have suggested a single underlying variable in behavioral and neural data. We advocate the usage of unidimensional models that are supported by data and have been successful in understanding memory deficits and in linking to neural data.

Bastin et al. advocate a dual-process model to understand memory deficits. While this model is a popular framework, the evidence for it is weak. Much of the argument for the dual-process model hinges on double dissociations in behavioral data, including remember-know responses and parameters of the dual-process signal-detection model (Yonelinas 2002), and in neural data, such as between the frontal-negativity component and the parietal late-positive component in event-related potentials (Rugg & Curran 2007) and between the hippocampus and surrounding cortical regions such as the perirhinal cortex in functional magnetic resonance imaging (fMRI) (Eichenbaum et al. 2007).

Unfortunately, a double dissociation is not sufficient evidence to infer the existence of more than one latent variable or processes (Dunn & Kirsner 1988). A more principled method is provided by state-trace analysis (Bamber 1979; Dunn & Kalish 2018; Newell & Dunn 2008). State-trace analysis evaluates the number of latent variables that are required to explain performance across multiple dependent variables. State-trace analysis in recognition memory consistently refutes dual-process theory, as it has not revealed evidence for more than one latent variable in remember-know responses (Dunn 2008), item recognition and source memory across development (Hayes et al. 2017), and event-related potentials (Brezis et al. 2017; Freeman et al. 2010).

Double dissociations in these paradigms are consistent with a monotonic but non-linear relationship between dependent measures, as illustrated in the hypothetical demonstration in our Figure 1. Although state-trace analysis has not yet been applied to fMRI data, Squire et al. (2007) proposed that dissociations between the hippocampus and perirhinal cortex can be explained by non-linear relationships between the two regions, and evidence

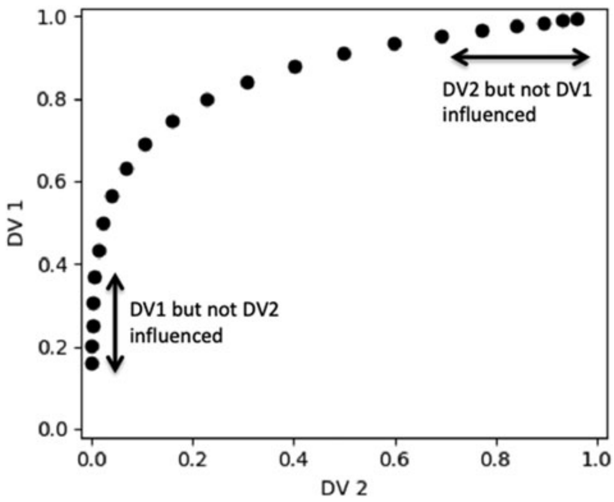

Figure 1 (Osth et al.). A hypothetical example of how manipulations can produce double dissociations between two dependent variables (DVs) within a unidimensional model where the relation between the two DVs is non-linear. The black dots depict performance across a range of manipulations.

for such a non-linearity has been found using fMRI (Song et al. 2011).

We argue that a more fruitful approach to understanding cognitive and neurological deficits in memory is to use models that contain a single underlying latent variable. One-dimensional models, such as signal-detection theory, have often been found to provide a better fit to receiver-operating characteristics than the dual-process model (Hayes et al. 2017; Heathcote 2003; Heathcote et al. 2006). Signal-detection theory has also been highly successful as a measurement model; even graded levels of memory deficits in Alzheimer's disease have been able to be identified using this model (Pooley et al. 2011).

The diffusion model of Ratcliff (1978) is an even better candidate for understanding memory deficits because it can also account for response times. In the diffusion model, evidence accumulates toward one of the two response boundaries corresponding to response alternatives, such as "old" and "new" in the case of recognition memory. Once a boundary is reached, the associated response is given and the time taken to reach the boundary plus time for non-decision processes is the response time. The rate at which evidence is accumulated is called the *drift rate* and is analogous to memory strength in signal-detection theory. As drift rate increases, the rate of correct responses increases and latency decreases.

The diffusion model is advantageous because, unlike signal-detection theory and the dual-process model, it leverages both accuracy and latency into relevant psychological variables. These include memory strength (measured by drift rate), speed of perception and motor processes (measured by non-decision time), and response caution (measured by response boundaries). The diffusion model has been highly successful in explaining data from recognition memory paradigms (Osth et al. 2017; 2018; Ratcliff 1978). Although recollection in the dual-process model has been described as being slower than the familiarity process, to date there is no formal instantiation of the dual-process model that has made contact with latency data.

The diffusion model has also been extremely fruitful as a measurement model. A noteworthy example is the study by Ratcliff et al. (2004), which compared younger and older adults' recognition performance. While both groups exhibited similar accuracy, latencies were much longer in older adults. Diffusion modeling revealed that older adults were more cautious in their responding and had higher non-decision times, but otherwise exhibited very similar drift rates. Without the aid of the model, researchers could easily be misled into believing that the older adults had slower rates of processing in the task. In other applications, diffusion model parameters such as the drift rate have been shown to be more sensitive to group-level differences than measures based on accuracy or latency alone (White et al. 2010).

Diffusion modeling applied to Alzheimer's disease is in its infancy, but shows promise. Memory deficits associated with a family history of Alzheimer's disease have been best described by differences in the drift-rate parameter (Aschenbrenner et al. 2016). Even more critically, the drift-rate parameter predicted group-level differences better than neuropsychological tests.

In addition, diffusion models have been extremely successful in linking to neural data. Ratcliff et al. (2016a) were able to explain variability in single-trial indices of memory strength using only the drift-rate parameter. In addition, a great deal of work in neuroscience has uncovered neural mechanisms that resemble evidence accumulation in the diffusion model (Gold & Shadlen 2007), suggesting that the neurological underpinnings of dementia may be able to be understood through the lens of diffusion models.

We suggest that adoption of a dual-process framework for recognition memory is unlikely to lead to progress in understanding memory deficits. It is not strongly supported by existing evidence and, if it is the wrong model of memory, will lead to misleading conclusions (Pazzaglia et al. 2013). Models that contain a single latent variable are consistent with the neural evidence and provide a framework for unifying accuracy and latency; they are suitable measurement models for memory impairment. In our view, the application of this framework will lead to a deeper understanding of the nature of memory deficits.

Understanding misidentification syndromes using the integrative memory model

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Abstract

Misidentification syndromes occur commonly in neuropsychiatric practice and can be explained through aberrant integration of recollection and familiarity, in keeping with a dysfunction at the level of the attributional system in the new integrative memory model. We examine neuroimaging findings associated with Fregoli and Capgras syndromes and compare these with the proposed neural substrate of the integrative memory model supporting the core and attribution functions.

There are a few prominent eponymous syndromes in psychiatry; two of the most well-known are the Capgras delusion and the Fregoli delusion. These are delusional misidentification syndromes: In the Capgras delusion, the sufferer believes that a close relative has been replaced by someone, or is not who they say they are, despite them physically resembling the person they have replaced. The original description (Capgras & Reboul-Lachaux 1923/1994) described the delusion as an "agnosia of individual identification" (p. 1) and not necessarily a symptom of false recognition, highlighting the separation between recognition and identification. In the Fregoli syndrome, the patient holds the delusional belief that one person is constantly changing his or her appearance and occupying different forms, thus appearing as different people. The Fregoli delusion was originally described in a 1927 publication as a complimentary antonym to Capgras syndrome (Courbon & Fail 1927/1994). In the Capgras delusion, the patient can recognize the similarity of the "imposter" to the close friend or relative and can recollect the facial detail of said person (Josephs 2007). An additional element for those suffering from Fregoli syndrome is that patients appreciate that the person looks different, but believe this is the same person despite the different superficial appearance (Langdon et al. 2014). Thus, both these syndromes reflect a dichotomy between recollection and familiarity. What does the new integrative memory model presented in the current target article by Bastin et al. suggest may be the issue in these psychiatric syndromes? Ostensibly, in the Capgras delusion there is intact recollection and a deficit in or absence of familiarity; while in the Fregoli delusion, there is a deficit in recollection and over-attribution of familiarity. The deficits could occur at the level of the initial or core processing, or at the higher-order attributional stage where recollection and familiarity are combined and contextualized.

These delusional misidentification syndromes commonly occur in schizophrenia and psychosis (Förstl et al. 1991) affecting around 15% of those suffering from schizophrenia (Feinberg & Roane 2005; Salvatore et al. 2014). However, delusional misidentification syndrome has also been attributed as a symptom of many other disease states, including dementia, epilepsy, Parkinson's disease, trauma, and other organic brain diseases (Oyebode & Sargeant 1996; Pandis & Poole 2017). Neuroimaging has highlighted the role of organic brain dysfunction in delusional misidentification syndrome (Atta et al. 2006). These studies of delusional misidentification syndrome have highlighted prominent dysfunction in frontal cortical regions, with a focus on right-hemispheric change, and in temporoparietal cortical regions, with an emphasis on left-hemisphere change. A few studies have suggested parahippocampal atrophy. Specific studies have demonstrated Fregoli's delusion associated with right-frontal and left-tempo-parietal contusions following trauma (Feinberg et al. 1999). Meta-analyses of delusional misidentification syndrome point to the involvement of the right frontal lobes (Atta et al. 2006; Feinberg & Roane 2005), with other changes observed in the left temporal lobes (Edelstyn & Oyebode 1999; Feinberg et al. 1999; Huang et al. 1999; Signer 1994). Further, neuroimaging data in delusional misidentification syndrome and schizophrenia have demonstrated structural volume reduction in the frontotemporal area of the brain (Turkiewicz et al. 2009), as well as reductions in structural magnetic resonance in the right frontal lobe (Coltheart et al. 2007). A few studies showed damage to the right fusiform gyrus and para/hippocampal atrophy indicating temporal lobe deficiencies (Hudson 2000).

In the integrative memory model, the fluency heuristic establishes familiarity, while the attribution system underpins recollection. These combine with the core systems generating the memory trace that is made available to these familiarity and recollection systems to ensure accurate memory-related decisions. The imaging data in delusional misidentification syndrome largely implicate dysfunction at the level of the fluency heuristic and attribution, based on the prefrontal cortex and possibly its connections with perirhinal regions, rather than reflecting any core dysfunction in the entity or relational processes associated more with the hippocampus and perirhinal regions. The model appears to lack parsimony as it proposes that a dissociation between familiarity and recollection can occur through damage to the hippocampus or the perirhinal cortex – but it is not clear how it is possible to distinguish the consequences of this from any prefrontal cortical dysfunction which will impact attribution and lead to misrecognition and impaired familiarity.

In summary, the structural and functional anomalies found in patients suffering from Capgras and Fregoli misidentification syndromes, that demonstrate aberrant integration of recollection and familiarity, fit with a dysfunction at the level of the attributional system rather than a core representational deficit in Bastin et al.'s new model. However, the authors propose that similar dissociations are also possible with a core dysfunction in hippocampus or perirhinal cortex, which suggests that the model may lack parsimony and potentially fits less well with the available data on dissociation.

The role of reference frames in memory recollection

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Abstract

In this commentary on Bastin et al., we suggest that spatial context plays a critical role in the encoding and retrieval of events. Specifically, the translation process between the viewpoint-independent content of a memory and the viewpoint-dependent stimuli activating the retrieval (mental frame syncing) plays a critical role in spatial memory recollection. This perspective also provides an explanatory model for pathological disturbances such as Alzheimer's disease.

In the target article, Bastin et al. convincingly propose an integrative memory model as a neurocognitive framework of episodic memory to describe the cognitive and neural mechanisms underlying both recollection and familiarity. However, a critical point not sufficiently addressed in their article is the role that spatial context plays in this process.

Each event we experience in our life is framed in a unique spatial scaffold (Bicanski & Burgess 2018; Bird et al. 2012; Byrne et al. 2007). Earlier, O'Keefe and Nadel (1978) pioneered the existence of a functional relationship between the episodic and spatial domain under the control of medial temporal lobes. This perspective has been revised and extended by the multiple trace theory (Nadel et al. 2000), and evidence from both amnesic patients with hippocampal damage and experimental studies have consistently suggested that hippocampus is involved in both episodic and spatial processing (for a review, see Graham et al. 2010).

In line with this perspective, the spatial mechanisms underlying episodic encoding and retrieval have been modeled in some detail (Burgess et al. 2001), stressing the role of information provided by space-related brain cells playing in concert in the medial temporal lobes (place cells: O'Keefe & Dostrovsky [1971]; head-direction: Taube et al. [1990]; grid cells: Hafting et al. [2005]; and boundary cells: Solstad et al. [2008]).

In brief, egocentric (i.e., *body-centered and corresponding to a specific point of view*) representations of the local sensory environment are transformed thanks to the retrosplenial cortex into viewpoint-independent (allocentric, or *world-centered*) representations for long-term storage in the medial temporal lobes (Byrne et al. 2007). In particular, head-direction cells (Bicanski

& Burgess 2018) allow the transformation from egocentric directions (left, right, ahead) in allocentrically referenced directions (north, south, east, west).

This process, however, is bidirectional. In fact, the reverse process is used in memory retrieval to reconstruct viewpoint-dependent egocentric representations in parietal areas from stored hippocampal-based allocentric representations, supporting both imagery and recollection. According to this perspective, episodic retrieval implies the construction of a transient egocentric representation (i.e., the distances of the elements in a scene from the left, the right, or ahead of the individual) that can be inspected and used to retrieve the past event or envision future/imaginary events (Gomez et al. 2009). This reconstructed egocentric scenario is also updated with the egocentric heading (i.e., our viewpoint in the scene) for both successful navigation and effective episodic retrieval (Julian et al. 2018; Serino & Riva 2013).

In our view, there is a specific cognitive process (i.e., the “mental frame syncing”) underlying this egocentric–allocentric transformation that is critical for the recollection of spatial scenarios (see our Figure 1). It is responsible for placing the egocentric heading into the stored abstract allocentric representation, providing the reconstructed scenario with the same viewpoint in respect to those of the encoding (Serino et al. 2015; Serino & Riva 2013). If there is a break in this process, we cannot use the retrieved representation to guide our spatial behavior.

The mental frame syncing hypothesis provides a useful framework that can also be applied to pathological conditions that report episodic memory deficits along with spatial reference impairments. As an example, the scientific outcomes of different systematic reviews have critically underlined the presence of both allocentric and allocentric-to-egocentric transformation impairments in Alzheimer’s disease (AD) population (Colombo et al. 2017; Lithfous et al. 2013; Serino et al. 2015; 2017), where the episodic memory impairments characterizing the clinical profile of these patients are also accompanied by a more profound deficit in the synchronization between allocentric and egocentric reference frames (Serino et al. 2015). In support of this, a recent proof-of-concept preliminary study demonstrated the efficacy of a novel virtual reality (VR) treatment based on enhancing the ability to synchronize an allocentric viewpoint-independent representation with an egocentric one, by providing participants with real-time information about their current egocentric heading in the environment (Serino et al. 2017). Results indicated a clear improvement in long-term spatial memory performance after the VR-based training for patients with AD.

Furthermore, a growing body of studies have highlighted that spatial factors might be implicated also in disordered awareness of memory deficits (commonly known as “anosognosia”). In particular, studies have suggested that the spatial perspective in which the information is presented (i.e., first- vs. third-person perspective) has a prominent role in affecting AD patients’ self-awareness of their memory deficits (Bertrand et al. 2016). Patients typically show better awareness when evaluating others’ abilities than their own, suggesting that shifting from a first-person perspective (i.e.,

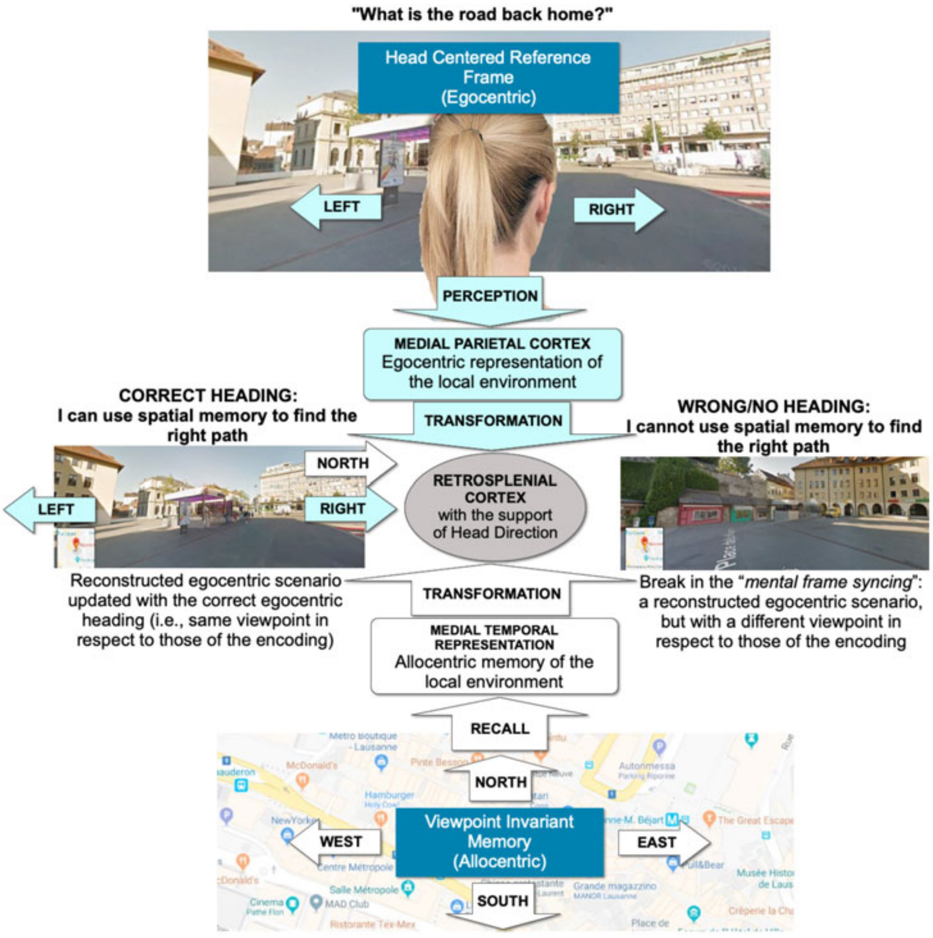

Figure 1 (Riva et al.). Mental Frame Syncing. Sensory inputs from the environment are processed in the egocentric reference frame in parietal areas and then transformed for long-term storage in hippocampal allocentric representations. When needed (for imagery or prompted by a retrieval cue), the reverse process permits the reconstruction of a parietal egocentric image from allocentric-based stored map. To correctly retrieve our location in space, it is necessary to synchronize our egocentric heading within the allocentric viewpoint-independent representation. Therefore, we have to update the retrieved allocentric representation with the correct egocentric heading. If there is a break in this process, we cannot use the retrieved representation to guide our spatial behavior.

egocentric) to third-person perspective (i.e., allocentric) might make them more aware of their deficits. Accordingly, it is possible to speculate that a "break" in the ability to update the allocentric representations (i.e., unrelated to the self) with egocentric information (i.e., related to the self) does not allow these patients to translate their spatial memories into a "lived space" that they can use to navigate and remember the past (Serino & Riva 2017). Moreover, the break can also produce an impairment in their ability to use their spatial memories to place themselves in a "future space" and consequently to use the content of such memories to update their first-person perspective, which is required for self-awareness (Serino & Riva 2017).

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Fluency: A trigger of familiarity for relational representations?

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Abstract

According to Bastin et al.'s integrative memory model, familiarity may be attributed to both entity representations and relational representations. However, the model does not specify what triggers familiarity for relational representations. I argue that fluency is a key player in the attribution of familiarity regardless of the type of representation. Two lines of evidence are reviewed in support of my claim.

Bastin et al. make a valiant attempt to rejuvenate the dual-process theory of recognition – a theory formulated more than 40 years ago, and which has triggered intense debate and research ever since (Dunn 2004; Wixted 2007; Wixted & Mickes 2010; Yonelinas 2002). Their attempt yields the integrative memory model. The most novel and significant aspect of this model is the clear distinction between mnemonic representations – entity and relational – and the subjective experiences – familiarity and recollection – that are attributed to reactivation of the corresponding representations. This distinction has been misleadingly blurred in previous dual-process model of recognition. According to the integrative memory model, familiarity is typically associated with entity representations and recollection is typically associated with relational representations. However, recollection and familiarity are not *necessarily* triggered by relational and entity representations, respectively. Thus, the model makes the novel prediction that the subjective experience of familiarity may also be triggered by relational representations and, likewise, the subjective experience of recollection may also be triggered by entity representations (though this latter point is only implied, and not explicitly mentioned in the target article). This is an important prediction – perhaps the most important prediction that the model makes. However, its implications are not fully explored by the authors and are not sufficiently elaborated on. In this commentary, I focus on one specific aspect of this prediction – namely, that reactivation of a trace in the relational core system may trigger familiarity.

Bastin et al. claim that "even if the relational representation core system reactivates specific item-context details, one may experience a feeling of familiarity" (sect. 3, para. 2). This claim begs the question: What gives rise to this feeling of familiarity? However, the model remains mute regarding the source for the experience of familiarity for relational representations. For *entity* representations, the source triggering familiarity is the fluency heuristic, defined as "the speed and ease with which a stimulus is processed" (sect. 2, para. 2). Importantly, while mentioning other factors that are potential sources of familiarity (e.g., proprioceptive and affective information), the authors acknowledge that these may also be intricately linked to fluency – either being a by-product of fluency, or by triggering fluency (see sect. 4.2.1). Thus, familiarity emerges predominantly from the fluency with which a stimulus is processed. In line with the vast majority of the relevant literature (e.g., Kleider & Goldinger 2004; Whittlesea et al. 1990; Whittlesea & Leboe 2000), Bastin et al. describe fluency only as a property of processing *entity* representations (e.g., single words, pictures). However, I maintain that there is no reason to preclude fluency as a relevant property of *relational* representations as well. Hence, a feasible source for the subjective experience of familiarity for relational representations is the fluency with which these representations are processed. Two lines of evidence support this notion.

First, though fluency is typically examined in the context of single entities, effects of fluency have also been demonstrated for information which can be construed as relational. Such relational information may include a variety of content types which, critically, involve the binding of two or more items – namely, forming a link between the items while preserving the meaning of each individual item (Eichenbaum et al. 1994). For instance, processing of arithmetic problems, which are comprised of several numbers and the relations between them, is affected by fluency (manipulated as the number of exposures to each problem; Paynter et al. 2009; Reder & Ritter 1992). Sentences are an additional instance of relational information whose representations include both their constituent elements (namely, the words) and the relationships between them. Fluency for sentences has been manipulated both visually, by comparing sentences written in a degraded font to those written in a clear font (Alter et al. 2007; Laham et al. 2009; Song & Schwarz 2008a), and aurally, by comparing sentences pronounced with a non-native accent versus a native accent (Lev-Ari & Keysar 2010). Interestingly, the effects of the fluency with which sentences got processed were demonstrated on various dependent measures, including syllogistic reasoning, speakers' credibility, and moral judgments. Going beyond sentences, fluency has been shown to affect processing of whole paragraphs (Diemand-Yauman et al. 2011; Song & Schwarz 2008b). Finally, fluency has also been shown to exert its effects on processing of ambiguous paintings which, as in previous examples of relational information, are composed of several elements and the relationships between them (Jakesch et al. 2013).

A second line of evidence supporting the relevance of fluency to relational representations concerns *repetition suppression* – reduction of neural activity to repeated presentations of stimuli. Repetition suppression is regarded by many (apparently, Bastin et al. included) as a neural marker for fluency (e.g., Ward et al. 2013). The target article describes several pieces of evidence for repetition suppression in the perirhinal cortex, a key structure in the entity representation core system. However, repetition suppression is not limited to neural structures within the entity representation system, and has also been demonstrated for relational representations in the hippocampus (Duncan et al. 2012; Düzel et al. 2003; Kumaran & Maguire 2006; 2007; 2009). For instance, in one study relational representations were operationalized as face–object and face–location associations (Düzel et al. 2003). Decreased activity in the hippocampus was found for repeated associations (intact pairs) versus novel associations (recombined pairs). Thus, the hippocampus – a key structure in the relational representation core system – also exhibits repetition suppression, the neural correlate of fluency.

To conclude, the integrative memory model makes the novel prediction that familiarity can be attributed to relational representations. However, the model does not specify what would lead to this attribution. Therefore, an exciting avenue for future research is to elucidate the sources of information or heuristics that may give rise to familiarity for relational representations. Based on the two lines of evidence reviewed above, I suggest considering fluency as a major candidate.

Dual processes in memory: Evidence from memory of time-of-occurrence of events

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Abstract

Bastin et al. present a framework that draws heavily on existing ideas of dual processes in memory in order to make predictions about memory deficits in clinical populations. It has been difficult to find behavioral evidence for multiple memory processes but we offer some evidence for dual processes in a related domain: memory for the time-of-occurrence of events.

Bastin et al. present a model that is designed to make predictions about memory deficits in clinical populations. This model draws upon dual-process views of episodic memory. Laboratory work analyzed using advanced methods such as state-trace analysis (Dunn 2008) and computational modeling (Wixted 2007) has failed to find evidence of multiple processes, bringing into question a fundamental assumption of the model. However, in the domain of *memory for the time-of-occurrence of events*, there is extensive literature on multiple memory processes. In an influential review, Friedman (1993) made a distinction between "distance-based" and "location-based" processes. Location-based processes involve retrieval of information associated with the available cues, which is then used to draw inferences about when the event occurred. Location-based processing, therefore, is analogous to recollection. Distance-based processes are very similar to familiarity in that they rely on some quality of memory (such as strength) to infer when the event took place. Friedman (1993) concluded that location-based processes are most common.

Much of the work in the domain of memory for the time-of-occurrence of events has relied on testing people's memories for events that are part of the public record or those that have been recorded in personal diaries (Kemp 1999). Most of these studies used event stimuli that occurred outside of the laboratory, but which could be dated because they were part of the public record or had been recorded in personal diaries (Kemp 1999). Many of the existing studies also asked people to determine the exact dates of occurrence of these events. The method of reporting, however, may influence the strategy that people employ. Furthermore, using public events may tend to emphasize unique flashbulb-type memories which, in turn, may not reflect how people retrieve the time-of-occurrence of everyday mundane and personally experienced events. We conducted several studies using smartphone-based sensors to record people's everyday life events and used those events to probe how they retrieved the week and day of occurrence of these events a few weeks after they occurred (Dennis et al. 2017; Sreekumar 2015; Yim et al. 2019). Using a hierarchical Bayesian model-comparison framework, we concluded that location-based processes were employed when people had to retrieve more precise information (i.e., day of occurrence) compared to distance-based strategies when asked about the week of occurrence. Therefore, experience sampling work suggests that when one looks at people's real-world memories that have not been stripped of cues necessary to form reliable inferences, one can see clear evidence of a distinction between what Friedman (1993) called "distance"- and "location"-based processes. The prior difficulty in dissociating location-based and distance-based processes behaviorally also led to neuropsychological research on the contribution of various brain regions to memory for time. For example, Curran and Friedman (2003) recorded event-related potentials (ERPs), where participants engaged in temporal memory tests that were designed to emphasize one of the two processes and showed greater late-frontal ERP effects under conditions that fostered location-based processing.

In memory-for-time experiments, it is easier to manipulate these different components than in a recognition memory experiment because it is possible to vary the nature of the query and the time-scale probed (e.g., month, week, day, hour, etc.). We also have access to a wider range of the ratio between retention interval and the temporal separation between probe events, which has been identified as another factor that plays a role in fostering one process over the other. Therefore, both neuropsychological and more recent behavioral experiments based on experience sampling provide evidence for multiple processes in memory for when an event occurred, where the dominant processes are very similar to recollection and familiarity in recognition memory.

While the multiple memory processes assumption has some support from the memory-of-time literature, Bastin et al. rely on findings of fMRI (functional magnetic resonance imaging) activation of brain regions in discrimination tasks to support the assumption that the perirhinal/anterolateral entorhinal cortex is specialized for pattern separation of entities (i.e., objects). Although the hippocampal circuit has known mechanisms that allow both pattern completion and pattern separation, the mechanisms that would allow the perirhinal/anterolateral entorhinal cortices to specifically pattern-separate entities are unclear. In fact, major types of computation in the brain seem to be redundant and distributed (e.g., Siegel et al. 2015; Tian et al. 2016). Furthermore, assigning "entity separation" computations to a very specific brain region seems somewhat contradictory to the goal of moving away from assigning processes to brain regions, to thinking about the type and complexity of representations they are capable of. Temporal context signals, which guide memory encoding and retrieval, are found everywhere in the brain (e.g., in various regions within the temporal lobe; El-Kalliny et al. 2019). Folkerts et al. (2018) found that even highly visually selective units participate in a gradually changing representation of temporal context. However, the rate at which these signals drift in time may depend on where the brain region lies along the representational hierarchy because temporal receptive windows follow the same hierarchy (Lerner et al. 2011). Within the lateral entorhinal cortex specifically, Tsao et al. (2018) reported that population states encoded temporal context information. They also previously identified a population of lateral entorhinal cortex cells that encoded object-location associations (Tsao et al. 2013) and, importantly, these cells were different from object-specific cells. Therefore, even the anterolateral entorhinal cortex (human homolog of the rodent lateral entorhinal cortex) "entity representational core" assumed in Bastin et al.'s model seems to have an important role to play in context and associative representations that extend beyond conjunctions of simpler features. Similarly, the hippocampal formation is not required for some context-discrimination tasks. For example, such contextual discrimination tasks can be readily learned even by animals with hippocampal lesions (see Rudy [2009] for a review).

In summary, Bastin et al.'s framework is motivated by dual-process accounts of memory which are well supported by both behavioral and neuroimaging data; but the distinctions made between entity and context representational systems may not accurately reflect the distributed nature of these representations in the brain.

Episodic memory is emotionally laden memory, requiring amygdala involvement

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Abstract

The memory impairment of neurological and psychiatric patients is seen as occurring mainly in the autobiographical-episodic memory domain and this is considered to depend on limbic structures such as the amygdala or the septal nuclei. Especially the amygdala is a hub for giving an emotional flavor to personal memories. Bastin et al. fail to include the amygdala in their integrative memory model.

As the title of Bastin et al.'s target article indicates, their integrative memory model is intended to "understand memory deficits."

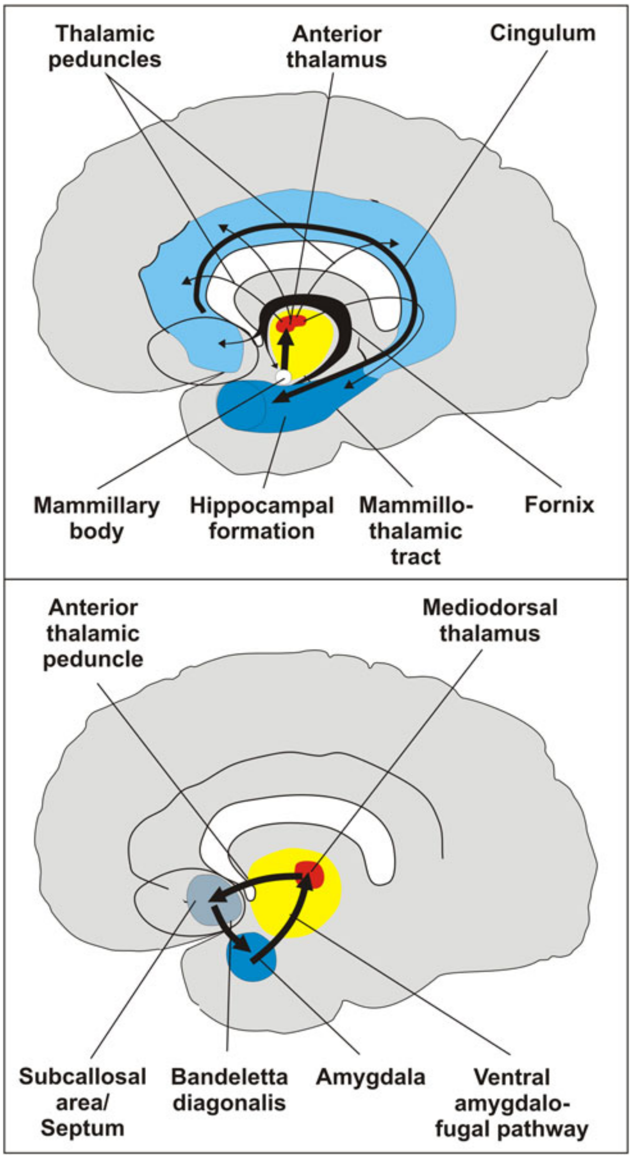


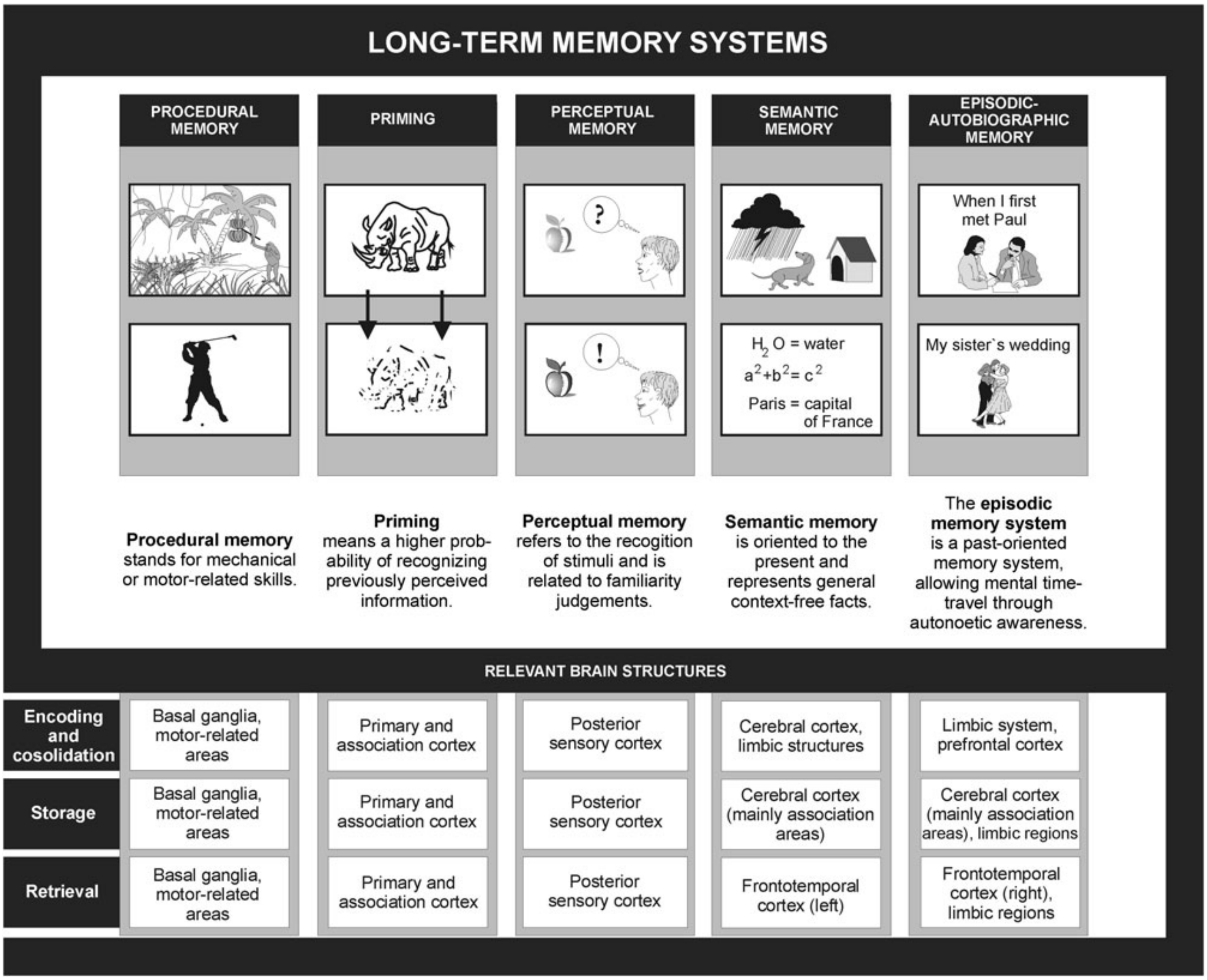
Figure 1 (Staniloiu & Markowitsch): Schematic sagittal sections through the human brain showing the arrangement of the two main circuits implicated in memory binding. (**Top**) The medial or Papez circuit. (**Bottom**) The basolateral limbic circuit. The medial circuit is probably associated with cognitive acts of memory processing and the basolateral circuit with the affective evaluation of information. Both circuits interact.

Memory processing is largely a product of structures of the limbic system, including (among others) the hippocampal formation, the amygdala, the basal forebrain (septal nuclei), thalamic and hypothalamic nuclei (mammillary bodies), and their interconnections (see our Figure 1) (Markowitsch 1999). As most structures of the limbic system are engaged in processing emotional stimuli, this implies that especially the most important memory system – namely, episodic-autobiographical memory (our Fig. 2) – is always emotion-based (e.g., Markowitsch & Staniloiu 2011; Stanley et al. 2017).

Piolino et al. (2009) formulated that:

> visual mental imagery and emotional experience are critical phenomenological characteristics of episodic AM [autobiographical memory] retrieval. Hence, the subjective sense of remembering almost invariably involves some sort of visual (Greenberg & Rubin 2003) and emotional (Rubin & Berntsen 2003) re-experiencing of an event. (Piolino et al. 2009, p. 2315).

This becomes most evident in patients with dissociative amnesia (Staniloiu & Markowitsch 2014), who – based on stressful or traumatic events – lose the capacity to recollect episodic-autobiographical memories, while still being (largely) unimpaired in semantic, and therefore mainly unemotional, memory. We (Brand et al. 2009) found in the brains of patients with dissociative amnesia hypometabolic zones in the right inferolateral prefrontal and anterior temporal regions (including the amygdala), indicating that in these patients the synchronization of "emotional and factual components of the personal past linked to the self" (Brand et al. 2009, p. 38) is no longer possible. But patients with clear structural damage in the amygdala or in the septal nuclei also demonstrate major deficits in episodic-autobiographical memory (Cramon et al. 1993; Markowitsch & Staniloiu 2011; 2012a; 2012b). This is most evident from the rare patients with symmetrical bilateral amygdalar damage due to Urbach–Wiethe disease (Cahill et al. 1995; Markowitsch et al. 1994; Siebert et al. 2003). And in normal individuals, the right amygdala is especially engaged in episodic-autobiographical memory retrieval (compared to fictitious memory retrieval) (Markowitsch et al. 2000).



Procedural memory stands for mechanical or motor-related skills.

Priming means a higher probability of recognizing previously perceived information.

Perceptual memory refers to the recognition of stimuli and is related to familiarity judgements.

Semantic memory is oriented to the present and represents general context-free facts.

The **episodic memory system** is a past-oriented memory system, allowing mental time-travel through autonoetic awareness.

RELEVANT BRAIN STRUCTURES

	Procedural memory	Priming	Perceptual memory	Semantic memory	Episodic-autobiographic memory
Encoding and cosolidation	Basal ganglia, motor-related areas	Primary and association cortex	Posterior sensory cortex	Cerebral cortex, limbic structures	Limbic system, prefrontal cortex
Storage	Basal ganglia, motor-related areas	Primary and association cortex	Posterior sensory cortex	Cerebral cortex (mainly association areas)	Cerebral cortex (mainly association areas), limbic regions
Retrieval	Basal ganglia, motor-related areas	Primary and association cortex	Posterior sensory cortex	Frontotemporal cortex (left)	Frontotemporal cortex (right), limbic regions

Figure 2 (Staniloiu & Markowitsch): The five long-term memory systems (after Markowitsch & Staniloiu 2012a; 2012b). Procedural memory refers to motor-based routines; priming to a higher likeliness of re-identifying already perceived stimuli. Perceptual memory allows us to distinguish an object based on distinct features. Semantic memory is factual memory (general world knowledge). Episodic-autobiographical memory is context-specific with respect to time and place, and allows mental time traveling; it is associated with an emotional overtone.

As researchers Bocchio et al. (2017) write, in the very first sentence of their Abstract: "The neuronal circuits of the basolateral amygdala (BLA) are crucial for acquisition, consolidation, retrieval, and extinction of associative emotional memories." Canli et al. (2000) identified a correlation between amygdala activation and episodic memory for highly emotional, but not for neutral stimuli. Similarly, many other researchers have emphasized amygdala activations in relation to memory consolidation (e.g., McGaugh 2015) and retrieval (e.g., Markowitsch et al. 2003). And already in the 1980s, in two reviews by Sarter and Markowitsch, it was argued that the human amygdala is responsible for activating or reactivating those mnemonic events which are of an emotional significance for the subjects' life history, and that this (re-)activation is performed by charging sensory information with appropriate emotional cues (Sarter & Markowitsch 1985a; 1985b).

The importance of the amygdala and related structures for episodic-autobiographical memory is therefore undisputed; and it is also stressed in Pessoa's review in which he states that the amygdala is in fact no longer viewed as a simple emotional brain structure, but rather as a hub that plays a critical role in integrating emotive and cognitive processes (Pessoa 2008). There are strong pathways between amygdala and hippocampus (Wang & Barbas 2018), as well as between amygdala and prefrontal cortex (Barbas 2000), a cortical region centrally implicated in memory recollection as well (Bahk & Choi 2018; Eichenbaum 2017b; Lepage et al. 2000).

On the other hand, Bastin et al. mention the amygdala only once and very cursorily by stating that the "extended anterior temporal system … also includes the ventral temporopolar cortex, lateral orbitofrontal cortex, and amygdala" (sect. 2.1.4, para. 1). They fail to include the amygdala (or the septal nuclei) in their integrative memory model. On account of this omission, their integrative memory model lacks essential neuroanatomical components that are necessary for memory recollection – a lack, particularly, when it comes to understanding the brain bases of memory deficits in neurological and psychiatric patients.

The other side of the coin: Semantic dementia as a lesion model for understanding recollection and familiarity

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Abstract

The syndrome of semantic dementia represents the "other side of the coin" to Alzheimer's disease, offering convergent evidence to help refine Bastin et al.'s integrative memory model. By considering the integrative memory model through the lens of semantic dementia, we propose a number of important extensions to the framework, to help clarify the complex neurocognitive mechanisms underlying recollection and familiarity.

Human lesion studies offer a powerful means of validating and refining neurocognitive models of memory (Irish & van Kesteren 2018). In their integrative memory model, Bastin et al. provide a compelling overview of the processes of recollection and familiarity, invoking evidence from Alzheimer's disease (AD) in support of its central tenets. Although this new framework can accommodate many of the memory and pathological changes in AD, we note significant gaps that warrant consideration.

We propose to extend the integrative memory model by considering complementary human lesion findings from the syndrome of semantic dementia; a neurodegenerative disorder characterized by progressive atrophy to core nodes of the entity representation (i.e., anterior temporal lobes and perirhinal cortex) and relational representation (i.e., hippocampus) systems (Brambati et al. 2009). The cognitive profile of semantic dementia is commonly taken to represent the "other side of the coin" to AD, with profound semantic processing impairments emerging in the context of relatively spared episodic memory (Hodges & Patterson 2007). Importantly, the neurocognitive sequelae of semantic dementia pose several challenges to the integrative memory model, which we address here.

First, the integrative memory model fails to consider how the inherent features of the to-be-remembered stimulus potentially influence processes underlying familiarity. The key role of the entity representation system in familiarity is primarily supported by evidence from nonverbal measures, such as object recognition tasks. Studies of recognition memory in semantic dementia, however, reveal the importance of stimulus modality in familiarity judgments. For example, when pictures of objects are used as stimuli, semantic dementia patients demonstrate intact recognition (Simons et al. 2002a), despite severely impaired recognition for words (Graham et al. 2002). As such, the anterior temporal lobe degeneration in semantic dementia does not manifest in an all-encompassing recognition deficit, but rather produces an impairment specific to verbal stimuli. As suggested by the integrative memory model, perceptual fluency signals, likely mediated by intact occipitotemporal regions, are co-opted to support recognition of pictorial stimuli in semantic dementia, even when the conceptual representation of that stimulus is degraded (Simons et al. 2002b). For verbal stimuli, however, no such compensatory strategy can be deployed, as the poor perceptual discriminability of written words precludes the use of perceptual fluency signals (Graham et al. 2002). Collectively, these findings from semantic dementia suggest that the relative weightings of perceptual versus conceptual fluency signals during familiarity judgments vary, contingent upon the nature of the to-be-remembered stimulus.

Building on this argument, the role of the anterior temporal lobe in supporting familiarity judgments may also scale, depending on the "meaningfulness" or conceptual loading of pictorial stimuli. In line with the integrative memory model, damage to the perirhinal cortex in semantic dementia has been shown to impair discrimination of objects with highly ambiguous perceptual features (Barense et al. 2010). Importantly, however, in semantic dementia these deficits are amplified for items embedded within a distinct semantic framework (e.g., animals) as compared with non-meaningful items (e.g., blobs). This disproportionate impairment of semantically loaded items likely manifests because of the co-occurrence of both perirhinal and temporopolar atrophy in semantic dementia. By contrast, amnesic patients with exclusive medial temporal (including perirhinal) damage, and spared temporal poles, are more accurate at discriminating between perceptually similar items that are meaningful, compared with novel ones, potentially by harnessing intact semantic constructs to boost recognition (see Barense et al. 2010). Accordingly, we propose an extension to the integrative memory model, in which the role of the anterior temporal lobes in familiarity judgments is particularly pertinent for stimuli that are both perceptually ambiguous and conceptually meaningful (see also Chiou & Lambon Ralph 2016).

Contemporary models of memory recognize the importance of a distributed core recollection network including medial temporal, frontal, and parietal regions in mediating successful episodic retrieval (Rugg & Vilberg 2013). While the hippocampus is an important node of this network, findings from semantic dementia suggest that models of episodic memory must look beyond the medial temporal lobes (Irish et al. 2016). Despite pronounced hippocampal atrophy from early in the disease course (Chapleau et al. 2016), semantic dementia patients demonstrate remarkably intact nonverbal memory retrieval. This profile of sparing reflects the preservation of frontal and parietal brain structures (Irish et al. 2016), including the angular gyrus, posterior cingulate cortex, and lateral prefrontal cortex. Moreover, when recollection is affected in semantic dementia, it relates primarily to prefrontal, rather than hippocampal, degeneration (Simons et al. 2002b). These findings emphasize the multifaceted nature of recollection, and its dependency upon lateral prefrontal and parietal brain regions. Further iterations of the integrative memory model should consider how distinct aspects of recollection, such as strategic retrieval (Rugg et al. 1999) and contextual binding (Ramanan et al. 2018), are differentially underwritten by subdivisions of lateral prefrontal and parietal cortices.

Finally, we believe it is important to validate the integrative memory model with respect to ecologically valid expressions of memory, which are essential for self-continuity and identity (Strikwerda-Brown et al. 2019). The integrative memory model is predicated largely on evidence from highly decontextualized experimental measures (e.g., object recognition, source memory). Although useful, such laboratory tasks fail to capture the idiosyncrasies of self-referential episodic recall as experienced in the real world. Autobiographical memory represents the prototypical expression of contextually detailed episodic retrieval, imbued with vivid sensory-perceptual and semantic elements, and strong self-referential and emotional connotations. Studies of autobiographical memory in semantic dementia reveal intact retrieval of recently experienced events (Irish et al. 2012; Piolino et al. 2003), attributable to preservation of sensory-perceptual representations stored in posterior parietal brain regions (Irish et al. 2018). In contrast, recall of remote autobiographical events is impoverished in semantic dementia (Irish et al. 2011), given the increased semanticization of episodic experiences with the passage of time (Moscovitch et al. 2006). Considering how profiles of autobiographical memory corroborate or challenge the integrative memory model framework will be crucial to validate and update the model with respect to self-defining expressions of the episodic memory system.

The ventral lateral parietal cortex in episodic memory: From content to attribution

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Abstract

The ventral lateral parietal cortex (VLPC) shows robust activation during episodic retrieval, and is involved in content representation, as well as in the evaluation of memory traces. This suggests that the VLPC has a crucial contribution to the quality of recollection and the subjective experience of remembering, and situates it at the intersection of the core and attribution systems.

The ventral lateral parietal cortex (VLPC) is one of the most active regions during successful episodic retrieval (reviewed by Levy 2012; Rugg & King 2018; Sestieri et al. 2017; Shimamura 2011; Vilberg & Rugg 2008; Wagner et al. 2005). Nevertheless, patients with VLPC lesions can often successfully retrieve episodic memories, and are not usually considered to be amnesic. This alleged discrepancy has led to growing interest in VLPC activation in the context of episodic memory.

In considering the contribution of the VLPC to episodic retrieval, the integrative memory model proposed in the target article by Bastin et al. builds on the attention-to-memory account (AtoM; Cabeza et al. 2008). AtoM associates VLPC activation during retrieval with bottom-up capture of attention by relevant memory cues and/or recovered memories. Accordingly, the integrative memory model suggests that the VLPC interacts with a connectivity hub (centred in the posterior cingulate) and a frontal attribution system, to support orientation of ecphory-related attention. Nevertheless, growing evidence suggests that the role of the VLPC in retrieval goes beyond the ancillary attentional function ascribed by the integrative memory model. More specifically, building on two separate lines of evidence – the first showing VLPC involvement in content representation and the second in the evaluation of the memory trace – I suggest that the VLPC should be considered an essential part of the connectivity hub that links together the core systems and the attribution system.

Recent evidence suggest that VLPC activation reflects retrieved information, either by holding an actual representation, or by linking distributed memory traces. Particularly compelling is evidence from studies that employed multi-voxel pattern classification to decode the content of the retrieved information in the VLPC. For example, Kuhl and Chun (2014) employed a task in which words were paired with pictures (faces/scenes) during an initial study phase, and subsequently used as cues in a cued-recall test, followed by a recognition test for pictures alone. Activity patterns elicited by word cues during recall were compared with activity patterns elicited by pictures during recognition. Strikingly, in the VLPC, patterns elicited by words were more similar to the specific pictures with which they were studied than with "unassociated" pictures from the same category, strongly suggesting that the

VLPC holds event-specific representations. Arguably, however, these retrieved representations are not passively held in the VLPC. Rather, their content is further evaluated and transformed into signals that can be used by the attribution system.

An influential account (Yazar et al. 2012) posits that the VLPC is involved in subjective aspects of recollection. This account derives from several studies showing that, while accuracy of recognition judgements is typically unaffected by VLPC lesions, patients consistently express lower confidence in their judgements, and are less likely to report that recognised items engendered a subjective experience of recollection (e.g., Hower et al. 2014; Simons et al. 2010). Thus, while "objective" memory performance, as expressed in response accuracy, exhibits no obvious decline in patients with VLPC lesions, "subjective" memory – that is, the personal experience of one's own episodic memory – is impaired. In support of this view, fMRI (functional magnetic resonance imaging) studies have shown that the relative number of "remember" (vs. "know") responses, high-confidence responses, and measures of richness, vividness, and specificity of retrieved episodic events, all correlate with VLPC activation (Qin et al. 2011; Richter et al. 2016; Tibon et al. 2019; Yazar et al. 2014). Taken together, these findings suggest that the VLPC is involved in the subjective evaluation of memory traces, and affords conscious access to the quality of the memory signal that serves as the basis for such judgements (e.g., Rugg & King 2018).

The integrative memory model suggests that the connectivity between core systems and the attribution system relies mostly on the posterior cingulate cortex. Of particular interest is the ventral posterior cingulate cortex (vPCC), which connects notably with the VLPC, and is assumed to support pattern completion of a whole memory trace by allowing the reactivation of the self-referential properties of personally experienced events. Arguably, these recovered traces are then processed by the VLPC, which computes the subjective evaluation of the trace (e.g., vivid memories will be evaluated as highly confident; memories that contain many contextual details will be evaluated as recollective). The memory trace, coupled with its evaluation, is then transferred to the attribution system, which translates the signal according to task demands and particular contexts (e.g., the memory will be endorsed as "Remembered"). Altogether, the interactions between these components contribute to the quality of recollection and the subjective experience of remembering.

In contrast to the integrative memory model, the current view suggests that the frontal attribution system relies mostly on VLPC output, which represents the evaluated memory trace, rather than on vPCC output. Moreover, the interactions between the vPCC and the VLPC are (generally) hierarchical: the vPCC generates self-referenced memory traces, which are subsequently evaluated by the VLPC.

Interestingly, a recent study confirms this suggested role of the VLPC in the intersection of the core and attribution systems: Following initial recognition of studied words, participants made a remember/know judgement, and then recalled the colour and the spatial position in which the word was studied. Importantly, on trials where *both* features were retrieved (but not on trials where one or neither source feature was retrieved) healthy controls were more likely to make Remember relative to Know judgements, whereas parietal patients could not do so. In their interpretation, Ciaramelli et al. (2017) argue that unlike patients, controls were able to use the richness of the experience accompanying the reinstatement of multiple features as an important basis for endorsing an item as "Remembered."

To conclude, the integrative memory model integrates a large corpus of findings and theories, and provides a framework that affords better understanding of memory deficits. It will, nevertheless, benefit from further specification of the processes that occur at the intersection of the core and attribution systems; some of which are supported by VLPC.

Cutting out the middleman: Separating attributional biases from memory deficits

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Abstract

Bastin and colleagues present an integrative model of how recollection- and familiarity-based memories are represented in the brain. While they emphasize the role of attribution mechanisms in shaping memory retrieval, prior work examining implicit memory suggests that memory deficits may be better understood by separating attributional biases from the underlying memory traces.

In the last decade, advances in functional magnetic resonance imaging (fMRI) have shifted the focus of cognitive neuroscience research toward understanding how memory traces are represented in the human brain. In their thoughtful synthesis of recent neurocognitive models, Bastin et al. illustrate the important role that attribution plays in recollection and familiarity, and incorporate multiple factors to put forth a holistic account of episodic memory. However, while the attribution system described in their integrative memory model is demonstrably essential for recollection and familiarity, it is secondary to the underlying memory representations.

Although judgments of recollection and familiarity are the measurable outputs in episodic memory tests, objective memory traces may sometimes be biased by the attribution system. For example, in a simultaneous fMRI and eye-tracking study, Hannula and Ranganath (2009) reported that hippocampal activation predicts eye gaze to the correct item during a relational memory test, even when limited to incorrect explicit memory responses (i.e., implicit memory). Moreover, functional connectivity between hippocampus and lateral prefrontal cortex was greater for correct than incorrect responses. Together, these results tie episodic memory traces to implicit behavior (i.e., eye gaze), unbiased by attribution, as well as to explicit behavior (i.e., memory response), biased by attribution signals from prefrontal cortex.

As Bastin et al. discuss, the entity representation and relational representation core systems are recruited in the service of cognitive tasks beyond episodic memory (Graham et al. 2010; Yonelinas 2013). Notably, there is evidence of shared neural substrates (Wang & Giovanello 2016) and cognitive mechanisms (Wang & Yonelinas 2012) between explicit forms of memory such as recollection and familiarity, and implicit forms of memory such as priming.

In other words, entities and relations may not need to be explicitly retrieved in order to involve recollection- and familiarity-based mechanisms. Consistent with the importance of these core systems for mnemonic representations, medial temporal lobe activation is related to *objective* oldness, rather than subjective or perceived oldness (Daselaar et al. 2006).

Therefore, in studying memory-impaired populations, it is essential to separate an inability to form mnemonic representations from attributional biases that affect the use of these representations. For example, memory-impaired patients with intact attribution systems may interpret processing fluency differently than healthy controls (Ozubko & Yonelinas 2014). The entity and relational systems are the backbones by which memories are encoded, and their retrieval can be most accurately assessed by cutting out the middleman – through implicit measures that do not rely on attributional systems. Moreover, separating attributional biases from memory deficits will also help to resolve inconsistent findings in the literature with regard to clinical populations. This perspective largely agrees with how Bastin et al. have described the integrative memory model. However, separating attributional biases is an important point of emphasis with both theoretical implications for how recollection- and familiarity-based memory is conceptualized, as well as practical implications for how residual memory function can be best harnessed in clinical populations.

Global matching and fluency attribution in familiarity assessment

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Abstract

In the integrative memory model proposed by Bastin et al., familiarity is thought to arise from attribution of fluency signals. We suggest that, from a computational and anatomical perspective, this conceptualization converges with a global-matching account of familiarity assessment. We also argue that consideration of global matching and evidence accumulation in decision making could help further our understanding of the proposed attribution system.

We commend Bastin et al. on developing an integrative dual-process model of recognition memory that considers the role of distinct brain regions in representing information, and in making attributions about experience-dependent changes to these representations, in memory decisions. In our view, such an integration has been missing in the extant cognitive neuroscience literature, which has typically focused exclusively either on representations or on cognitive processes when characterizing the role of different structures (e.g., Bussey & Saksida 2007 versus Brown & Aggleton 2001). Past accounts of recognition memory that have made reference to attribution have discussed it in relation to fluency, with attribution of fluency to prior experience being at the core of familiarity-based judgments (Dew & Cabeza 2013; Jacoby et al. 1989). In the current model, the authors take a similar stance when specifying the role of perirhinal cortex (PrC) and anterolateral entorhinal cortex in providing fluency signals. As the authors acknowledge, this fluency account contrasts, at least on the surface, with another dominant account of familiarity assessment that focuses on global-matching computations, which have also been linked to PrC (LaRocque et al. 2013; Norman 2010).

We would like to point out that global matching and fluency accounts of familiarity may not be mutually exclusive. In the integrative model proposed here, fluency can arise from repetition (i.e., prior exposure) of perceptual or conceptual features at different levels of a representational hierarchy, with PrC being sensitive to repetition at the entity level where features are highly conjunctive and can differentiate between different exemplars of objects with high feature overlap. Critically, feature overlap also plays a key role in global matching and has been linked to behavioral evidence, such as false alarm rates to lures similar to targets, in recognition-memory judgments (Montefinese et al. 2015). In the influential MINERVA 2 model (Hintzman 1984) of global matching in recognition memory, a retrieval cue induces an echo whose intensity is directly based on a scalar measure of feature overlap between the cue and all stored memory traces. Fluency may be a signal that simply reflects this intensity measurement.

Global matching and fluency can also be linked to a common neural phenomenon in terms of changes to representations that occur with repeated exposures: namely, repetition suppression. Repetition suppression is well documented in the perirhinal cortex (Suzuki & Naya 2014) and has been suggested to reflect a fluency signal that can inform decisions on a variety of tasks, including but not limited to familiarity-based memory judgments (Dew & Cabeza 2013). Although the functional significance and underlying mechanisms of repetition suppression in neural recordings remain contentious (Barron et al. 2016; Grill-Spector et al. 2006), at least one of the proposed mechanisms, "sharpening," can support both computations of global matching and fluency signaling. In a sharpening account, neural representations of a stimulus become sparser over repetitions, as neurons that initially responded weakly to a stimulus gradually "drop out." In the complementary learning system neural network model (Norman & O'Reilly 2003; see also Norman 2010), such sharpening is the result of a competitive Hebbian learning process between neurons in neocortical regions; it is linked to global matching by virtue of stimuli with high degree of feature overlap also being represented with overlapping neural patterns. Inasmuch as repetition suppression in single cell recordings and in fMRI (functional magnetic resonance imaging) BOLD signals is not limited to the PrC, and has also been shown to occur, for example, in other ventral visual pathway regions (Barron et al. 2016), wide-spread repetition suppression effects are consistent with the proposal in the present integrative memory model that fluency signals can arise at multiple levels.

Considering global-matching computations (and their link to fluency) may also be of value when trying to understand the mechanisms that underlie the attribution process in recognition memory as proposed in the integrative memory model. It is our impression that this attribution system is currently less well specified, and supported by less empirical evidence overall, than the proposed representation system. In the integrative memory model, the attribution system interprets changes in representations toward the goal of making overt memory decisions. A promising account that may help to elaborate on how attribution processes lead to memory judgments is provided by the drift-diffusion model (Ratcliff 1978; see also Ratcliff et al. 2016b). This model addresses the temporal unfolding of memory retrieval and treats the comparison of feature overlap between cues and stored traces during this retrieval process as accumulating noisy evidence. Because all memory traces are compared in parallel, these computations can be understood as global matching, with fluency reflecting the combined speed of these parallel accumulation streams.

An emerging body of evidence from functional neuroimaging and other recording techniques points to a role for lateral parietal cortex in evidence accumulation during decision making, including but not limited to memory judgments (Wagner et al. 2005). Some studies have even identified specific neurons in the lateral intraparietal sulcus whose activity profile can be interpreted as evidence accumulation (Shadlen & Newsome 2001). Against this background, the specification of structures involved in memory attribution in the integrative memory model may require expansion beyond prefrontal cortex, and additional emphasis on lateral parietal cortex as a key player. At present, the latter structure is primarily concerned with attentional mechanisms in this model. There is some evidence to suggest, however, that attention effects observed in the lateral parietal lobe are at least in part spatially distinct from memory effects (Hutchinson et al. 2009; 2014). Therefore, exclusive reference to attentional mechanisms may not fully capture its role in attribution processes as part of the decision making just described.

Authors' Response

Interactions with the integrative memory model

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Abstract

The integrative memory model formalizes a new conceptualization of memory in which interactions between representations and cognitive operations within large-scale cerebral networks generate subjective memory feelings. Such interactions allow to explain the complexity of memory expressions, such as the existence of multiples sources for familiarity and recollection feelings and the fact that expectations determine how one recognizes previously encountered information.

The integrative memory model takes into account the complexity of memory, from the representations of elements of past experiences to the subjective feelings accompanying memory retrieval. As suggested by commentators **Curot & Barbeau**, the model could have been called the interaction memory model, as interactions between representations and cognitive operations within large-scale cerebral networks are at the core of the proposal. The majority of the commentaries follow the path of this integration/interaction scheme. We are grateful to all commentators for the insightful comments and the abundance of new ideas to be tested. In this response, we will address the issues raised in the commentaries by relating them to the key aspects of our integrative memory model: the representation core systems (sect. R1), the attribution system (sect. R2) and the subjective experiences of memory (sect. R3).

R1. Representation core systems

The idea that the content of past experiences are encoded in core systems that specialize in specific kinds of representations shaped by dedicated computational operations and the level of associativity that characterize constituent brain regions has been approved explicitly (**Axmacher**; **Brady & Utochkin**; **Gainotti**; **Patchitt & Shergill**; **Sadeh**) or tacitly by the large majority of the commentators. There is some controversy, however, concerning (1) the role of specific regions, (2) the specific nature of the computational operations distinguishing the various core systems, and (3) the consideration of additional types of information, such as emotion. In the sections below, we group the commentators' arguments by focusing in turn on the postulated core systems – the entity, the context, and the relational representation core systems – before considering interactions with the self and emotion.

R1.1. The entity representation core system

In the target article, we propose that encountered entities pertaining to experienced events are encoded hierarchically in terms of the complexity of the representation: from individual features (e.g., shape, texture, color) in ventral occipitotemporal areas and conceptual features in anterior temporal areas, to unique conjunctive representations allowing the resolution of ambiguity in the face of objects with overlapping features and the identification of objects in a viewpoint-invariant manner.

Gainotti points to the lateralization of the representations, with faces and voices prominently stored in right temporal areas and names lateralized to the left temporal areas. There is indeed a degree of hemispheric specialization in the medial and lateral temporal lobes. This is notably seen in material-specific double dissociation between recall and recognition memory in patients with selective unilateral hippocampal versus perirhinal lesions (Barbeau et al. 2011). In semantic dementia, some material-specific effects are also described, with better recognition memory for objects than for words (Graham et al. 2002; Simons et al. 2002a). However, in this case, the reason for material-specific dissociation is to be found in the pathology affecting the anterior temporal lobe (**Strikwerda-Brown & Irish**). We agree with Strikwerda-Brown & Irish, as well as with **Ionita, Talmi, & Taylor** (**Ionita et al.**), that the inherent features of the stimuli will determine the kind of information supporting memory decisions, and notably feelings of familiarity. Words will rely much more on conceptual features than will object pictures, and consequently words are particularly vulnerable to the anterior temporal pathology in semantic dementia. Critically, however, the interaction between the anterior temporal lobe and the perirhinal cortex is important for the discrimination of objects that can be confused because of high perceptual and/or conceptual feature overlap. Amnesic patients with damage to the perirhinal cortex, but intact anterior temporal lobes, are impaired at discriminating between objects with a high, not low, degree of perceptual feature ambiguity, but their difficulty is attenuated when objects are meaningful (Barense et al. 2010). In semantic dementia, when both anterior temporal and perirhinal regions are affected, the deficit in discrimination between confusable objects is exacerbated for conceptually meaningful stimuli (Barense et al. 2010). Finally, discrimination between semantically confusable objects is more impaired in patients who suffer from combined anterior temporal/perirhinal damage than in patients whose damage is limited to the anterior temporal lobe (Wright et al. 2015).

By shedding light on the role of the anterior temporal lobe, **Strikwerda-Brown & Irish** join **Axmacher** in calling for more consideration of representations in neocortical areas. We acknowledge that we placed much emphasis on the anterolateral entorhinal/perirhinal region and its proposed role in representing entities. Because of the historically central role of the medial temporal lobe (MTL), we wanted to make the point that the perirhinal cortex is not supporting familiarity per se, but rather a particular kind of representations (i.e., entities). Nevertheless, implicit in the inclusion of neocortical areas within representation core systems, and in the claim of representations being shaped by unique computational operations, is the idea that the formats of representations are determined by the properties of underlying neocortical (and MTL) regions (as suggested by Axmacher). Furthermore, Axmacher argues that these representational properties may be determinant features of the subjective experience of memory rather than attribution mechanisms, a point to which we return in section R3.

Additionally, the fact that our model includes interactions between hierarchically organized representation regions is emphasized by **Curot & Barbeau**, who point out a related prediction: activation of these regions should follow a precise order. This opens a whole avenue for research using various techniques that allow an evaluation of temporal dynamics in neural activity. Some preliminary EEG data centered on the time course of identification of objects via a 1-back task (in which one tells whether an object is the same as the one seen just before) at various levels of the hierarchy within the entity core representation system indicate that access to an entity representation comes later than access to a conceptual representation, which itself arises later than access to a low-level perceptual representation (data from an as-yet unpublished study by Besson and colleagues). More work remains to be done, however, notably by using methods that enable us to examine the temporal dynamics of precisely localized regions, such as intracranial EEG (Curot & Barbeau).

Our hypothesis of entity-level representations in the anterolateral entorhinal/perirhinal cortex is somewhat challenged by **Brady & Utochkin** who argue that entities also require relational coding and binding (see also **Hakobyan & Cheng**; **Sreekumar, Yim, Zaghloul, & Dennis** [**Sreekumar et al.**], for related suggestions). Indeed, numerous studies - from working memory to long-term memory, on arbitrary to semantically meaningful objects – do not support the idea of a pure perceptually unitized representation of objects (Brady et al. 2013; Chalfonte & Johnson 1996; Fougnie & Alvarez 2011); and we acknowledge that this was overlooked when we wrote that “at the level of the perirhinal cortex and anterolateral entorhinal… all visual features are integrated in a single complex representation of the object” (target article, sect. 4.1., para. 3). Behind this sentence and our definition of the entity representation lies the idea that at this level, entities could be distinguished as a whole rather than as a sum of overlapping features represented in order to distinguish objects at their individual level. Cognitive data showing separate coding of the exemplar and the object state also directly suggest that exemplar recognition operates despite object state or pose (Brady et al. 2013; Utochkin & Brady 2019). Our view is that the entity-level representations in the anterolateral entorhinal/perirhinal cortex correspond to the higher level of representation of the object, both anatomically and functionally, and as such represent the individual object in a way abstracted from its presentation characteristics (viewpoint, perceptual conditions of presentation, functional state or pose, etc.). In that sense, the features integrated at this level in a single complex representation of the object are those that the system considers to be *characterizing* and defining the object as a unique member of its category. Such defining features may be contextual in nature (e.g., the classic coffee mug of a specific brand used by a colleague at the lab might be encoded as a distinct entity, as the exact same one that I use at home). They must be distinguished from any other feature that the system considers as *associated* with but not defining the object. In order to retrieve any of this second class of features that were related to the object, the flexible and relational representation offered by the hippocampus might be critical.

R1.2. The context representation core system

In the target article we proposed that the contextual setting for an event is represented first by elements of the environment (e.g., sounds, visual details, space perception…) stored in posterior occipitoparietal sites and that these elements become more integrated as scenes and spatial configurations in the parahippocampal cortex. Moreover, the posteromedial entorhinal cortex would encode an internally generated grid of the spatial environment. If some of these elements become the focus of attention in a memory task (e.g., a building), they can be recognized and can, for example, generate a feeling of familiarity. Alternatively, they will provide the context within which an event occurs or a specific item is encountered, so that the context representation is bound together with other information into the relational representation core system.

Several commentators reproached us for not elaborating on this core system sufficiently; but they did not question its relevance (**Axmacher**; **Hakobyan & Cheng**; **Riva, Di Lernia, Serino, & Serino** [**Riva et al.**]). The commentators are right in underlining that more can be said about this system and they highlight some dimensions that could help characterize the respective content and representation formats of the context representation core system (Axmacher). In particular, the case of scenes is a puzzling issue. In our model, we suggested that scenes are represented in the parahippocampal cortex, given evidence of a specific response of this region to scene familiarity (Kafkas et al. 2017; Preston et al. 2010). In contrast, Hakobyan & Cheng regard scenes as part of the "what" information that is supported by the ventral visual stream culminating in the perirhinal cortex. Yet, other views are conveyed by Zeidman and Maguire (2016) who suggest that the hippocampus is involved in the construction of spatially coherent scene representations, and by Howett et al. (2019) who relate impaired virtual reality navigation within scenes to atrophy of the posteromedial entorhinal cortex in prodromal Alzheimer's disease (AD). There is clearly a need for further research on this topic. It may be that there are qualitatively different kinds of scenes, depending on the nature of constituent elements (e.g., buildings, landscape, spatial configuration, etc.). It could also be that the role of the scene in a given event, as focus of attention versus as background context, would determine how it is represented.

Another dimension that we overlooked in our model is the egocentric/allocentric distinction (**Axmacher**; **Riva et al.**). This distinction is particularly interesting when framing the role of the retrosplenial cortex. We placed this region within the context representation core system because it should enable cortical reinstatement of the content of memories as a gateway between the hippocampus and regions storing the sensory-perceptual details of the memory (Aggleton 2010). A more detailed description of its role in both encoding and retrieval of events could indeed be the transformation of egocentric representations (mediated by posterior parietal areas) into allocentric representations (mediated by the hippocampus and entorhinal cortex), and vice versa (Aggleton 2010; Serino et al. 2015; Vann et al. 2009a). Several studies have shown deficient translation between egocentric and allocentric frames of reference in Alzheimer's disease (Serino et al. 2015), especially in early-onset cases (Pai & Yang 2013) and in the stage of mild cognitive impairment (MCI; Ruggiero et al. 2018) where the retrosplenial cortex shows prominent damage (Boccia et al. 2016). Following on this, one could predict that the early hypometabolism and atrophy of the retrosplenial cortex in Braak Stage 3 would disturb the recollection of details from past events because of such translation difficulty. Relatedly, the observation of decreased "field" recall of personal past events (i.e., event visualized through one's own eyes, in the first-person perspective) and increased "observer" recall (i.e., event seen as a spectator from a third-person perspective) in Alzheimer's disease may possibly also be associated with retrosplenial-related impaired egocentric-allocentric synchronization (El Haj et al. 2019a; **Kapogiannis & El Haj**). However, distinct roles for the parahippocampal and retrosplenial cortices have been reported in spatial navigation (Auger et al. 2012), and reconciliation between spatial and non-spatial roles of the retrosplenial cortex was recently identified as a scientific challenge (Mitchell et al. 2018).

R1.3. The relational representation core system

Our view of the organization of the relational representation core system matches traditional influential models of the role of the hippocampus and the extended hippocampal system, by proposing that it rapidly encodes a detailed representation of the item bound to associated contextual information, or more generally complex high-resolution bindings, via relational pattern separation (Aggleton & Brown 1999; Aggleton et al. 2011; Eichenbaum et al. 2007; Montaldi & Mayes 2010; Ranganath & Ritchey 2012; Yonelinas 2013). We do not make any novel proposal regarding this core system and so we did not feel it necessary in the target article to describe data showing that damage to each part of the system (i.e., hippocampus, fornix, mammillary bodies, and anterior thalamus nuclei) leads to memory disorders, especially affecting recollection. This omission is regretted by **Aggleton**. Although this was beyond the scope of our proposal, we agree that further research needs to assess whether the mammillary body–anterior thalamic axis contributes a specific function beyond that supported by the hippocampus in the encoding and retrieval of complex events. In addition to examining the specific memory (and non-memory) profile of patients with diencephalic lesions, ultra-high resolution MRI and functional connectivity analyses as well as examination of coupling of neural oscillations may provide some insight about the interplay between the medial diencephalon and other regions (notably, the hippocampus, retrosplenial cortex, and prefrontal cortex). Indeed, the specific role of each component of the relational representation core system may depend on its specific afferent-efferent profile and, therefore, in the kind of information it processes and how it is brought into the system or transferred for further processing by other regions (Aggleton 2012; Ketz et al. 2015; Vann 2010).

R1.4. Self and emotion

A few commentators deplored that we did not take into account the emotional flavor of memories that can be provided through the amygdala (**Axmacher**; **Nephew, Chumachenko, & Forester** [**Nephew et al.**]; **Staniloiu & Markowitsch**; **Strikwerda-Brown & Irish**). As we stated in the conclusion of the target article, our proposed model is certainly not comprehensive and should evolve to incorporate more brain regions (notably the amygdala and basal forebrain) and more mechanisms. In terms of the psycho-affective flavor of memories, we mainly described how interactions with a self-referential system give self-relatedness and personal meaningfulness to stored representations. Indeed, personal memories are strongly interconnected with the self (Conway 2005) and these interactions contribute to the subjective feeling of reliving past events (Tulving 2002). In contrast, as most of the evidence that we reviewed relied on memory for neutral events, we did not elaborate on the role of emotion in shaping representations and subjective memory experiences. However, Staniloiu & Markowitsch are right to point out that this dimension is needed to understand the nature of memory deficits in patients with lesions to the amygdala and in psychiatric cases, such as dissociative amnesia (Markowitsch & Staniloiu 2011; Staniloiu & Markowitsch 2014).

The role of the amygdala appears to be the modulation of cognitive functions with emotional cues so as to incorporate the biological and social significance of events and actions. In the case of episodic autobiographical memories, the amygdala will tag them with their specific emotional significance and facilitate their retrieval (Markowitsch & Staniloiu 2011). According to the emotional binding account, when an event involves an emotional response, the amygdala binds this emotional response to representations of items in the perirhinal cortex (Ritchey et al. 2019; Yonelinas & Ritchey 2015). Another dimension that modulates memories is stress and anxiety (**Nephew et al.**). For example, acute stress could act as a memory filter at encoding, favoring events that elicited a strong neural activity in the medial temporal lobe (Ritchey et al. 2017). Nephew et al. further emit the interesting idea that anxiety may affect task context and metacognition, which would modify recollection and familiarity outputs by changing expectations and attentional focus. An intriguing example that could support this idea is psychogenic déjà-vu, where an individual with a high level of anxiety reported a form of persistent déjà-vu without any neurological explanation (Wells et al. 2014).

Patchitt & Shergill interpret two psychiatric syndromes, the Capgras delusion and the Fregoli syndrome, in light of the integrative memory model. We have reported the case of a patient with probable Alzheimer's disease who presented symptoms of Capgras syndrome with regard to her husband (Jedidi et al. 2015). Compared to other probable Alzheimer's disease patients without any misidentification symptoms, the patient showed decreased metabolism in the posterior cingulate gyrus/precuneus and the dorsomedial prefrontal cortex. We interpreted the Capgras syndrome in this patient as related to impaired recognition of a familiar face and impaired reflection on personally relevant knowledge about a face. Other interpretations include a disconnection between regions supporting face representations and regions encoding the emotional significance of the face (Breen et al. 2000). Investigating the role of a disruption of the attribution system due to frontal dysfunction, as suggested by Patchitt & Shergill, is certainly worthwhile, but we believe that this is an example of a disorder for which the role of emotion must be taken into account (see **Staniloiu & Markowitsch**).

R2. The attribution system

One of the most critical claims of the integrative memory model is that the attribution system modulates the use of memory traces reactivated in representation core systems as a function of expectations, task context, and goals, thus modulating subjective experiences and explicit judgments. In other words, we incorporated mechanisms from attribution theories (Bodner & Lindsay 2003; McCabe & Balota 2007; Voss et al. 2012; Westerman et al. 2002; Whittlesea 2002) into more traditional recollection/familiarity views. This proposal, approved by many commentators (**Bodner & Bernstein**; **Curot & Barbeau**; **Hakobyan & Cheng**; **Kelley & Jacoby**; **Patchitt & Shergill**; **Sadeh**; **Tibon**; **Wang**; **Yang & Köhler**), raises new questions for future work (Curot & Barbeau; Hakobyan & Cheng; Kelley & Jacoby; **Strikwerda-Brown & Irish**; Tibon; Wang; Yang & Köhler), but also generates controversy (**Aggleton**; **Axmacher**; **Ionita et al.**). These commentaries refer mainly to fluency cues, attribution mechanisms, and false memories.

R2.1. Fluency cues

In the target article, we argue that fluency cues are important signals for familiarity when recognizing studied items. More precisely, when a previously encountered item is repeated in a memory task, processing of the item and its constituent components (perceptual and conceptual features and their unique configuration as entity) is facilitated. This easier and more rapid processing (i.e., fluency), when in contrast with the expected baseline fluency of processing, produces a vague experience of ease (Masson & Caldwell 1998; Oppenheimer 2008; Reber et al. 2004b; Whittlesea & Williams 2000) which is attributed to past occurrence and generates a feeling of familiarity. The translation from the repetition-related facilitated processing into a feeling of familiarity thus requires the attribution system (see sect. R2.2). Familiarity for fluent items is not obligatory, as the attribution system may lead to disqualification of fluency cues.

While **Aggleton** thinks that too much importance is given to fluency in the generation of feelings of familiarity, other commentators support our point of view and even reinforce it with additional suggestions (**Ionita et al.**; **Sadeh**; **Wang**; **Yang & Köhler**). It is likely that part of the controversy is due to a blurry definition of fluency in our target article. In our view, perceptual fluency as a "change in threshold for information that has been previously experienced" (Aggleton) may correspond to the full fluency heuristic, given that the setting of the decision threshold falls within the duty of the attribution system. Like Sadeh, and Yang & Köhler, we define *repetition-related fluency,* at the behavioral level, as facilitated perceptual/conceptual/entity-level processing of repeated stimuli; and, at the neural level, as reduced activity of neurons where these features were first processed (Bogacz et al. 2001; Reber 2013; Suzuki & Naya 2014). While Ionita et al. refer to repetition-related fluency as a "non-mnemonic" signal, we would argue that it is mnemonic when it concerns a stimulus that has been encountered at least once before (even if we are not aware of that). As underlined by Yang & Köhler, reduced neuronal activity for repeated stimuli (or repetition suppression) has been interpreted as sharpening (Norman 2010).Yang & Köhler further suggest that sharpening may be a neural phenomenon common to both fluency and global matching (which indexes the degree of feature overlap between a cue and stored representations). Finally, Sadeh proposes that fluency is a key player in the attribution of familiarity even when information is retrieved from the relational representation core system. This author points to different findings to support this hypothesis, such as fluency effects for relational information in the form of facilitated judgments in a variety of tasks, as well as repetition suppression in the hippocampus for repeated associations. Another argument can be found in a study by Gomes et al. (2016), which showed a hippocampal deactivation linked to fluency-based supraliminal associative priming (size judgments for pairs of objects). However, one needs to determine whether relational fluency is interpreted as a feeling of familiarity or an experience of recollection in explicit memory tasks.

As reminded by **Wang**, repetition-related fluency is a mechanism shared by explicit forms of memory (e.g., familiarity) and implicit forms of memory (e.g., priming). On this basis, Wang suggests that implicit measures may best capture the status of representations in the core systems, contrary to explicit judgments in memory tasks that are biased by attribution mechanisms. We think that, more than the implicit or explicit character of the task, it is important to consider its objective demand (Whittlesea & Price 2001). The performance-oriented priming tests with objective measures, such as word-stem completion or picture naming, are probably the best to capture the status of representations, compared to more subjective implicit memory tasks that rely also on attributional processes, such as mere exposure effect or fame effect paradigms, or other illusion-oriented implicit memory measures (Buchner & Brandt 2003). In addition, some studies shed light on the role of fluency attribution even in performance-oriented priming tests, such as the possible-impossible decision task. Indeed, in this task, fluency seems to lead subjects to respond "possible" to both possible and impossible objects that have been previously studied (Marsolek & Burgund 2005; Ratcliff & McKoon 1995; Willems & Van der Linden 2009).

Nevertheless, beyond repetition-related fluency, there are other sources of fluency that we would regard as *non-mnemonic fluency*, but which can also lead to a feeling of familiarity (**Ionita et al.**). The existence of these non-mnemonic sources of fluency could help to explain partially the finding, pointed by **Aggleton**, that some patients with amnesia are not able to use fluency as a cue for recognition memory, despite successfully completing priming tasks (Levy et al. 2004), a fact that has led several authors to conclude that fluency has no or only small influence on people's memory decisions (Conroy et al. 2005; Squire & Dede 2015). Recently, however, studies have shown that changes in *how* amnesic patients *attribute* fluency to the past could account for this pattern of results (Geurten et al. 2019; Geurten & Willems 2017; Ozubko & Yonelinas 2014). For instance, Geurten et al. (2017; 2019) examined the influence of the introduction of an alternative (non-mnemonic) source of fluency on amnesic patients' recognition decisions by manipulating the perceptual quality of stimuli during a forced-choice recognition test. They found that patients disregard fluency when they detect an alternative source that can explain the easy processing of the stimulus, as do healthy subjects in the same paradigm (Willems & Van der Linden 2006). However, amnesic patients detect this alternative source more readily than healthy participants and thus disqualify more often fluency as a cue for memory. Patients' underuse of fluency could result from a learned reinterpretation of fluency as a poor cue for memory rather than from a real inability to rely on it. Because of the high number of situations where fluency leads to memory errors in patients' daily lives, the ecological validity of the correlation between fluency and past occurrence gradually decreases. In order to reduce fluency-based memory errors, patients would progressively learn to implement strategies to track biasing fluency sources. Behaviorally, this leads them to rely on fluency only when they can attribute it to their memory with a high level of confidence (Geurten et al. 2017; 2019).

An alternative and complementary explanation to the priming-without-recognition pattern in amnesia can be found in the retrieval mode, attention orientation, and processing style adopted by participants in some contexts. This idea is compatible with **Kelley & Jacoby**'s pre-access control hypothesis. More precisely, qualitatively different processing strategies – analytic versus non-analytic – have been shown to ensure or prevent the fluency experience (Whittlesea & Price 2001; Willems et al. 2010; Willems et al. 2008; Willems & Van der Linden 2009). An analytic form of processing consists in isolating some component parts of a stimulus – for example, to determine whether any of them acts as a cue for recalling diagnostic details. This style of processing can be preferred when a given recognition memory task appears as a considerable challenge. On the other hand, a non-analytic mode corresponds to examining the stimulus as a whole. Healthy participants and patients with Alzheimer's disease sometimes believe that their only hope of discriminating new from old stimuli is by discovering some specific details that they could recognize (Willems et al. 2008). However, Whittlesea and Price (2001) demonstrated that, even when a stimulus is presented in the same form as it was encountered earlier, if the participants analyze the stimulus into parts at testing, they will not experience enhanced processing fluency.

Within the integrative memory model, such a pattern of results can be explained by the interaction between metacognitive knowledge and components that create the retrieval mode during memory search (top-down attention and cue specification/memory search supported by dorsal parietal and ventrolateral and dorsolateral prefrontal cortex). This allows individuals' expectations and beliefs to constrain the type of information that will be favored during memory retrieval, as illustrated above. But also, as emphasized by **Kelley & Jacoby**, this can guide inferential mechanisms in order to avoid misattributions, such as false memories. For instance, Kelley & Jacoby describe a capture effect by which older adults, patients with Alzheimer's disease, and patients with traumatic brain injury are more prone to falsely remember misleading primes than young and healthy individuals (Dockree et al. 2006; Jacoby et al. 2005a; Millar et al. 2018).

R2.2. Attribution mechanisms

We claim that the attribution system is a key player in the generation of subjective experiences of memory and explicit judgments in memory tasks by modulating the use of reactivated content in core systems through the lens of metacognitive, monitoring, and attention mechanisms. This seems a contentious proposal as some commentators believe that such attribution mechanisms may not always be necessary (**Axmacher**; **Ionita et al.**), while others abound in our direction and evoke mechanisms that could contribute to the functioning of such a system (**Hakobyan & Cheng**; **Kelley & Jacoby**; **Tibon**; **Wang**; **Yang & Köhler**). We readily acknowledge that the description of the attribution system and of the role of the parietal regions in our target article was poorly elaborated. Our aim was first to put forward its role in shaping subjective and explicit outputs. But there is clearly a need to unpack its underlying mechanisms and associated neural correlates. We are delighted to see that, when admitted, many ideas for refining our understanding of the functioning of this attribution system arise (Hakobyan & Cheng; Kelley & Jacoby; Tibon; Yang & Köhler).

First of all, it may be that the term "attribution" is fuzzy and misleading and does not fully capture the complexity of inferential mechanisms that lead to subjective feelings and explicit judgments. For instance, **Ionita et al.** posit that recollection does not need attribution mechanisms because the details from past experiences that are reactivated in the relational representation core system are mnemonic in nature and diagnostic of past encounters and, therefore, do not require interpretation by an attribution system, in contrast to familiarity which may arise from non-mnemonic fluency cues (e.g., perceptual clarity). So, Ionita et al. suggest that attribution comes into play only when there are several possible signals, either mnemonic or non-mnemonic, that could be interpreted as evidence of prior exposure and, thus, when there is a possibility of misattribution (e.g., interpreting a non-mnemonic signal as due to memory). Actually, our meaning behind "attribution" was more in line with Whittlesea and Williams' (2000) view and refers to subconscious inferential processes that allow one to make sense of the quality of different data and processing (and not only as source attribution processes), and that can be applied to any kind of memory experiences (i.e., recollection and familiarity) and also to non-memory judgments (e.g., aesthetic judgments, preference judgments).

According to this definition, inferential "attribution" processes are necessary to explain the fact that some non-mnemonic processes, such as metacognitive expectations, may influence recollection-based memory decisions. For example, Simmons-Stern et al. (2012) have found that people held the (wrong) metacognitive belief that they would recollect more information after encoding some materials via a song than after a spoken encoding, leading them to adopt a more conservative response criterion regarding the amount of information they feel they should be able to recollect after studying sung materials. This results in a reduction of both correct and false recognitions on a subsequent memory test. Such a pattern is difficult to explain without the intervention of some metacognitive processes that, in the integrative memory model, are included in the attribution system. Another kind of evidence comes from studies that found a fluency effect on recollection responses. **Ionita et al.** point out that one hallmark of the attribution processes is the presence of fluency-based false alarms that signal the occurrence of misattribution. This pattern was noted by Kurilla and Westerman (2008) in experiments showing that perceptual and conceptual priming at test increased claims of recollection and familiarity (via remember/know responses), with a larger effect for lures than for targets.

However, we agree that some of the control/monitoring processes involved in familiarity and recollection decisions are probably more of a pre-retrieval than of a post-retrieval nature (**Kelley & Jacoby**; see also sect. R2.1). Restricting what comes to mind, depending on task context and people's goals, is probably an important step to avoid memory misattribution. The context or the task demand could influence metacognitive expectations and the retrieval mode adopted by the participants, favoring fluency (Whittlesea & Price 2001; Willems et al. 2008) or the search for some specific types of details (Bodner & Lindsay 2003; Bodner & Richardson-Champion 2007). The interaction between the pre- and post-access monitoring processes is thus expected to influence the quality of the evaluation, producing a feeling of coherence or discrepancy responsible for the emergence of familiarity and recollection.

The role of parietal regions in memory is clearly a larger subject that requires more in-depth discussion than the concise treatment we gave in the target article. Indeed, we mainly linked ventral parietal activity to bottom-up attention following the attention-to-memory model (Cabeza et al. 2012). According to this model, the presentation of a cue or an output captures the focus of attention in both memory and perception tasks. **Tibon** argues that ventral parietal activity should not only be attributed to attention processes, but also to the representational quality and the subjective evaluation of the memory trace, justifying its position at the intersection of the core and attribution systems. Previous fMRI studies found increased brain activity in the ventral parietal cortex during episodic memory retrieval, but whether this pattern of activity resulted from the engagement of attention or memory processes was unclear (Rugg & King 2018). Interestingly, Kuhl and Chun (2014) showed that the angular gyrus was not only sensitive to whether an item was correctly remembered but it also represented what the item was, which suggests that the parietal cortex may hold some item representations, in line with the idea that representational features are not only stored in the medial temporal lobe (MTL) (**Axmacher**; Tibon). Nevertheless, the role of parietal regions seems to go beyond mere representation. Many fMRI studies found activity in the ventral parietal cortex when participants assigned *remember* judgments (Wang et al. 2016), vividness ratings (Richter et al. 2016; Tibon et al. 2019) or confidence judgments (Qin et al. 2011). These findings are congruent with the view that the parietal cortex, and more precisely the angular gyrus, contributes to our subjective experience of remembering (Yazar et al. 2012). More direct support for this assumption comes from neuropsychological data showing reduced confidence ratings but spared "objective" source memory performance in patients with parietal lesions (Simons et al. 2010).

As noted by **Yang & Köhler**, it is most likely that different parietal regions support different functions. To give only one illustration, the angular gyrus was found to track the strength of recollection, whereas the temporoparietal junction was more active during incorrect source memory than true recollection (Hutchinson et al. 2014). Rather than adopting a modular view, examination of gradients within the parietal areas (notably, in terms of connectivity) may help to resolve the complex nature of the interplay between parietal areas and key regions from the representation core systems and attribution system (Huntenburg et al. 2018). Therefore, within the parietal cortex, some parts may be more involved in attention-to-memory mechanisms and others in the generation of subjective aspects of memory. **Tibon** proposes the interesting idea that some parietal areas may provide an index of the quality or quantity of signals reactivated in core systems that will be used by the attribution system to make some inference and that will lead to subjective experience of remembering (see also Rugg & King 2018). Additionally, Yang & Köhler evoke the role of parietal regions in evidence accumulation. In this view, the parietal cortex would accumulate signals about a situation until a decision is made (Wagner et al. 2005). In the case of a memory task, this would imply integrating signals from the MTL and the posterior cingulate hub on which prefrontal-related decision processes can apply. How exactly parietal and prefrontal areas interact during the retrieval process is an unresolved issue that is central to the understanding of the attribution system (**Strikwerda-Brown & Irish**).

In the search for an operationalization of the steps leading from representations to overt memory decisions, **Yang & Köhler** suggest that the diffusion model (Ratcliff et al. 2016b) may provide a promising framework (see also **Osth, Dunn, Heathcote, & Ratcliff** [**Osth et al.**]). According to the diffusion model, in a recognition memory task, decision about whether or not a stimulus has been previously encountered relies on the accumulation of evidence until a threshold is reached in favor of one of the choices (i.e., yes/no). Moreover, **Hakobyan & Cheng** draw a parallel between the attribution system and the retrieval process described in terms of attractor dynamics (Greve et al. 2010). However, this view is quite different from our own as Greve et al. (2010) propose that recollection and familiarity emerge from distinct retrieval processes applied to a single representation, whereas we argue that recollection and familiarity memory experiences usually rely on qualitatively different representations which undergo processing in a single (but complex) attribution system. Notwithstanding, we fully agree that more elaboration of this attribution system is needed and that existing models, such as the diffusion model, could help to describe operations – but this would need to incorporate the critical role of metacognition.

R2.3. False memories

A few commentators regret that we did not elaborate on how false memories are generated, in particular false recollections (**Bodner & Bernstein**; **Hakobyan & Cheng**; **Ionita et al.**). Notably, Bodner & Bernstein refer to several phenomena in which false recollections occur, such as the misinformation effect, the Deese-Roediger-McDermott (DRM) effect, or rich false memories in which people believe that they remember entire events that actually never happened.

In the integrative memory model, false recollections can be understood when considering that the subjective experiences of recollection and familiarity are generated through a unitary attribution system, so that a recollective experience could occur regardless of whether or not a test item was studied, provided that the test item acts as an effective retrieval cue for past events even if they do not concern the experimental context. This fits with the source misattribution account (McCabe & Geraci 2009), according to which false recollections are the result of a misattribution of the source of the information within the attribution system. In such cases, unstudied test items cue the actual (true) recollection of extra-list contextual information that are erroneously attributed to the study context. For example, a participant may experience a feeling of remembering when an object picture reactivates a past encounter with this object outside the experimental task, but if this exact source is not identified, this may induce him or her to endorse the object picture as recollected in a recognition memory task. The way such extra-list information would be cued within the core representational systems could be assimilated to the process of pattern completion (Yassa & Stark 2011).

Ionita et al. suggest that certain types of materials may be more prone to misattribution (see also **Strikwerda-Brown & Irish** for suggestion of material-related differences). They point out that studies supporting the idea of an attribution system for recollection often use less distinctive stimuli (i.e., words) that are more commonly encountered outside the laboratory than objects or scenes, and that are often presented in visually impoverished encoding conditions. In such cases, recollection decisions would rely heavily on the reactivation of contextual elements from the encoding episode, which are likely to be internal rather than external. We agree that retrieval mechanisms differ as a function of the nature of the materials. However, this is not incompatible with the source misattribution account, if both internal and external contextual elements represent the source of the occurrence of a given stimulus, considering that our definition of "attribution" is not restricted to non-mnemonic signals (see sect. R2.2). This implies that the difference between true and false recollections is not so much in the quality or veracity of the representations within the representation core systems, but, rather, false recollections would differentiate themselves from true memories by the erroneous attribution of a given representation within the core systems to the wrong past episode.

Also, **Hakobyan & Cheng** tackle the question of false recognition of lures with features that highly overlap with targets features, which we suggest are dependent upon the perirhinal and entorhinal cortices as pattern separators of individual entities. Precisely, Hakobyan & Cheng argue that some results from patients with selective hippocampal lesions challenge this idea, since these patients show increased false alarms toward similar lures with no increase toward unrelated lures. We can only agree that the hippocampus might contribute somewhat to entity pattern discrimination. However, we also note that, in these studies, most patients actually do manage to perform the task well above chance (Bayley et al. 2008; Holdstock et al. 2002), suggesting that they do have some ability to discriminate highly similar lures. Therefore, the hippocampus could contribute, while not being necessary, to entity pattern separation.

Bodner & Bernstein further suggest that the case of false memory could help in understanding how the neuroarchitecture underlying recollection and familiarity develops and shifts across the lifespan. Notably, they wonder how our integrative memory model might handle the fact that the "likelihood of different memory errors shifts in childhood and adulthood," with misinformation and rich false memories following a U-shaped development (Brainerd & Reyna 2005) and the DRM illusion following a linear trajectory. We postulate that the metacognitive component of the attribution system could help explain these patterns. Indeed, metacognitive abilities undertake dramatic changes throughout the course of childhood, changes that have been shown to impact children's memory performance and, particularly, false memories. For instance, Geurten et al. (2018) have found age-related differences in how 4-, 6-, and 8-year-old children relied on their metacognitive expectations about the quality of their memory to guide memory decisions in a recognition memory test. Indeed, younger children have more difficulties than older children in determining how much information they should be able to recollect and in setting a well-adjusted decision threshold. Moreover, in a study examining familiarity-based memory illusions (Geurten et al. 2017), 8-year-old children and adults relied more on fluency when it was greater than expected in a given context (i.e., for lures more than for targets). In contrast, 4- and 6-year-old children based their memory decision on the absolute level of fluency (i.e., the more fluent an item, the more likely to be called "studied"). These results are important because they suggest that changes in children's metacognitive expectations about what is a fluent item in a specific context could account for the developmental decrease observed in the frequency of false memories during childhood.

R3. How are subjective experiences of memory generated?

In many memory situations, the explicit judgments and the subjective experience that the individuals report match the nature of the representations that are reactivated in representation core systems (e.g., the reactivation of item-study context associations during item-recognition memory would lead to a feeling of recollecting the encoding episode). However, sometimes, the qualitative and subjective experience in a given memory task may dissociate from the memory reconstructed by a core system. One example is the disqualification of fluency cues (see sect. R2.1). In the target article, we argue that the inclusion of an attribution system is necessary to explain the modulation of the translation of reactivated content into outputs. This idea is supported by many commentators (**Curot & Barbeau**; **Hakobyan & Cheng**; **Kapogiannis & El Haj**; **Kihlstrom**), who evoke the diversity of the explicit outputs and the subjective experiences that we can have and how they are modified in pathology. **Axmacher** nevertheless questions the extent to which the attribution system defines the subjective quality of memories.

R3.1. Do attribution mechanisms shape subjective experiences of memory?

Axmacher argues that the representational formats of contents within the medial temporal lobe and the neocortex are sufficient to determine the subjective qualities of the explicit memory experience without the need for an attribution system. We strongly agree that the subjective quality of a memory is mainly shaped by its content or representational properties, and does not come from the attribution system itself. In many cases, inferential processes only validate the adequacy of retrieved content to expectations for a given decision. In this view, the subjective memory experience of recollection or vivid recall (e.g., a *remember* response or a vividness rating) is based on the reinstatement of the context and relational representations. For instance, using trial-by-trial analyses, we found that subjective vividness judgments are based on the properties of a remembered episode – the objective amount of retrieved details (Folville et al. 2019).

Nevertheless, it can happen that participants report a memory decision (e.g., old/new) or a particular subjective experience that does not match the reactivated representation. For example, a crime scene detail of medium retrieval difficulty elicits a remember judgment more often when mixed with difficult details than easy details (Bodner & Richardson-Champion 2007). Another example is the observation that amnesic patients reject fluent old stimuli, instead of using the fluency signal as a cue for oldness as healthy people do (Geurten & Willems 2017; Geurten et al. 2019; Ozubko & Yonelinas 2014). Another illustration is the finding that healthy older people claim that their memory for a given scene or episode is very vivid despite the small amount of details they can recall about it (Hashtroudi et al. 1990; Robin & Moscovitch 2017). These examples and others suggest that the explicit memory report given by a participant is also modulated by metamemory, monitoring, and pre-access control mechanisms (sect. R2.2; see also **Kelley & Jacoby**). For instance, Folville et al. (2019) have shown that the amount of recalled details about a scene predicted the associated vividness ratings for memory of the scene in young and older adults, but this relationship was significantly smaller in older participants. An interpretation for this observation is that both young and older adults used the properties or the details of memories to shape their vividness feeling, but older adults monitored/weighted these details differently when calibrating their subjective ratings (Johnson et al. 2015; Mitchell & Hill 2019).

Axmacher raises a very good point by asking, "if feelings of familiarity or recollection do not match with the typical representational format of the corresponding memories, are these feelings really the same as in more common cases?" At face value, the endorsement of categorical responses (remember/know; old/new; high versus low vividness) does not allow us to distinguish atypical from typical experiences. fMRI cortical reinstatement analyses would likely show that the representations behind the judgments are not the same; yet this does not tell us anything about the detailed phenomenology of the feelings. This may be a topic for future studies.

R3.2. The diversity of subjective memory experiences

Kihlstrom underlines that other types of memory experiences than the classical remembering and feeling of familiarity could be considered as well, such as "recognition-by-knowing," "recognition-by-feeling," and "remembering-as-believing." With the remember/know paradigm, *know* responses are assigned to memory experiences devoid of the retrieval of contextual encoding details. Therefore, a know response could be assigned to a face, for instance, either in a situation in which one individual recognizes that face with a high degree of confidence but is not able to consciously remember where and when this person was met (recognition-by-knowing), or in a situation in which one individual feels that this face is intriguingly familiar but with a poorer degree of confidence about this feeling (recognition-by-feeling). So, know responses may include memory experiences that vary not only in their content but also in their cognitive and neural bases (Kihlstrom). To assess these, subjective self-paced reports of Remembering and Knowing should be complemented with verbal justifications (Bodner & Lindsay 2003), electrophysiological measures such as event-related potentials (ERPs) (Woodruff et al. 2006), or cardiovascular measures (Fiacconi et al. 2016). In the current context, verbal justifications would allow experimenters to verify whether participants' know responses indeed corresponded to knowing, feeling, or believing recognition experiences. Besides, accompanying the subjective self-reports with more "objective" memory measures is of particular interest for the study of populations that have a decreased ability to precisely assess their subjective memory experience (reflected in know responses, vividness or confidence ratings), such as older adults or patients with Alzheimer's disease (Duarte et al. 2008; El Haj & Antoine 2017; Folville et al. 2019; Wong et al. 2012).

Beyond feelings of familiarity and recollection, the outputs of processing within the systems described in the integrative memory model may take other forms, such as thinking about future events, preference judgments, and so forth. **Sreekumar et al.** give the example of judgments about the temporal context in which an event took place. For instance, when people are asked to judge whether a stimulus was seen in the first or second part of an experiment, they can use two kinds of strategies (Friedman 1993). On the one hand, location-based processes involve the reconstruction of the time of occurrence, based on the contextual information encoded with the event (likely to be recovered from the relational representation core system). On the other hand, distance-based processes involve evaluation of the time elapsed since the event occurred, based on the global strength of the memory. This could be indexed by the output of attribution system evaluating the speed and/or the amount of details during memory retrieval.

R3.3. Subjective experiences of memory in the pathology

Kapogiannis & El Haj argue that declines in the components of the subjective experience of remembering, such as reliving, mental time travel, or vividness, could account for the recollection deficit observed in Alzheimer's disease (AD). We agree that mental imagery processes may certainly influence how the memory representation is shaped when it is consciously brought back to mind. However, we assume that the deterioration of mechanisms taking place earlier may account to a greater extent for the impaired recollective abilities observed in AD. In our view, impaired recollection abilities is first related to the deterioration of item-context bindings in the relational representation core system (Braak's Stage 3) and impaired pattern completion in the hippocampus (Ally et al. 2013; Xue 2018). As the disease progresses, pathology extends to posterior regions such as the retrosplenial and posterior cingulate cortices, affecting the reinstatement of complex representations and autonoetic consciousness of remembered episodes (Genon et al. 2013), and decreasing the ability to have the subjective feeling of mentally reliving the past (El Haj et al. 2016).

At the same time, AD patients have difficulties switching between egocentric and allocentric representations during retrieval (**Riva et al.**; Serino et al. 2015; see also sect. R1.2). Of interest is the finding that taking a first-person perspective and recalling episodic details when remembering are both related to the volume of the precuneus (Ahmed et al. 2018). Moreover, changes in visual perspective during memory retrieval are associated with changes in precuneus activity (St. Jacques et al. 2017). An atrophy of the precuneus is observed in AD (Ryu et al. 2010) and it may arise along with the more global atrophy found in posterior brain regions during Braak's Stages 4 to 6. Together, these findings highlight that AD is associated with a decline in recollection abilities that may result first from an impairment in the relational representation core system supporting pattern completion, along with progressive dysfunctions of posterior regions supporting autonoetic consciousness, mental imagery, and visual perspective.

R4. Concluding remarks

A last question needs to be considered: Is the integrative memory model a dual-process model of recognition memory? As reminded by **Osth et al.**, whether memory retrieval is best explained by the involvement of two processes (i.e., recollection and familiarity), or by a single process, has been a matter of debate for the past 20 years at least. Rather than taking side in this debate, we would like to emphasize that the critical notion in our framework is interaction. The subjective feelings and the explicit judgments provided in a memory task are qualitatively different because they rely on the reactivation of qualitatively different representations (core systems). In fact, there are not only two possible outputs (recollection versus familiarity), but a variety of feelings and judgments that can arise (see sect. R3.2). The distinction between outputs and representations is critical, and the nature of the output in a given situation will depend on the interaction between reactivated representations and inferential operations that rely on metacognitive, monitoring, control, and attention mechanisms. We believe that future research on memory should unravel the dynamics of this interactive system.

References

[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

Addis D. R. & Schacter D. L. (2012) The hippocampus and imagining the future: Where do we stand? *Frontiers in Human Neuroscience* **5**: article no. 173. Available at: https://doi.org/10.3389/fnhum.2011.00173. [JC]

Aggleton J. P. (2010) Understanding retrosplenial amnesia: Insights from animal studies. *Neuropsychologia* **48**(8):2328–38. doi: 10.1016/j.neuropsychologia.2009.09.030. [arCB]

Aggleton J. P. (2012) Multiple anatomical systems embedded within the primate medial temporal lobe: Implications for hippocampal function. *Neuroscience and Biobehavioral Reviews* **36**(7):1579–96. doi: 10.1016/j.neubiorev.2011.09.005. [arCB]

Aggleton J. P. & Brown M. W. (1999) Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences* **22**:425–89. [arCB, JPA]

Aggleton J. P. & Brown M. W. (2006) Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences* **10**(10):455–63. [JPA]

Aggleton J. P., Dumont J. R. & Warburton E. C. (2011) Unraveling the contributions of the diencephalon to recognition memory: A review. *Learning and Memory* **18**(6):384–400. doi: 10.1101/lm.1884611. [arCB]

Aggleton J. P., O'Mara S. M., Vann S. D., Wright N. F., Tsanov M. & Erichsen J. T. (2010) Hippocampal–anterior thalamic pathways for memory: Uncovering a network of direct and indirect actions. *European Journal of Neuroscience* **31**(12):2292–307. [JPA]

Aggleton J. P., Pralus A., Nelson A. J. & Hornberger M. (2016) Thalamic pathology and memory loss in early Alzheimer's disease: Moving the focus from the medial temporal lobe to Papez circuit. *Brain* **139**(7):1877–90. [JPA]

Ahmed S., Irish M., Loane C., Baker I., Husain M., Thompson S., Blanco-Duque C., Mackay C., Zamboni G., Foxe D., Hodges J. R., Piguet O. & Butler C. (2018) Association between precuneus volume and autobiographical memory impairment in posterior cortical atrophy: Beyond the visual syndrome. *NeuroImage: Clinical* **18**:822–34. doi: 10.1016/j.nicl.2018.03.008. [rCB]

Albert M. S., DeKosky S. T., Dickson D., Dubois B., Feldman H. H., Fox, Gamst A., Holtzman D. M., Jagust W. J., Petersen R. C., Snyder P. J., Carrillo M. C., Thies B. & Phelps C. H. (2011) The diagnosis of mild cognitive impairment due to Alzheimer's disease: Recommendations from the National Institute on Aging-Alzheimer's Association workgroups on diagnostic guidelines for Alzheimer's disease. *Alzheimer's and Dementia* **7**(3):270–79. doi: 10.1016/j.jalz.2011.03.008. [aCB]

Ally B. A., Hussey E. P., Ko P. C. & Molitor R. J. (2013) Pattern separation and pattern completion in Alzheimer's disease: Evidence of rapid forgetting in amnestic mild cognitive impairment. *Hippocampus* **23**(12):1246–58. doi: 10.1002/hipo.22162. [rCB]

Alter A. L., Oppenheimer D. M., Epley N. & Eyre R. N. (2007) Overcoming intuition: Metacognitive difficulty activates analytic reasoning. *Journal of Experimental Psychology: General* **136**(4):569–76. [TS]

Aly M., Yonelinas A. P., Kishiyama M. M. & Knight R. T. (2011) Damage to the lateral prefrontal cortex impairs familiarity but not recollection. *Behavioral Brain Research* **225**(1):297–304. doi: 10.1016/j.bbr.2011.07.043. [aCB]

Anderson J. R. & Bower G. H. (1972) Recognition and retrieval processes in free recall. *Psychological Review* **79**(2):97–123. [JFK]

Anderson N. D., Davidson P. S., Mason W. P., Gao F., Binns M. A. & Winocur G. (2011) Right frontal lobe mediation of recollection- and familiarity-based verbal recognition memory: Evidence from patients with tumor resections. Journal of Cognitive Neuroscience **23**(12):3804–16. doi: 10.1162/jocn_a_00050. [aCB]

Andrews-Hanna J. R., Reidler J. S., Sepulcre J., Poulin R. & Buckner R. L. (2010) Functional-anatomic fractionation of the brain's default network. *Neuron* **65**:550–62. [aCB]

Aschenbrenner A. J., Balota D. A., Gordon B. A., Ratcliff R. & Morris J. C. (2016) A diffusion model analysis of episodic recognition in preclinical individuals with a family history for Alzheimer's Disease: The adult children study. *Neuropsychology* **30**:225–38. [AFO]

Atta K., Forlenza N., Gujski M., Hashmi S. & Isaac G. (2006) Delusional misidentification syndromes: Separate disorders or unusual presentations of existing DSM-IV categories? *Psychiatry* **3**(9):56–61. [JP]

Auger S. D., Mullally S. L. & Maguire E. A. (2012) Retrosplenial cortex codes for permanent landmarks. *PLOS ONE* **7**(8):e43620. doi: 10.1371/journal.pone.0043620. [rCB]

Azizi A. H., Schieferstein N. & Cheng S. (2014) The transformation from grid cells to place cells is robust to noise in the grid pattern. *Hippocampus* **24**(8):912–19. Available at: https://doi.org/10.1002/hipo.22306. [OH]

Bahk Y. C. & Choi K. H. (2018) The relationship between autobiographical memory, cognition, and emotion in older adults: A review. Neuropsychology, Development, and Cognition. Section B: Aging, Neuropsychology and Cognition **25**:874–92. [AS]

Balestrini S., Francione S., Mai R., Castana L., Casaceli G., Marino D., Provinciali L., Cardinale F. & Tassi L. (2015) Multimodal responses induced by cortical stimulation of the parietal lobe: A stereo-electroencephalography study. *Brain* **138**(9):2596–607. Available at: https://doi.org/10.1093/brain/awv187. [JC]

Balota D. A. & Duchek J. M. (2015) Attention, variability, and biomarkers in Alzheimer's Disease. In: *Remembering: Attributions, processes, and control in human memory: Essays in honor of Larry L. Jacoby*, ed. S. Lindsay, H. L. Roediger, III C. M. Kelley & A. Yonelinas, pp. 285–303. Psychology Press. [CMK]

Bamber D. (1979) State-trace analysis: A method of testing simple theories of causation. *Journal of Mathematical Psychology* **19**:137–81. [AFO]

Bar M., Aminoff E. & Schacter D. L. (2008) Scenes unseen: The parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *Journal of Neuroscience* **28**(34):8539–44. doi: 10.1523/JNEUROSCI.0987-08.2008. [aCB]

Barbas H. (2000) Connections underlying the synthesis of cognition, memory, and emotion in primate prefrontal cortices. *Brain Research Bulletin* **52**:319–30. [AS]

Barbeau E., Wendling F., Regis J., Duncan R., Poncet M., Chauvel P. & Bartolomei F. (2005) Recollection of vivid memories after perirhinal region stimulations: Synchronization in the theta range of spatially distributed brain areas. *Neuropsychologia* **43**(9):1329–37. doi: 10.1016/j.neuropsychologia.2004.11.025. [aCB]

Barbeau E. J., Pariente J., Felician O. & Puel M. (2011) Visual recognition memory: A double anatomo-functional dissociation. *Hippocampus* **21**(9):929–34. doi: 10.1002/hipo.20848. [arCB]

Barbeau E. J., Taylor M. J., Regis J., Marquis P., Chauvel P. & Liégeois-Chauvel C. (2008) Spatio temporal dynamics of face recognition. *Cerebral Cortex* **18**(5):997–1009. Available at: https://doi.org/10.1093/cercor/bhm140. [JC]

Barense M. D., Rogers T. T., Bussey T. J., Saksida L. M. & Graham K. S. (2010) Influence of conceptual knowledge on visual object discrimination: Insights from semantic dementia and MTL amnesia. Cerebral Cortex **20**(11):2568–82. doi: 10.1093/cercor/bhq004. [CS-B, rCB]

Barense M. D., Warren J. D., Bussey T. J. & Saksida L. M. (2016) The temporal lobes. In: *Oxford textbook of cognitive neurology and dementia*, ed. M. Husain & J. Schott, pp. 39–49. Oxford University Press. [aCB]

Barron H. C., Garvert M. M. & Behrens T. E. J. (2016) Repetition suppression: A means to index neural representations using BOLD? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **371**(1705). Available at: https://doi.org/10.1098/rstb.2015.0355. [HY]

Barry D. N. & Maguire E. A. (2019) Remote memory and the hippocampus: A constructive critique. *Trends in Cognitive Sciences* **23**(2):128–42. [NA]

Bartlett F. C. (1932) *Remembering: A study in experimental and social psychology*. Cambridge University Press. [JFK]

Bartolomei F., Barbeau E., Gavaret M., Guye M., McGonigal A., Regis J. & Chauvel P. (2004) Cortical stimulation study of the role of rhinal cortex in deja vu and reminiscence of memories. *Neurology* **63**(5):858–64. [aCB]

Bastin C., Bahri M. A., Miévis F., Lemaire C., Collette F., Genon S., Simon J., Guillaume B., Diana R. A., Yonelinas A. P. & Salmon E. (2014) Associative memory and its cerebral correlates in Alzheimer's disease: Evidence for distinct deficits of relational and conjunctive memory. *Neuropsychologia* **63**:99–106. Available at: http://dx.doi.org/10.1016/j.neuropsychologia.2014.08.023. [aCB]

Bayley P. J., Wixted J. T., Hopkins R. O. & Squire L. R. (2008) Yes/no recognition, forced-choice recognition, and the human hippocampus. *Journal of Cognitive Neuroscience* **20**(3):505–12. doi: 10.1162/jocn.2008.20038. Available at: https://doi.org/10.1162/jocn.2008.20038. [rCB, OH]

Beer Z., Vavra P., Atucha E., Rentzing K., Heinze H.-J. & Sauvage M. M. (2018) The memory for time and space differentially engages the proximal and distal parts of the hippocampal subfields CA1 and CA3. *PLOS Biology* **16**(8):e2006100. Available at: https://doi.org/10.1371/journal.pbio.2006100. [OH]

Bernstein D. M. & Loftus E. F. (2009) How to tell if a particular memory is true or false. *Perspectives on Psychological Science* **4**:370–74. [GEB]

Berron D., Schutze H., Maass A., Cardenas-Blanco A., Kuijf H. J., Kumaran D. & Duzel E. (2016) Strong evidence for pattern separation in human dentate gyrus. *Journal of Neuroscience* **36**(29):7569–79. doi: 10.1523/JNEUROSCI.0518-16.2016. [aCB]

Bertrand E., Landeira-Fernandez J. & Mograbi D. C. (2016) Metacognition and perspective-taking in Alzheimer's disease: A mini-review. *Frontiers in Psychology* **7**: article no.1812. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5112262/. [GR]

Besson G., Ceccaldi M., Didic M. & Barbeau E. J. (2012) The speed of visual recognition memory. *Visual Cognition* **20**(10):1131–52. Available at: https://doi.org/10.1080/13506285.2012.724034. [JC]

Besson G., Ceccaldi M., Tramoni E., Felician O., Didic M. & Barbeau E. J. (2015) Fast, but not slow, familiarity is preserved in patients with amnestic mild cognitive impairment. *Cortex* **65**:36–49. doi: 10.1016/j.cortex.2014.10.020. [aCB]

Besson G., Simon J., Salmon E. & Bastin C. (2017) Testing a new memory task sensitive to early entorhinal/perirhinal atrophy in Alzheimer's disease. *Alzheimer's & Dementia* **13** (7):P477. doi: 10.1016/j.jalz.2017.06.505. [aCB]

Bicanski A. & Burgess N. (2018) A neural-level model of spatial memory and imagery. *eLife* **7**: e33752. (Online publication). doi:10.7554/eLife.33752. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6122954/. [GR]

Bird C. M., Bisby J. A. & Burgess N. (2012) The hippocampus and spatial constraints on mental imagery. *Frontiers in Human Neuroscience* **6**: article no. 142. doi:10.3389/fnhum.2012.00142. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3354615/. [GR]

Bird C. M., Keidel J. L., Ing L. P., Horner A. J. & Burgess N. (2015) Consolidation of complex events via reinstatement in posterior cingulate cortex. *Journal of Neuroscience* **35** (43):14426–34. doi:10.1523/JNEUROSCI.1774-15.2015. [aCB]

Bocchio M., Nabavi S. & Capogna M. (2017) Synaptic plasticity, engrams, and network oscillations in amygdala circuits for storage and retrieval of emotional memories. *Neuron* **94**:731–43. [AS]

Boccia M., Silveri M. C., Sabatini U., Guariglia C. & Nemmi F. (2016) Neural underpinnings of the decline of topographical memory in mild cognitive impairment. *American Journal of Alzheimer's Disease and Other Dementias* **31**(8):618–30. doi: 10.1177/1533317516654757. [rCB]

Bodner G. E. & Lindsay D. S. (2003) Remembering and knowing in context. *Journal of Memory and Language* **48**:563–80. [arCB]

Bodner G. E. & Richardson-Champion D. D. L. (2007) Remembering is in the details: Effects of test-list context on memory for an event. *Memory* **15**(7):718–29. [arCB]

Bogacz R. & Brown M. W. (2003) An anti-Hebbian model of familiarity discrimination in the perirhinal cortex. *Neurocomputing* **52–54**:1–6. Available at: https://doi.org/10.1016/S0925-2312(02)00738-5. [aCB]

Bogacz R., Brown M. W. & Giraud-Carrier C. (2001) Model of familiarity discrimination in the perirhinal cortex. *Journal of Computational Neuroscience* **10**(1):5–23. [arCB]

Borghesani V., Narvid J., Battistella G., Shwe W., Watson C., Binney R. J., Sturm V., Miller Z., Mandelli M. L., Miller B. & Gorno-Tempini M. L. (2019) "Looks familiar, but I do not know who she is": The role of the anterior right temporal lobe in famous face recognition. *Cortex* **115**:72–85. Available at: https://doi.org/10.1016/j.cortex.2019.01.006. [GG]

Bowles B., Crupi C., Mirsattari S. M., Pigott S. E., Parrent A. G., Pruessner J. C., Yonelinas A. P. & Köhler S. (2007) Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proceedings of the National Academy of Sciences USA* **104**(41):16382–87. [aCB]

Bowles B., Crupi C., Pigott S., Parrent A., Wiebe S., Janzen L. & Kohler S. (2010) Double dissociation of selective recollection and familiarity impairments following two different surgical treatments for temporal-lobe epilepsy. *Neuropsychologia* **48**(9):2640–47. doi: 10.1016/j.neuropsychologia.2010.05.010. [aCB]

Braak H. & Braak E. (1991) Neuropathological stageing of Alzheimer-related changes. *Acta Neuropathologica* **82**:239–59. [aCB]

Braak H. & Braak E. (1995) Staging of Alzheimer's disease-related neurofibrillary changes. *Neurobiology of Aging* **16**(3):271–84. [aCB]

Braak H. & Del Tredici K. (2015) The preclinical phase of the pathological process underlying sporadic Alzheimer's disease. *Brain* **138**(Pt 10):2814–33. doi: 10.1093/brain/awv236. [aCB]

Brady T. F., Konkle T. & Alvarez G. A. (2011) A review of visual memory capacity: Beyond individual items and towards structured representations. *Journal of Vision*, **11**(5):4, 1–34. [TFB]

Brady T. F., Konkle T., Alvarez G. A. & Oliva A. (2013) Real-world objects are not represented as bound units: Independent forgetting of different object details from visual memory. *Journal of Experimental Psychology: General* **142**(3):791–808. doi: 10.1037/a0029649. [rCB, TFB]

Brainerd C. J. & Reyna V. F. (2005) *The science of false memory*. Oxford University Press. [GEB, rCB]

Brainerd C. J., Reyna V. F. & Ceci S. J. (2008) Developmental reversals in false memory: A review of data and theory. *Psychological Bulletin* **134**, 343–82. [GEB]

Brambati S. M., Rankin K. P., Narvid J., Seeley W. W., Dean D., Rosen H. J., Miller B. L., Ashburner J. & Gorno-Tempini M. L. (2009) Atrophy progression in semantic dementia with asymmetric temporal involvement: A tensor-based morphometry study. *Neurobiology of Aging* **30**(1):103–11. doi: 10.1016/j.neurobiolaging.2007.05.014. [CS-B]

Brand M., Eggers C., Reinhold N., Fujiwara E., Kessler J., Heiss W.-D. & Markowitsch H. J. (2009) Functional brain imaging in fourteen patients with dissociative amnesia reveals right inferolateral prefrontal hypometabolism. *Psychiatry Research* **174**:32–39. [Neuroimaging section] [AS]

Brandt K. R., Eysenck M. W., Nielsen M. K. & von Oertzen T. J. (2016) Selective lesion to the entorhinal cortex leads to an impairment in familiarity but not recollection. *Brain and Cognition* **104**:82–92. doi: 10.1016/j.bandc.2016.02.005. [aCB]

Breen N., Caine D. & Coltheart M. (2000) Models of face recognition and delusional misidentification: A critical review. *Cognitive Neuropsychology* **17**(1):55–71. doi: 10.1080/026432900380481. [rCB]

Brettschneider J., Del Tredici K., Lee V. M. & Trojanowski J. Q. (2015) Spreading of pathology in neurodegenerative diseases: A focus on human studies. *Nature Reviews: Neuroscience* **16**(2):109–20. doi: 10.1038/nrn3887. [aCB]

Brewin C. R., Dalgleish T. & Joseph S. (1996) A dual representation theory of posttraumatic stress disorder. *Psychological Review*, **103**(4):670–86. [NA]

Brezis N., Bronfman Z. Z., Yovel G. & Goshen-Gottstein Y. (2017) The electrophysiological signature of remember-know is confounded with memory strength and cannot be interpreted as evidence for dual-process theory of recognition. *Journal of Cognitive Neuroscience* **29**:322–36. [AFO]

Brown A. A. & Bodner G. E. (2011) Re-examining dissociations between remembering and knowing: Binary judgments vs. independent ratings. *Journal of Memory and Language* **65**(2):98–108. Available at: http://dx.doi.org/10.1016/j.jml.2011.04.003. [aCB]

Brown M. W. & Aggleton J. P. (2001) Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nature Reviews. Neuroscience* **2**(1):51–61. Available at: https://doi.org/10.1038/35049064. [HY, OH]

Bruffaerts R., Dupont P., Peeters R., De Deyne S., Storms G. & Vandenberghe R. (2013) Similarity of fMRI activity patterns in left perirhinal cortex reflects semantic similarity between words. *Journal of Neuroscience* **33**(47):18597–607. doi: 10.1523/JNEUROSCI.1548-13.2013. [aCB]

Buchner A. & Brandt M. (2003) Further evidence for systematic reliability differences between explicit and implicit memory tests. *Quarterly Journal of Experimental Psychology A* **56**(2):193–209. doi: 10.1080/02724980244000260. [rCB]

Buckner R. L., Andrews-Hanna J. R. & Schacter D. L. (2008) The brain's default network. *Annals of the New York Academy of Sciences* **1124**:1–38. [aCB]

Burgess N., Becker S., King J. A. & O'Keefe J. O. (2001) Memory for events and their spatial context: Models and experiments. *Philosophical Transactions of the Royal Society of London*, **356**, 1493–503. [GR]

Burgess P. W. & Shallice T. (1996) Confabulation and the control of recollection. *Memory* **4**(4):359–411. [CMK]

Bussey T. J. & Saksida L. M. (2007) Memory, perception, and the ventral visual-perirhinal-hippocampal stream: Thinking outside of the boxes. *Hippocampus* **17**(9):898–908. Available at: https://doi.org/10.1002/hipo.20320. [HY]

Byrne P., Becker S. & Burgess N. (2007) Remembering the past and imagining the future: A neural model of spatial memory and imagery. *Psychological Review* **114**(2):340–75. [GR, NA]

Bzdok D., Heeger A., Langner R., Laird A. R., Fox P. T., Palomero-Gallagher N., Vogt B. A., Zilles K. & Eickhoff S. B. (2015) Subspecialization in the human posterior medial cortex. *NeuroImage* **106**:55–71. doi: 10.1016/j.neuroimage.2014.11.009. [aCB]

Cabeza R., Ciaramelli E. & Moscovitch M. (2012) Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences* **16** (6):338–52. doi: 10.1016/j.tics.2012.04.008. [arCB]

Cabeza R., Ciaramelli E., Olson I. R. & Moscovitch M. (2008) The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience* **9**(8):613–25. Available at: http://doi.org/10.1038/nrn2459. [aCB, RT]

Cahill L., Babinsky R., Markowitsch H. J. & McGaugh J. L. (1995) Involvement of the amygdaloid complex in emotional memory. *Nature* **377**:295–96. [AS]

Canli T., Zhao Z., Brewer J., Gabrieli J. D. E. & Cahill L. (2000) Event-related activation in the human amygdala associates with later memory for individual emotional experience. *Journal of Neuroscience* **20**:RC99. Available at: https://doi.org/10.1523/JNEUROSCI.20-19-j0004.200. [AS]

Capgras J. & Reboul-Lachaux J. (1923/1994) L'Illusion des "sosies" dans un délire systématisé chronique [Illusion of negative doubles in chronic systematized delusion].

History of Psychiatry **5**(17):119–33. doi: 10.1177/0957154x9400501709. (Original work published in 1923). [JP]

Carlesimo G. A., Lombardi M. G. & Caltagirone C. (2011) Vascular thalamic amnesia: A reappraisal. *Neuropsychologia* **49**(5):777–89. [JPA]

Chalfonte B. L. & Johnson M. K. (1996) Feature memory and binding in young and older adults. *Memory & Cognition* **24**(4):403–16. [rCB]

Chapleau M., Aldebert J., Montembeault M. & Brambati S. M. (2016) Atrophy in Alzheimer's disease and semantic dementia: An ALE meta-analysis of voxel-based morphometry studies. *Journal of Alzheimer's disease* **54**(3):941–55. [CS-B]

Chen J., Leong Y. C., Honey C. J., Yong C. H., Norman K. A. & Hasson U. (2017) Shared memories reveal shared structure in neural activity across individuals. *Nature Neuroscience* **20**(1):115–25. doi: 10.1038/nn.4450. [aCB]

Cheng S. (2013) The CRISP theory of hippocampal function in episodic memory. *Frontiers in Neural Circuits* **7**: article no. 88. Available at: https://doi.org/10.3389/fncir.2013.00088. [OH]

Cheng S. & Werning M. (2016) What is episodic memory if it is a natural kind? *Synthese* **193**(5):1345–85. Available at: https://doi.org/10.1007/s11229-014-0628-6. [OH]

Cheng S., Werning M. & Suddendorf T. (2016) Dissociating memory traces and scenario construction in mental time travel. *Neuroscience & Biobehavioral Reviews* **60**:82–89. Available at: https://doi.org/10.1016/j.neubiorev.2015.11.011. [NA, OH]

Chetelat G., Desgranges B., de la Sayette V., Viader F., Berkouk K., Landeau B., Lalevée C., Le Doze F., Dupuy B., Hannequin D., Baron J. C. & Eustache F. (2003) Dissociating atrophy and hypometabolism impact on episodic memory in mild cognitive impairment. *Brain* **126**(Pt 9):1955–67. doi: 10.1093/brain/awg196. [aCB]

Chiou R. & Lambon Ralph M. A. (2016) The anterior temporal cortex is a primary semantic source of top-down influences on object recognition. *Cortex* **79**:75–86. Available at: https://doi.org/10.1016/j.cortex.2016.03.007. [CS-B]

Chua E., Pergolizzi D. & Weintraub R. R. (2014) The cognitive neuroscience of metamemory monitoring: Understanding metamemory processes, subjective levels expressed, and metacognitive accuracy. In: *The cognitive neuroscience of metacognition*, ed. S. M. Fleming & C. D. Frith, pp. 267–91. Springer. [aCB]

Ciaramelli E., Faggi G., Scarpazza C., Mattioli F., Spaniol J., Ghetti S. & Moscovitch M. (2017) Subjective recollection independent from multifeatural context retrieval following damage to the posterior parietal cortex. *Cortex* **91**, 114–25. Available at: https://doi.org/10.1016/j.cortex.2017.03.015. [RT]

Ciaramelli E., Grady C. L. & Moscovitch M. (2008) Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* **46**:1828–51. [aCB]

Clark I. A. & Maguire E. A. (2016) Remembering preservation in hippocampal amnesia. *Annual Review of Psychology* **67**:51–82. doi: 10.1146/annurev-psych-122414-033739. [aCB]

Clarke A. & Tyler L. K. (2015) Understanding what we see: How we derive meaning from vision. *Trends in Cognitive Sciences* **19**(11):677–87. doi: 10.1016/j.tics.2015.08.008. [aCB]

Colombo D., Serino S., Tuena C., Pedroli E., Dakanalis A., Cipresso P. & Riva G. (2017) Egocentric and allocentric spatial reference frames in aging: A systematic review. *Neuroscience and Biobehavioral Reviews* **80**, 605–21. doi:10.1016/j.neubiorev.2017.07.012. [GR]

Coltheart M. (2006) What has functional neuroimaging told us about the mind (so far)? *Cortex* **42**:323–31. [JFK]

Coltheart M., Langdon R. & McKay R. (2007) Schizophrenia and Monothematic Delusions. *Schizophrenia Bulletin* **33**(3):642–47. doi: 10.1093/schbul/sbm017. [JP]

Conroy M. A., Hopkins R. O. & Squire L. R. (2005) On the contribution of perceptual fluency and priming to recognition memory. *Cognitive and Affective Behavioral Neuroscience* **5**(1):14–20. [arCB]

Conway M. A. (2005) Memory and the self. *Journal of Memory and Language* **53**:594-628. [rCB]

Conway M. A. & Pleydell-Pearce C. W. (2000) The construction of autobiographical memories in the self-memory system. *Psychological Review* **107**:261–88. [NA]

Courbon P. & Fail G. (1927/1994) Syndrome d'illusion de Frégoli et schizophrénie [Fregoli illusion syndrome and schizophrenia]. *History of Psychiatry* **5**(17):134–38. (Original work published in 1923). doi: 10.1177/0957154x9400501710. [JP]

Cowell R. A., Bussey T. J. & Saksida L. M. (2006) Why does brain damage impair memory? A connectionist model of object recognition memory in perirhinal cortex. *Journal of Neuroscience* **26**(47):12186–97. doi: 10.1523/jneurosci.2818-06.2006. [aCB]

Cowell R. A., Bussey T. J. & Saksida L. M. (2010) Components of recognition memory: Dissociable cognitive processes or just differences in representational complexity? *Hippocampus* **20**(11):1245–62. doi: 10.1002/hipo.20865. [aCB]

Cramon D. Y von, Markowitsch H. J. & Schuri U. (1993) The possible contribution of the septal region to memory. *Neuropsychologia* **31**:1159–80. [AS]

Curot J., Busigny T., Valton L., Denuelle M., Vignal J. P., Maillard L., Chauvel P., Pariente J., Trebuchon A., Bartolomei F. & Barbeau E. J. (2017) Memory scrutinized through electrical brain stimulation: A review of 80 years of experiential phenomena. *Neuroscience and Biobehavioral Reviews* **78**:161–77. Available at: https://doi.org/10.1016/j.neubiorev.2017.04.018. [JC]

Curran T. & Friedman W. J. (2003) Differentiating location- and distance-based processes in memory for time: An ERP study. *Psychonomic Bulletin and Review* **10**(3):711–17. [VS]

Danet L., Pariente J., Eustache P., Raposo N., Sibon I., Albucher J.-F., Bonneville F., Péran P. & Barbeau E. J. (2017) medial thalamic stroke and its impact on familiarity and recollection. *eLife* **6**:e28141. doi: 10.7554/eLife.28141. [aCB]

D'Argembeau A. (2013) On the role of the ventromedial prefrontal cortex in self-processing: The valuation hypothesis. *Frontiers in Human Neuroscience* **7**: article no. 372. (Online publication). doi: 10.3389/fnhum.2013.00372. [aCB]

D'Argembeau A., Collette F., Van der Linden M., Laureys S., Del Fiore G., Degueldre C., Luxen A. & Salmon E. (2005) Self-referential reflective activity and its relationship with rest: A PET study. *NeuroImage* **25**:616–24. [aCB]

Daselaar S. M., Fleck M. S., Prince S. E. & Cabeza R. (2006) The medial temporal lobe distinguishes old from new independently of consciousness. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* **26**(21):5835–39. Available at: https://doi.org/10.1523/JNEUROSCI.0258-06.2006. [W-CW]

Davachi L. (2006) Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology* **16**(6):693–700. doi: 10.1016/j.conb.2006.10.012. [aCB]

Davachi L., Mitchell J. P. & Wagner A. D. (2003) Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences USA* **100**(4):2157–62. [aCB]

David O., Job A. S., De Palma L., Hoffmann D., Minotti L. & Kahane P. (2013) Probabilistic functional tractography of the human cortex. *NeuroImage* **80**:307–17. Available at: https://doi.org/10.1016/j.neuroimage.2013.05.075. [JC]

Deese J. (1959) On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology* **58**:17–22. [GEB]

Dehaene S. & Naccache L. (2001) Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition* **79**:1–37. [aCB]

Delhaye E., Bahri M. A., Salmon E. & Bastin C. (2019) Impaired perceptual integration and memory for unitized representations are associated with perirhinal cortex atrophy in Alzheimer's disease. *Neurobiology of Aging* **73**:135–44. doi: 10.1016/j.neurobiolaging.2018.09.021. [aCB]

Dennis S. J., Yim H., Sreekumar V., Evans N. J., Garrett P. & Sederberg P. (2017) A hierarchical Bayesian model of "memory for when" based on experience sampling data. In: *Proceedings of the 39th Annual Conference of the Cognitive Science Society*, ed. G. Bunzelmann, A. Howes, T. Tenbrink & E. Davelaar, pp. 295–300. Cognitive Science Society. [VS]

Dew I. T. Z. & Cabeza R. (2013) A broader view of perirhinal function: From recognition memory to fluency-based decisions. *Journal of Neuroscience* **33**(36):14466–74. doi: 10.1523/JNEUROSCI.1413-13.2013. [aCB, HY]

Diana R. A., Yonelinas A. P. & Ranganath C. (2007) Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences* **11**(9):379–86. doi: 10.1016/j.tics.2007.08.001. [aCB]

Diana R. A., Yonelinas A. P. & Ranganath C. (2010) medial temporal lobe activity during source retrieval reflects information type, not memory strength. *Journal of Cognitive Neuroscience* **22**(8):1808–18. [aCB]

Diana R. A., Yonelinas A. P. & Ranganath C. (2013) Parahippocampal cortex activation during context reinstatement predicts item recollection. *Journal of Experimental Psychology: General* **142**(4):1287–97. doi: 10.1037/a0034029. [aCB]

Diemand-Yauman C., Oppenheimer D. M. & Vaughan E. B. (2011) Fortune favors the Bold (and the Italicized): Effects of disfluency on educational outcomes. *Cognition* **118**(1):111–15. [TS]

Dockree P. M., O'Keeffe F. M., Moloney P., Bishara A. J., Carton S., Jacoby L. L. & Robertson I. H. (2006) Capture by misleading information and its false acceptance in patients with traumatic brain injury. *Brain* **129**(Pt 1):128–40. doi: 10.1093/brain/awh664. [CMK, rCB]

Dodson C. S. & Schacter D. L. (2001) "If I had said it I would have remembered it": Reducing false memories with distinctiveness heuristic. *Psychonomic Bulletin and Review* **8**(1):155–61. [aCB]

Doeller C. F., Barry C. & Burgess N. (2010) Evidence for grid cells in a human memory network. *Nature* **463**(7281):657–61. doi: 10.1038/nature08704. [aCB]

Donovan N. J., Locascio J. J., Marshall G. A., Gatchel J., Hanseeuw B. J., Rentz D. M., Johnson K. A. & Sperling R. A. (2018) Longitudinal association of amyloid beta and anxious-depressive symptoms in cognitively normal older adults. *American Journal of Psychiatry* **175**(6):530–37. doi: 10.1176/appi.ajp.2017.17040442. [BCN]

Du A. T., Schuff N., Amend D., Laakso M. P., Hsu Y. Y., Jagust W. J., Yaffe K., Kramer J. H., Reed B., Norman D., Chui H. C. & Weiner M. W. (2001) Magnetic resonance imaging of the entorhinal cortex and hippocampus in mild cognitive impairment and Alzheimer's disease. *Journal of Neurology, Neurosurgery, and Psychiatry* **71** (4):441–47. [OH]

Duarte A., Henson R. N. & Graham K. S. (2008) The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex* **18**:2169–80. [rCB]

Duarte A., Ranganath C. & Knight R. T. (2005) Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience* **25**(36):8333–37. doi: 10.1523/JNEUROSCI.1392-05.2005. [aCB]

Duke D., Fiacconi C. M. & Köhler S. (2014) Parallel effects of processing fluency and positive affect on familiarity-based recognition decisions for faces. *Frontiers in Psychology* **5**: article no. 328. doi: 10.3389/fpsyg.2014.00328. [aCB]

Duncan K., Ketz N., Inati S. J. & Davachi L. (2012) Evidence for area CA1 as a match/mismatch detector: A high-resolution fMRI study of the human hippocampus. *Hippocampus* **22**(3):389–98. [TS]

Dunn C. J., Duffy S. L., Hickie I. B., Lagopoulos J., Lewis S. J., Naismith S. L. & Shine J. M. (2014) Deficits in episodic memory retrieval reveal impaired default mode network connectivity in amnestic mild cognitive impairment. *NeuroImage: Clinical* **4**:473–80. doi: 10.1016/j.nicl.2014.02.010. [aCB]

Dunn J. C. (2004) Remember-know: A matter of confidence. *Psychological Review* **111** (2):524–42. [TS]

Dunn J. C. (2008) The dimensionality of the remember–know task: A state-trace analysis. *Psychological Review* **115**:426–46. doi: 10.1037/0033-295X.115.2.426. [AFO, VS]

Dunn J. C. & Kalish M. L. (2018) *State-trace analysis*. Springer. [AFO]

Dunn J. C. & Kirsner K. (1988) Discovering functionally independent mental processes: The principle of reversed association. *Psychological Review* **95**:91–101. [AFO]

Düzel E., Habib R., Rotte M., Guderian S., Tulving E. & Heinze H.-J. (2003) Human hippocampal and parahippocampal activity during visual associative recognition memory for spatial and nonspatial stimulus configurations. *Journal of Neuroscience* **23** (28):9439–44. [TS]

Dzieciol A. M., Bachevalier J., Saleem K. S., Gadian D. G., Saunders R., Chong W. K., Banks T., Mishkin M. & Vargha-Khadem F. (2017) Hippocampal and diencephalic pathology in developmental amnesia. *Cortex* **86**:33–44. [JPA]

Edelstyn N. M. J., Grange J. A., Ellis S. J. & Mayes A. R. (2016) A deficit in familiarity-driven recognition in a right-sided mediodorsal thalamic lesion patient. *Neuropsychology* **30**(2):213–24. doi: 10.1037/neu0000226. [aCB]

Edelstyn N. M. J. & Oyebode F. (1999) A review of the phenomenology and cognitive neuropsychological origins of the Capgras syndrome. *International Journal Of Geriatric Psychiatry* **14**(1):48–59. doi: 10.1002/(sici)1099-1166(199901)14:1 < 48::aid-gps891 > 3.3.co;2-s. [JP]

Eichenbaum H. (2013) Memory on time. *Trends in Cognitive Sciences* **17**(2):81–88. doi: 10.1016/j.tics.2012.12.007. [aCB]

Eichenbaum H. (2017a) On the integration of space, time, and memory. *Neuron* **95** (5):1007–1018. Available at: https://doi.org/10.1016/j.neuron.2017.06.036. [JC]

Eichenbaum H. (2017b) Prefrontal cortex: A mystery of belated memories. *Current Biology* **27**:R418–20. [AS]

Eichenbaum H. (2017c) The role of the hippocampus in navigation is memory. *Journal of Neurophysiology* **117**(4):1785–96. doi: 10.1152/jn.00005.2017. [aCB]

Eichenbaum H. & Cohen N. J. (2014) Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron* **83**(4):764–70. doi: 10.1016/j.neuron.2014.07.032. [aCB]

Eichenbaum H., Otto T. & Cohen N. J. (1994) Two functional components of the hippocampal memory system. *Behavioral and Brain Sciences* **17**(3):449–72. [TS]

Eichenbaum H., Yonelinas A. P. & Ranganath C. (2007) The medial temporal lobe and recognition memory. *Annual Review of Neuroscience* **30**:123–52. doi: 10.1146/annurev.neuro.30.051606.094328. [arCB, AFO]

Ekstrom A. D. & Ranganath C. (2018) Space, time, and episodic memory: The hippocampus is all over the cognitive map. *Hippocampus* **28**(9):680–87. Available at: https://doi.org/10.1002/hipo.22750. [JC]

El Haj M. & Antoine P. (2017) Discrepancy between subjective autobiographical reliving and objective recall: The past as seen by Alzheimer's disease patients. *Consciousness and Cognition* **49**:110–16. doi: 10.1016/j.concog.2017.01.009. [rCB]

El Haj M., Antoine P., Nandrino J. L. & Kapogiannis D. (2015) Autobiographical memory decline in Alzheimer's disease, a theoretical and clinical overview. *Ageing Res Rev* **23** (Pt B):183–92. doi: 10.1016/j.arr.2015.07.001. [DK]

El Haj M., Gallouj K. & Antoine P. (2019a) Mental imagery and autobiographical memory in Alzheimer's disease. *Neuropsychology* **33**(5):609–16. doi: 10.1037/neu0000521. [rCB, DK]

El Haj M., Kapogiannis D. & Antoine P. (2016) Phenomenological reliving and visual imagery during autobiographical recall in Alzheimer's disease. *Journal of Alzheimer's Disease* **52**(2):421–31. doi: 10.3233/JAD-151122. [rCB, DK]

El Haj M., Moustafa A. A., Gallouj K. & Robin F. (2019b) Visual imagery: The past and future as seen by patients with Alzheimer's disease. *Consciousness and Cognition* **68**:12–22. Available at: https://doi.org/10.1016/j.concog.2018.12.003. [DK]

El-Kalliny M. M., Wittig J. H., Sheehan T. C., Sreekumar V., Inati S. K. & Zaghloul K. A. (2019) Changing temporal context in human temporal lobe promotes memory of distinct episodes. *Nature Communications* **10**(1): article no. 203. [VS]

Erez J., Cusack R., Kendall W. & Barense M. D. (2016) Conjunctive coding of complex object features. *Cerebral Cortex* **26**:2271–82. doi: 10.1093/cercor/bhv081. [aCB]

Failes E., Sommers M. & Jacoby L. (unpublished manuscript). Blurring past and present: Comparing false memory and false hearing in older adults. [CMK]

Fang J., Demic S. & Cheng S. (2018a) The reduction of adult neurogenesis in depression impairs the retrieval of new as well as remote episodic memory. *PLOS ONE*, **13**(6): e0198406. Available at: https://doi.org/10.1371/journal.pone.0198406. [OH]

Fang J., Rüther N., Bellebaum C., Wiskott L. & Cheng S. (2018b) The Interaction between Semantic Representation and Episodic Memory. *Neural Computation* **30**(2):293–332. Available at: https://doi.org/10.1162/neco_a_01044. [OH]

Feinberg T., Eaton L., Roane D. & Giacino J. (1999) Multiple Fregoli Delusions after Traumatic Brain Injury. *Cortex* **35**(3):373–87. doi: 10.1016/s0010-9452(08)70806-2. [JP]

Feinberg T. & Roane D. (2005) Delusional misidentification. *Psychiatric Clinics Of North America* **28**(3):665–83. doi: 10.1016/j.psc.2005.05.002. [JP]

Fiacconi C. M., Peter E. L., Owais S. & Köhler S. (2016) Knowing by heart: Visceral feedback shapes recognition memory judgments. *Journal of Experimental Psychology: General* **145**(5):559–72. doi: 10.1037/xge0000164. [arCB]

Folkerts S., Rutishauser U. & Howard M. W. (2018) Human episodic memory retrieval is accompanied by a neural contiguity effect. *Journal of Neuroscience* **38**(17):4200–211. [VS]

Folville A., D'Argembeau A. & Bastin C. (2019) Deciphering the relationship between objective and subjective aspects of recollection in healthy aging. *PsyArXiv*. doi:10.31234/osf.io/hjfe4. Available at: https://www.researchgate.net/publication/333906623_Deciphering_the_Relationship_between_Objective_and_Subjective_Aspects_of_Recollection_in_Healthy_Aging. [rCB]

Förstl H., Almeida O., Owen A., Burns A. & Howard R. (1991) Psychiatric, neurological and medical aspects of misidentification syndromes: A review of 260 cases. *Psychological Medicine* **21**(04):905. doi: 10.1017/s0033291700029895. [JP]

Foster B. L., Dastjerdi M. & Parvizi J. (2012) Neural populations in human posteromedial cortex display opposing responses during memory and numerical processing. *Proceedings of the National Academy of Sciences USA* **109**(38):15514–19. doi: 10.1073/pnas.1206580109. [aCB]

Foster B. L. & Parvizi J. (2017) Direct cortical stimulation of human posteromedial cortex. *Neurology* **88**(7):685–91. doi: 10.1212/wnl.0000000000003607. [aCB, JC]

Fougnie D. & Alvarez G. A. (2011) Object features fail independently in visual working memory: Evidence for a probabilistic feature-store model. *Journal of Vision* **11**(12). (Online publication). doi: 10.1167/11.12.3. [rCB]

Freeman E., Dennis S. & Dunn J. C. (2010) An examination of the ERP correlates of recognition memory using state-trace analysis. In: *Proceedings of the 32nd Annual Conference of the Cognitive Science Society*, ed. S. Ohlsson & R. Catrambone, pp. 97–102. Cognitive Science Society. [AFO]

Frenda S. J., Nichols R. M. & Loftus E. F. (2011) Current issues and advances in misinformation research. *Current Directions in Psychological Science* **20**:20–23. [GEB]

Friedman W. J. (1993) Memory for the time of past events. *Psychological Bulletin* **113** (1):44–66. [rCB, VS]

Gainotti G. (2007) Face familiarity feelings, the right temporal lobe and the possibile underlying neural mechanisms. *Brain Research Reviews* **56**:214–35. Available at: https://doi.org/10.1016/j.brainresrev.2007.07.009. [GG]

Gainotti G. (2012) The format of conceptual representations disrupted in semantic dementia: A position paper. *Cortex* **48**:521–29. Available at: https://doi.org/10.1016/j.cortex.2011.06.019. [GG]

Gainotti G. (2013) Laterality effects in normal subjects' recognition of familiar faces, voices and names. Perceptual and representational components. *Neuropsychologia* **51**:1151–60. Available at: https://doi.org/10.1016/j.neuropsychologia.2013.03.009. [GG]

Gainotti G. & Marra C. (2011) Differential contribution of right and left temporo-occipital and anterior temporal lesions to face recognition disorders. *Frontiers in Human Neuroscience* **5**: article no.55. Available at: http://dx.doi.org/10.3389/fnhum.2011.00055. [GG]

Gallagher D., Coen R., Kilroy D., Belinski K., Bruce I., Coakley D., Walsh B., Cunningham C. & lawlor B. A. (2011) Anxiety and behavioural disturbance as markers of prodromal Alzheimer's disease in patients with mild cognitive impairment. *International Journal of Geriatric Psychiatry* **26**(2):166–72. doi:10.1002/gps.2509. [BCN]

Gallistel C. R. (1999) Themes of thought and thinking [Review of *The Nature of Cognition*, ed. by R. J. Sternberg]. *Science* **285**:842–43. [JFK]

Gallo D. A. (2010) False memories and fantastic beliefs: 15 years of the DRM illusion. *Memory & Cognition* **38**:833–48. [GEB, JFK]

Gallo D. A., Foster K. T., Wong J. T. & Bennett D. A. (2010) False recollection of emotional pictures in Alzheimer's disease. *Neuropsychologia* **48**(12):3614–18. doi: 10.1016/j.neuropsychologia.2010.08.011. [aCB]

Gardiner J. M. (1988) Functional aspects of recollective experience. *Memory & Cognition* **16**:309–13. [JFK]

Genon S., Bahri M. A., Collette F., Angel L., d'Argembeau A., Clarys D., Kalenzaga S., Salmon E. & Bastin C. (2014) Cognitive and neuroimaging evidence of impaired interaction between self and memory in Alzheimer's disease. *Cortex* **51**:11–24. doi: 10.1016/j.cortex.2013.06.009. [aCB]

Genon S., Collette F., Feyers D., Phillips C., Salmon E. & Bastin C. (2013) Item familiarity and controlled associative retrieval in Alzheimer's disease: An fMRI study. *Cortex* **49**:1566–84. [arCB]

Geurten M., Bastin C., Salmon E. & Willems S. (2019) Hunting down the source: How amnesic patients avoid fluency-based memory errors. *Neuropsychology*. (Advance online publication.) doi: 10.1037/neu0000566. Available at: http://dx.doi.org/10.1037/neu0000566. [rCB]

Geurten M., Lloyd M. & Willems S. (2017) Hearing "quack" and remembering a duck: Evidence for fluency attribution in young children. *Child Development* **88**(2):514–22. doi: 10.1111/cdev.12614. [arCB]

Geurten M., Meulemans T. & Willems S. (2018) A closer look at children's metacognitive skills: The case of the distinctiveness heuristic. *Journal of Experimental Child Psychology* **172**:130–48. doi: 10.1016/j.jecp.2018.03.007. [rCB]

Geurten M. & Willems S. (2017) The learned reinterpretation of fluency in amnesia. *Neuropsychologia* **101**:10–16. doi: 10.1016/j.neuropsychologia.2017.05.012. [arCB]

Ghetti S. (2003) Memory for nonoccurrences: The role of metacognition. *Journal of Memory and Language* **48**(4):722–39. doi: 10.1016/s0749-596x(03)00005-6. [aCB]

Gold J. I. & Shadlen M. N. (2007) The neural basis of decision making. *Annual Review of Neuroscience* **30**:535–74. [AFO]

Gomes C. A., Figueiredo P. & Mayes A. (2016) Priming for novel object associations: Neural differences from object item priming and equivalent forms of recognition. *Hippocampus* **26**(4):472–91. doi: 10.1002/hipo.22537. [rCB]

Gomez A., Rousset S. & Baciu M. (2009) Egocentric-updating during navigation facilitates episodic memory retrieval. *Acta Psychologica (Amsterdam)* **132**(3):221–27. doi:10.1016/j.actpsy.2009.07.003. [GR]

Gonsalves B. D., Kahn I., Curran T., Norman K. A. & Wagner A. D. (2005) Memory strength and repetition suppression: Multimodal imaging of medial temporal cortical contributions to recognition. *Neuron* **47**:751–61. [aCB]

Graham K. S., Barense M. D. & Lee A. C. (2010) Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia* **48**(4):831–53. doi: 10.1016/j.neuropsychologia.2010.01.001. [aCB, GR, W-CW]

Graham K. S., Patterson K., Powis J., Drake J. & Hodges J. R. (2002) Multiple inputs to episodic memory: Words tell another story. *Neuropsychology* **16**(3):380–89. [CS-B, rCB]

Greenberg D. L. & Rubin D. C. (2003) The neuropsychology of autobiographical memory. *Cortex* **39**:687–728. [AS]

Greenberg D. L. & Verfaellie M. (2010) Interdependence of episodic and semantic memory: Evidence from neuropsychology. *Journal of the International Neuropsychol ogical Society* **16**:748–53. Available at: https://doi.org/10.1017/S1355617710000676. [GG]

Greicius M. D., Supekar K., Menon V. & Dougherty R. F. (2009) Resting-state functional connectivity reflects structural connectivity in the default mode network. *Cerebral Cortex* **19**:72–78. [aCB]

Greve A., Donaldson D. I. & van Rossum M. C. W. (2010) A single-trace dual-process model of episodic memory: A novel computational account of familiarity and recollection. *Hippocampus* **20**(2):235–51. doi: 10.1002/hipo.20606. [OH, rCB]

Griffiths S., Scott H., Glover C., Bienemann A., Ghorbel M. T., Uney J., Brown M. W., Warburton E. C. & Bashir Z. I. (2008) Expression of long-term depression underlies visual recognition memory. *Neuron* **58**(2):186–94. [JPA]

Grill-Spector K., Henson R. & Martin A. (2006) Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences* **10**(1):14–23. Available at: https://doi.org/10.1016/j.tics.2005.11.006. [HY]

Grober E., Dickson D., Sliwinski M. J., Buschke H., Katz M., Crystal H. & Lipton R. B. (1999) Memory and mental status correlates of modified Braak staging. *Neurobiology of Aging* **20**(6):573–79. [aCB]

Hafting T., Fyhn M., Molden S., Moser M. B. & Moser E. I. (2005) Microstructure of a spatial map in the entorhinal cortex. *Nature* **436**(7052):801–806. doi:10.1038/nature03721. [GR]

Hagmann P., Cammoun L., Gigandet X., Meuli R., Honey C. J., Wedeen V. J. & Sporns O. (2008) Mapping the structural core of human cerebral cortex. *PLoS Biology* **6**(7):e159. doi: 10.1371/journal.pbio.0060159. [aCB]

Halbwachs M. (1980) *The collective memory*. Harper & Row Colophon. [aCB]

Hamann S. B. & Squire L. R. (1997) Intact Perceptual Memory in the Absence of Conscious Memory. *Behavioral Neuroscicnce* **III**(4):850–54. doi: 10.1037/0735-7044.111.4.850. [CFI]

Hannula D. E. & Ranganath C. (2009) The eyes have it: Hippocampal activity predicts expression of memory in eye movements. *Neuron* **63**(5):592–99. Available at: https://doi.org/10.1016/j.neuron.2009.08.025. [W-CW]

Hanseeuw B. J., Van Leemput K., Kavec M., Grandin C., Seron X. & Ivanoiu A. (2011) Mild cognitive impairment: Differential atrophy in the hippocampal subfields. *American Journal of Neuroradiology* **32**(9):1658–61. doi: 10.3174/ajnr.A2589. [aCB]

Hashtroudi S., Johnson M. K. & Chrosniak L. D. (1990) Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology of Aging* **5**(1):119–26. [rCB]

Haskins A. L., Yonelinas A. P., Quamme J. R. & Ranganath C. (2008) Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron* **59**:554–60. [aCB]

Hatfield G. (2000) The brain's "new" science: Psychology, neurophysiology, and constraint. *Philosophy of Science* **67**(3):388–404. Available at: https://philarchive.org/archive/HATTBN. [JFK]

Hayes B. K., Dunn J. C., Joubert A. & Taylor R. (2017) Comparing single- and dual-process models of memory development. *Developmental Science* **20**:1–14. [AFO]

Heathcote A. (2003) Item recognition memory and the receiver operating characteristic. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **29**:1210–30. [AFO]

Heathcote A., Raymond F. & Dunn J. C. (2006) Recollection and familiarity in recognition memory: Evidence from ROC curves. *Journal of Memory and Language* **55**:495–514. [AFO]

Henson R. N. A., Rugg M. D., Shallice T., Josephs O. & Dolan R. J. (1999) Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *The Journal of Neuroscience* **19**(10):3962–72. [aCB]

Herholz K., Salmon E., Perani D., Baron J. C., Holthoff V., Frolich L., Schonknecht P., Ito K., Mielke R., Kalbe E., Zuendorf G., Delbeuck X., Pelati O., Anchisi D., Fazio F., Kerrouche N., Desgranges B., Eustache F., Beuthien-Baumann B., Menzel C., Schroder J., Kato T., Arahata Y., Henze M. & Heiss W. D. (2002) Discrimination between Alzheimer dementia and controls by automated analysis of multicenter FDG PET. *NeuroImage* **17**(1):302–16. [aCB]

Higham P. A. & Vokey J. R. (2004) Illusory recollection and dual-process models of recognition memory. *Quarterly Journal of Experimental Psychology A* **57**(4):714–44. doi: 10.1080/02724980343000468. [aCB]

Hintzman D. L. (1984) MINERVA 2: A simulation model of human memory. *Behavior Research Methods, Instruments & Computers* **16**(2):96–101. Available at: https://doi.org/10.3758/BF03202365. [HY]

Hirabayashi T., Takeuchi D., Tamura K. & Miyashita Y. (2013) Microcircuits for hierarchical elaboration of object coding across primate temporal areas. *Science* **341** (6142):191–95. doi: 10.1126/science.1236927. [aCB]

Hirst W., Yamashiro J. K. & Coman A. (2018) Collective memory from a psychological perspective. *Trends in Cognitive Sciences* **22**(5):438–51. doi: 10.1016/j.tics.2018.02.010. [aCB]

Hodges J. R. & Patterson K. (2007) Semantic dementia: A unique clinicopathological syndrome. *The Lancet Neurology* **6**(11):1004–1014. [CS-B]

Holdstock J. S., Mayes A. R., Roberts N., Cezayirli E., Isaac C. L., O'Reilly R. C. & Norman K. A. (2002) Under what conditions is recognition spared relative to recall after selective hippocampal damage in humans? *Hippocampus* **12**(3):341–51. doi: 10.1002/hipo.10011. [OH, rCB]

Holscher C., Rolls E. T. & Xiang J. (2003) Perirhinal cortex neuronal activity related to long-term familiarity memory in the macaque. *European Journal of Neuroscience* **18** (7):2037–46. [JPA]

Hoppstädter M., Baeuchl C., Diener C., Flor H. & Meyer P. (2015) Simultaneous EEG-fMRI reveals brain networks underlying recognition memory ERP old/new effects. *NeuroImage* **116**:112–22. Available at: https://doi.org/10.1016/j.neuroimage.2015.05.026. [JC]

Hower K. H., Wixted J., Berryhill M. E. & Olson I. R. (2014) Impaired perception of mnemonic oldness, but not mnemonic newness, after parietal lobe damage. *Neuropsychologia* **56**(1):409–17. Available at: http://doi.org/10.1016/j.neuropsychologia.2014.02.014. [RT]

Howett D., Castegnaro A., Krzywicka K., Hagman J., Marchment D., Henson R., Rio M., King J. A., Burgess N. & Chan D. (2019) Differentiation of mild cognitive impairment using an entorhinal cortex-based test of virtual reality navigation. *Brain* **142**(6):1751–66. doi: 10.1093/brain/awz116. [rCB]

Huang T., Liu C. & Yang Y. (1999) Capgras syndrome: Analysis of nine cases. *Psychiatry And Clinical Neurosciences* **53**(4):455–60. doi: 10.1046/j.1440-1819.1999.00582.x. [JP]

Hudson A. (2000) Misidentification syndromes related to face specific area in the fusiform gyrus. *Journal Of Neurology, Neurosurgery & Psychiatry* **69**(5):645–48. doi: 10.1136/jnnp.69.5.645. [JP]

Huntenburg J. M., Bazin P. L. & Margulies D. S. (2018) Large-scale gradients in human cortical organization. *Trends in Cognitive Sciences* **22**(1):21–31. doi: 10.1016/j.tics.2017.11.002. [rCB]

Hutchinson J. B., Uncapher M. R. & Wagner A. D. (2009) Posterior parietal cortex and episodic retrieval: Convergent and divergent effects of attention and memory. *Learning & Memory (Cold Spring Harbor, N.Y.* **16**(6):343–56. Available at: https://doi.org/10.1101/lm.919109. [HY]

Hutchinson J. B., Uncapher M. R., Weiner K. S., Bressler D. W., Silver M. A., Preston A. R. & Wagner A. D. (2014) Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cerebral Cortex* **24**(1):49–66. doi: 10.1093/cercor/bhs278. [HY, rCB]

Ingram K. M., Mickes L. & Wixted J. T. (2012) Recollection can be weak and familiarity can be strong. *Journal of Experimental Psychology. Learning, Memory, and Cognition* **38**(2):325–39. Available at: https://doi.org/10.1037/a0025483. [OH]

Inhoff M. C. & Ranganath C. (2015) Significance of objects in the perirhinal cortex. *Trends in Cognitive Sciences* **19**(6):302–303. Available at: http://dx.doi.org/10.1016/j.tics.2015.04.008. [aCB]

Irish M., Addis D. R., Hodges J. R. & Piguet O. (2012) Considering the role of semantic memory in episodic future thinking: Evidence from semantic dementia. *Brain* **135**(7):2178–91. doi: 10.1093/brain/aws119 [doi]. [CS-B]

Irish M., Bunk S., Tu S., Kamminga J., Hodges J. R., Hornberger M. & Piguet O. (2016) Preservation of episodic memory in semantic dementia: The importance of regions beyond the medial temporal lobes. *Neuropsychologia* **81**:50–60. [CS-B]

Irish M., Hornberger M., Lah S., Miller L., Pengas G., Nestor P. J., Hodges J. R. & Piguet O. (2011) Profiles of recent autobiographical memory retrieval in semantic dementia, behavioural-variant frontotemporal dementia, and Alzheimer's disease. *Neuropsychologia* **49**(9):2694–702. doi:S0028-3932(11)00266-1 [pii] 10.1016/j.neuropsychologia.2011.05.017 [doi]. [CS-B]

Irish M., Landin-Romero R., Mothakunnel A., Ramanan S., Hsieh S., Hodges J. R. & Piguet O. (2018) Evolution of autobiographical memory impairments in Alzheimer's disease and frontotemporal dementia – a longitudinal neuroimaging study. *Neuropsychologia* **110**:14–25. doi:10.1016/j.neuropsychologia.2017.03.014. [CS-B]

Irish M. & van Kesteren M. T. R. (2018) New perspectives on the brain lesion approach – implications for theoretical models of human memory. *Neuroscience* **374**:319–22. Available at: https://doi.org/10.1016/j.neuroscience.2017.10.049. [CS-B]

Jack Jr. C. R., Bennett D. A., Blennow K., Carrillo M. C., Dunn B., Haeberlein S. B., Holtzman D. M., Jagust W., Jessen F., Karlawish J., Liu E., Molinuevo J. L., Montine T., Phelps C., Rankin K. P., Rowe C. C., Scheltens P., Siemers E., Snyder H. M. & Sperling R. (2018) NIA-AA research framework: Toward a biological definition of Alzheimer's disease. *Alzheimer's and Dementia* **14**(4):535–62. doi: 10.1016/j.jalz.2018.02.018. [aCB]

Jack C. R., Knopman D. S., Jagust W. J., Petersen R. C., Weiner M. W., Aisen P. S., Shaw L. M., Vemuri P., Wiste H. J., Weigand S. D., Lesnick T. G., Pankratz M. C., Donohue M. C. & Trojanowski J. Q. (2013) Tracking pathophysiological processes in Alzheimer's disease: An updated hypothetical model of dynamic biomarkers. *The Lancet Neurology* **12**(2):207–16. doi: 10.1016/s1474-4422(12)70291-0. [aCB]

Jacoby L. L. (1991) A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language* **13**:513–41. [JFK]

Jacoby L. L., Bishara A. J., Hessels S. & Toth J. P. (2005a) Aging, subjective experience, and cognitive control: Dramatic false remembering by older adults. *Journal of Experimental Psychology: General* **134**(2):131–48. doi: 10.1037/0096-3445.134.2.131. [rCB, CMK]

Jacoby L. L. & Dallas M. (1981) On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General* **110**(3):306–40. [aCB, CMK]

Jacoby L. L., Kelley C. M. & Dywan J. (1989) Memory attributions. In: *Varieties of memory and consciousness: Essays in honour of Endel Tulving*, ed. H. L. Roediger & F. I. M. Craik, pp. 391–422. Erlbaum. [aCB, CMK, HY]

Jacoby L. L., Shimizu Y., Velanova K. & Rhodes M. G. (2005b) Age differences in depth of retrieval: Memory for foils. *Journal of Memory and Language* **52**:493–504. [CMK]

Jacoby L. L. & Whitehouse K. (1989) An illusion of memory: False recognition influenced by unconscious perception. *Journal of Experimental Psychology* **118**(2):126–35. doi: 10.1037/0096-3445.118.2.126. [CFI]

Jacoby L. L., Yonelinas A. P. & Jennings J. M. (1997) The relation between conscious and unconscious (automatic) influences: A declaration of independence. In: *Scientific approaches to consciousness*, ed. J. D. Cohen & J. W. Schooler pp. 13–47. Erlbaum. [aCB]

Jakesch M., Leder H. & Forster M. (2013) Image ambiguity and fluency. *PLOS ONE* **8**(9): e74084. Available at: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0074084. [TS]

Jankowski M. M., Passecker J., Islam M. N., Vann S., Erichsen J. T., Aggleton J. P. & O'Mara S. M. (2015) Evidence for spatially-responsive neurons in the rostral thalamus. *Frontiers in Behavioral Neuroscience* **9**: article no. 256. Available at: https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00256/full. [JPA]

Jedidi H., Daury N., Capa R., Bahri M. A., Collette F., Feyers D., Bastin C., Maquet P. & Salmon E. (2015) Brain metabolic dysfunction in Capgras delusion during Alzheimer's disease: A positron emission tomography study. *American Journal of Alzheimer's Disease and Other Dementias* **30**(7):699–706. doi: 10.1177/1533317513495105. [rCB]

Johnson J. D., McDuff S. G., Rugg M. D. & Norman K. A. (2009) Recollection, familiarity, and cortical reinstatement: A multivoxel pattern analysis. *Neuron* **63**(5):697–708. doi: 10.1016/j.neuron.2009.08.011. [aCB]

Johnson J. D., Suzuki M. & Rugg M. D. (2013) Recollection, familiarity, and content-sensitivity in lateral parietal cortex: A high-resolution fMRI study. *Frontiers in Human Neuroscience* **7**: article no. 219. doi: 10.3389/fnhum.2013.00219. [aCB]

Johnson M. K., Kuhl B. A., Mitchell K. J., Ankudowich E. & Durbin K. A. (2015) Age-related differences in the neural basis of the subjective vividness of memories: Evidence from multivoxel pattern classification. *Cognitive, Affective, and Behavioral Neuroscience* **15**(3):644–61. doi: 10.3758/s13415-015-0352-9. [rCB]

Jonin P.-Y., Besson G., La Joie R., Pariente J., Belliard S., Barillot C. & Barbeau E. J. (2018) Superior explicit memory despite severe developmental amnesia: In-depth case study and neural correlates. *Hippocampus* **28**(12):867–85. doi: 10.1002/hipo.23010. [aCB]

Jonin P.-Y., Calia C., Muratot S., Belliard S., Duché Q., Barbeau E. J. & Parra M. A. (2019) Refining understanding of working memory buffers through the construct of binding: Evidence from a single case informs theory and clinical practise. *Cortex* **112**:37–57. Available at: https://doi.org/10.1016/j.cortex.2018.08.011. [aCB]

Josephs K. (2007) Capgras Syndrome and Its Relationship to Neurodegenerative Disease. *Archives Of Neurology* **64**(12):1762. doi: 10.1001/archneur.64.12.1762. [JP]

Julian J. B., Keinath A. T., Marchette S. A. & Epstein R. A. (2018) The Neurocognitive Basis of Spatial Reorientation. *Current Biology* **28**(17):R1059–R1073. doi:10.1016/j.cub.2018.04.057. [GR]

Kafkas A., Migo E. M., Morris R. G., Kopelman M. D., Montaldi D. & Mayes A. R. (2017) Material specificity drives medial temporal lobe familiarity but not hippocampal recollection. *Hippocampus* **27**(2):194–209. doi: 10.1002/hipo.22683. [arCB]

Kaiser N. C., Liang L.-J., Melrose R. J., Wilkins S. S., Sultzer D. L. & Mendez M. F. (2014) Differences in anxiety among patients with early-versus late-onset Alzheimer's disease. *The Journal of Neuropsychiatry and Clinical Neurosciences* **26**(1):73–80. doi:10.1176/appi.neuropsych.12100240. [BCN]

Kassin S. M. (2008) False confessions: Causes, consequences, and implications for reform. *Current Directions in Psychological Science* **17**(4):249–53. [JFK]

Kassin S. M. (2017) False confessions: How can psychology so basic be so counterintuitive? *American Psychologist* **72**(9):951–64. [JFK]

Keane M. M., Orlando F. & Verfaellie M. (2006) Increasing the salience of fluency cues reduces the recognition memory impairment in amnesia. *Neuropsychologia* **44**(5):834–39. [aCB]

Keene C. S., Bladon J., McKenzie S., Liu C. D., O'Keefe J. & Eichenbaum H. (2016) Complementary functional organization of neuronal activity patterns in the perirhinal, lateral entorhinal, and medial entorhinal cortices. *Journal of Neuroscience* **36**(13):3660–75. doi: 10.1523/jneurosci.4368-15.2016. [aCB]

Kelley C. M. & Alban M. W. (2015) Constrained retrieval in recognition memory. In: *Remembering: Attributions, processes, and control in human memory: Essays in honor of Larry L. Jacoby*, ed. S. Lindsay, H. L. Roediger III, C. M. Kelley & A. Yonelinas, pp. 198–212. Psychology Press. [CMK]

Kelley C. M. & Rhodes M. G. (2002) Making sense and nonsense of experience: Attributions in memory and judgment. In: *The psychology of learning and motivation: Advances in research and theory, vol. 41*, ed. B. H. Ross, pp. 293–320. Academic Press. [aCB, CMK]

Kemp S. (1999) An associative theory of estimating past dates and past prices. *Psychonomic Bulletin & Review* **6**(1):41–56. [VS]

Kensinger E. A. & Schacter D. L. (2006) Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *Journal of Neuroscience* **26**(9):2564–70. doi: 10.1523/jneurosci.5241-05.2006. [aCB]

Kent B. A., Hvoslef-Eide M., Saksida L. M. & Bussey T. J. (2016) The representational–hierarchical view of pattern separation: Not just hippocampus, not just space, not just memory? *Neurobiology of Learning and Memory* **129**(Suppl. C):99–106. Available at: https://doi.org/10.1016/j.nlm.2016.01.006. [aCB]

Ketz N. A., Jensen O. & O'Reilly R. C. (2015) Thalamic pathways underlying prefrontal cortex-medial temporal lobe oscillatory interactions. *Trends in Neuroscience* **38**(1):3–12. doi: 10.1016/j.tins.2014.09.007. [rCB]

Kihlstrom J. F. (1998) Exhumed memory. In: *Truth in memory*, ed. S. J. Lynn & K. M. McConkey, pp. 3–31. Guilford Press. [JFK]

Kihlstrom J. F. (2006) Trauma and memory revisited. In: *Memory and emotions: Interdisciplinary perspectives*, ed. B. Uttl, N. Ohta & A. L. Siegenthaler, pp. 259–91. Blackwell. [JFK]

Kihlstrom J. F. (2010) Social neuroscience: The footprints of Phineas Gage. *Social Cognition* **28**(6):757–83. [JFK]

Kihlstrom J. F. (in press) Varieties of recollective experience. *Neuropsychologia*. [JFK]

Kim H. (2010) Dissociating the roles of the default mode, dorsal, and ventral networks in episodic memory retrieval. *NeuroImage* **50**:1648–57. [aCB]

Kishiyama M. M., Yonelinas A. P. & Knight R. T. (2009) Novelty enhancements in memory are dependent on lateral prefrontal cortex. *Journal of Neuroscience* **29**(25):8114–18. doi: 10.1523/jneurosci.5507-08.2009. [aCB]

Kivisaari S. L., Monsch A. U. & Taylor K. I. (2013) False positives to confusable objects predict medial temporal lobe atrophy. *Hippocampus* **23**(9):832–41. doi: 10.1002/hipo.22137. [aCB]

Kivisaari S. L., Tyler L. K., Monsch A. U. & Taylor K. I. (2012) medial perirhinal cortex disambiguates confusable objects. *Brain* **135**(Pt 12):3757–69. doi: 10.1093/brain/aws277. [aCB]

Kleider H. M. & Goldinger S. D. (2004) Illusions of face memory: Clarity breeds familiarity. *Journal of Memory and Language* **50**(2):196–211. Available at: https://doi.org/10.1016/j.jml.2003.09.001. [TS]

Klein S. B. & Nichols S. (2012) Memory and the sense of personal identity. *Mind* **121**(483):677–702. doi: 10.1093/mind/fzs080. [aCB]

Kloth N., Dobel C., Schweinberger S. R., Zwitserlood P., Bölte J. & Junghöfer M. (2006) Effects of personal familiarity on early neuromagnetic correlates of face perception. *European Journal of Neuroscience* **24**:3317–21. Available at: http://dx.doi.org/10.1111/j.1460-9568.2006.05211.x. [GG]

Knott L. M., Dewhurst S. A. & Howe M. L. (2012) What factors underlie associative and categorical memory illusions? The roles of backward associative strength and interitem connectivity. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **38**(1):229–39. [JFK]

Kobayashi Y. & Amaral D. G. (2003) Macaque monkey retrosplenial cortex: II. Cortical afferents. *Journal of Comparative Neurology* **466**(1):48–79. doi: 10.1002/cne.10883. [aCB]

Koen J. D. & Yonelinas A. P. (2014) The effects of healthy aging, amnestic mild cognitive impairment, and Alzheimer's disease on recollection and familiarity: A meta-analytic review. *Neuropsychological Review* **24**(3):332–54. doi: 10.1007/s11065-014-9266-5. [aCB]

Krieg J., Koessler L., Jonas J., Colnat-Coulbois S., Vignal J. P., Bénar C. G. & Maillard L. G. (2017) Discrimination of a medial functional module within the temporal lobe using an effective connectivity model: A CCEP study. *NeuroImage* **161**:219–31. Available at: https://doi.org/10.1016/j.neuroimage.2017.07.061. [JC]

Kubota Y., Enatsu R., Gonzalez-Martinez J., Bulacio J., Mosher J., Burgess R. C. & Nair D. R. (2013) In vivo human hippocampal cingulate connectivity: A corticocortical evoked potentials (CCEPs) study. *Clinical Neurophysiology* **124**(8):1547–56. Available at: https://doi.org/10.1016/j.clinph.2013.01.024. [JC]

Kuhl B. A. & Chun M. M. (2014) Successful remembering elicits event-specific activity patterns in lateral parietal cortex. *Journal of Neuroscience* **34**(23):8051–60. doi: 10.1523/JNEUROSCI.4328-13.2014. [rCB, RT]

Kukushkin N. V. & Carew T. J. (2017) Memory takes time. *Neuron* **95**(2):259–79. Available at: https://doi.org/10.1016/j.neuron.2017.05.029. [JC]

Kumaran D. & Maguire E. A. (2006) An unexpected sequence of events: Mismatch detection in the human hippocampus. *PLOS Biology* **4**(12):e424. Available at: https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.0040424. [TS]

Kumaran D. & Maguire E. A. (2007) Match–mismatch processes underlie human hippocampal responses to associative novelty. *Journal of Neuroscience* **27**(32):8517–24. [TS]

Kumaran D. & Maguire E. A. (2009) Novelty signals: A window into hippocampal information processing. *Trends in Cognitive Sciences* **13**(2):47–54. [TS]

Kurilla B. P. & Gonsalves B. D. (2012) An ERP investigation into the strategic regulation of the fluency heuristic during recognition memory. *Brain Research* **1442**:36–46. doi: 10.1016/j.brainres.2011.12.060. [aCB]

Kurilla B. P. & Westerman D. L. (2008) Processing fluency affects subjective claims of recollection. *Memory & Cognition* **36**(1):82–92. [arCB]

Kurilla B. P. & Westerman D. L. (2010) Source memory for unidentified stimuli. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **36**(2):398–410. doi: 10.1037/a0018279. [aCB]

Lacot E., Vautier S., Kohler S., Pariente J., Martin C. B., Puel M., Lotterie J. A. & Barbeau E. J. (2017) Familiarity and recollection vs representational models of medial temporal lobe structures: A single-case study. *Neuropsychologia* **104**:76–91. doi: 10.1016/j.neuropsychologia.2017.07.032. [aCB]

Laham S. M., Alter A. L. & Goodwin G. P. (2009) Easy on the mind, easy on the wrongdoer: Discrepantly fluent violations are deemed less morally wrong. *Cognition* **112**(3):462–66. Available at: https://doi.org/10.1016/j.cognition.2009.06.001. [TS]

Langdon R., Connaughton E. & Coltheart M. (2014) The Fregoli Delusion: A Disorder of Person Identification and Tracking. *Topics In Cognitive Science* **6**(4):615–31. doi: 10.1111/tops.12108. [JP]

Lanska M., Olds J. M. & Westerman D. L. (2014) Fluency effects in recognition memory: Are perceptual fluency and conceptual fluency interchangeable. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **40**(1):1–11. doi: 10.1037/a0034309. [aCB]

LaRocque K. F., Smith M. E., Carr V. A., Witthoft N., Grill-Spector K. & Wagner A. D. (2013) Global similarity and pattern separation in the human medial temporal lobe predict subsequent memory. *Journal of Neuroscience* **33**(13):5466–74. doi: 10.1523/JNEUROSCI.4293-12.2013. [aCB, HY]

Lavenex P. & Amaral D. G. (2000) Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus* **10**:420–30. [aCB]

Lavenex P., Suzuki W. A. & Amaral D. G. (2002) Perirhinal and parahippocampal cortices of the macaque monkey: Projections to the neocortex. *Journal of Comparative Neurology* **447**(4):394–420. doi: 10.1002/cne.10243. [aCB]

Leal S. L. & Yassa M. A. (2018) Integrating new findings and examining clinical applications of pattern separation. *Nature Neuroscience* **21**(2):163–73. doi: 10.1038/s41593-017-0065-1. [aCB]

Leboe-McGowan J. P. (2019) Constructions on an unwelcome exit: Bruce W. A. Whittlesea, 1950–2018. *Canadian Journal of Experimental Psychology* **73**:64–68. [GEB]

Lee A. C., Yeung L. K. & Barense M. D. (2012) The hippocampus and visual perception. *Frontiers in Human Neuroscience* **6**: article 91. doi: 10.3389/fnhum.2012.00091. [aCB]

Leech R., Kamourieh S., Beckmann C. F. & Sharp D. J. (2011) Fractionating the default mode network: Distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *Journal of Neuroscience* **31**(9):3217–24. doi: 10.1523/JNEUROSCI.5626-10.2011. [aCB]

Leech R. & Sharp D. J. (2014) The role of the posterior cingulate cortex in cognition and disease. *Brain* **137**:12–32. doi: 10.1093/brain/awt162. [aCB]

Lepage M., Ghaffar O., Nyberg L. & Tulving E. (2000) Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences USA* **97**(1):506–11. [aCB, AS]

Lerner Y., Honey C. J., Silbert L. J. & Hasson U. (2011) Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *The Journal of Neuroscience* **31**(8):2906–15. [VS]

Lev-Ari S. & Keysar B. (2010) Why don't we believe non-native speakers? The influence of accent on credibility. *Journal of Experimental Social Psychology* **46**(6):1093–96. [TS]

Levy D. A. (2012) Towards an understanding of parietal mnemonic processes: Some conceptual guideposts. *Frontiers in Integrative Neuroscience* **6**: article no. 41. Available at: http://doi.org/10.3389/fnint.2012.00041. Also available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3389369/. [RT]

Levy D. A., Stark C. E. L. & Squire L. R. (2004) Intact conceptual priming in the absence of declarative memory. *Psychological Science* **15**(10):680–86. doi: 10.1111/j.0956-7976.2004.00740.x. [arCB]

Li B., Taylor J. R., Wang W., Gao C. & Guo C. (2017) Electrophysiological signals associated with fluency of different levels of processing reveal multiple contributions to recognition memory. *Consciousness and Cognition* **53**:1–13. doi: 10.1016/j.concog.2017.05.001. [aCB, CFI]

Libby L. A., Ekstrom A. D., Ragland J. D. & Ranganath C. (2012) Differential connectivity of perirhinal and parahippocampal cortices within human hippocampal subregions revealed by high-resolution functional imaging. *Journal of Neuroscience* **32**(19):6550–60. doi: 10.1523/JNEUROSCI.3711-11.2012. [aCB]

Lithfous S., Dufour A. & Despres O. (2013) Spatial navigation in normal aging and the prodromal stage of Alzheimer's disease: Insights from imaging and behavioral studies. *Ageing Research Review* **12**(1):201–13. doi:10.1016/j.arr.2012.04.007. [GR]

Liuzzi A. G., Bruffaerts R., Dupont P., Adamczuk K., Peeters R., De Deyne S., Storms G. & Vandenberghe R. (2015) Left perirhinal cortex codes for similarity in meaning between written words: Comparison with auditory word input. *Neuropsychologia* **76**:4–16. doi: 10.1016/j.neuropsychologia.2015.03.016. [aCB]

Loftus E. F. (2005) Planting misinformation in the human mind: A 30-year investigation of the malleability of memory. *Learning and Memory* **12**(4):361–66. [JFK]

Loftus E. F. (2018) Eyewitness science and the legal system. *Annual Review of law and Social Science* **14**:1–10. [GEB]

Loftus E. F., Miller D. G. & Burns H. J. (1978) Semantic integration of verbal information into a visual memory. *Journal of Experimental Psychology: Human Learning and Memory* **4**:19–31. [GEB]

Loftus E. F. & Palmer J. C. (1974) Reconstruction of automobile destruction: An example of the interaction between language and memory. *Journal of Verbal Learning and Verbal Behavior* **13**:585–89. [JFK]

Lucas H. D. & Paller K. A. (2013) Manipulating letter fluency for words alters electrophysiological correlates of recognition memory. *NeuroImage* **83**:849–61. doi: 10.1016/j.neuroimage.2013.07.039. [aCB]

Maass A., Berron D., Libby L. A., Ranganath C. & Düzel E. (2015) Functional subregions of the human entorhinal cortex. *eLife* **4**:e06426. doi: 10.7554/eLife.06426. [aCB]

MacPherson S. E., Bozzali M., Cipolotti L., Dolan R. J., Rees J. H. & Shallice T. (2008) Effect of frontal lobe lesions on the recollection and familiarity components of recognition memory. *Neuropsychologia* **46**(13):3124–32. doi: 10.1016/j.neuropsychologia.2008.07.003. [aCB]

Maddock R. J. & Buonocore M. H. (1997) Activation of left posterior cingulate gyrus by the auditory presentation of threat-related words: An fMRI study. *Psychiatry Research: Neuroimaging* **75**(1):1–14. doi:10.1016/S0925-4927(97)00018-8. [BCN]

Madore K. P., Thakral P. P., Beaty R. E., Addis D. R. & Schacter D. L. (2019) Neural mechanisms of episodic retrieval support divergent creative thinking. *Cerebral Cortex* **29**(1):150–66. doi: 10.1093/cercor/bhx312. [aCB]

Mahr J. B. & Csibra G. (2018) Why do we remember? The communicative function of episodic memory. *Behavioral and Brain Sciences* **41**:e1. (Online publication). doi: 10.1017/S0140525X17000012. [aCB]

Mandler G. (1980) Recognizing: The judgement of previous occurence. *Psychological Review* **87**(3):252–71. [aCB, JFK]

Mandler G., Pearlstone Z. & Koopmans H. S. (1969) Effects of organization and semantic similarity on recall and recognition. *Journal of Verbal Learning and Verbal Behavior* **8**(3):410–23. [aCB]

Margulies D. S., Vincent J. L., Kelly C., Lohmann G., Uddin L. Q., Biswal B. B., Villringer A., Castellanos F. X., Milham M. P. & Petrides M. (2009) Precuneus shares intrinsic functional architecture in humans and monkeys. *Proceedings of the National Academy of Sciences USA* **106**(47):20069–74. doi: 10.1073/pnas.0905314106. [aCB]

Markowitsch H. J. (1999) Limbic system. In: *The MIT encyclopedia of the cognitive sciences*, ed. R. Wilson & F. Keil, pp. 472–75. MIT Press. [AS]

Markowitsch H. J., Calabrese P., Würker M., Durwen H. F., Kessler J., Babinsky R., Brechtelsbauer D., Heuser L. & Gehlen W. (1994) The amygdala's contribution to memory – A PET-study on two patients with Urbach-Wiethe disease. *NeuroReport* **5**:1349–52. [AS]

Markowitsch H. J. & Staniloiu A. (2011) Amygdala in action: Relaying biological and social significance to autobiographical memory. *Neuropsychologia* **49**(4):718–33. doi: 10.1016/j.neuropsychologia.2010.10.007. [rCB, AS]

Markowitsch H. J. & Staniloiu A. (2012a) Amnesic disorders. *Lancet* **380**:1429–40. [AS]

Markowitsch H. J. & Staniloiu A. (2012b) The contribution of the amygdala for establishing and maintaining an autonomous self and autobiographical memory. In: *Insights into the amygdala: Structure, function and implications for disorders*, ed. D. Yilmazer-Hanke, pp. 277–318. Nova Science. [AS]

Markowitsch H. J., Thiel A., Reinkemeier M., Kessler J., Koyuncu A. & Heiss W.-D. (2000) Right amygdalar and temporofrontal activation during autobiographic, but not during fictitious memory retrieval. *Behavioural Neurology* **12**:181–90. [AS]

Markowitsch H. J., Vandekerckhove M. M. P., Lanfermann H. & Russ M. O. (2003) Engagement of lateral and medial prefrontal areas in the ecphory of sad and happy autobiographical memories. *Cortex* **39**:643–65. [AS]

Marsolek C. J. & Burgund E. D. (2005) Initial storage of unfamiliar objects: Examining memory stores with signal detection analyses. *Acta Psychologica (Amsterdam)* **119** (1):81–106. doi: 10.1016/j.actpsy.2004.11.001. [rCB]

Martin C. B., Cowell R. A., Gribble P. L., Wright J. & Kohler S. (2016) Distributed category-specific recognition-memory signals in human perirhinal cortex. *Hippocampus* **26**(4):423–36. doi: 10.1002/hipo.22531. [aCB]

Martin C. B., Douglas D., Newsome R. N., Man L. L. & Barense M. D. (2018) Integrative and distinctive coding of visual and conceptual object features in the ventral visual stream. *eLife* **7**. Available at: https://elifesciences.org/articles/31873. doi: 10.7554/eLife.31873. [aCB]

Martin C. B., McLean D. A., O'Neil E. B. & Kohler S. (2013) Distinct familiarity-based response patterns for faces and buildings in perirhinal and parahippocampal cortex. *Journal of Neuroscience* **33**(26):10915–23. doi: 10.1523/JNEUROSCI.0126-13.2013. [aCB]

Masson M. E. J. & Caldwell J. I. (1998) Conceptually-driven encoding episodes create perceptual misattributions. *Acta Psychologica* **98**:183–210. [rCB]

Mayes A., Montaldi D. & Migo E. (2007) Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences* **11**(3):126–35. doi: 10.1016/j.tics.2006.12.003. [aCB]

McCabe D. P. & Balota D. A. (2007) Context effects on remembering and knowing: The expectancy heuristic. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **33**(3):536–49. doi: 10.1037/0278-7393.33.3.536. [arCB]

McCabe D. P. & Geraci L. (2009) The role of extralist associations in false remembering: A source misattribution account. *Memory & Cognition* **37**(2):130–42. doi: 10.3758/mc.37.2.130. [rCB]

McGaugh J. L. (2015) Consolidating memories. *Annual Reviews of Psychology* **66**:1–24. [AS]

McNally R. J. (2003) *Remembering trauma*. Harvard University Press. [JFK]

Meyer P., Mecklinger A. & Friederici A. D. (2010) On the processing of semantic aspects of experience in the anterior medial temporal lobe: An event-related fMRI study. *Journal of Cognitive Neuroscience* **22**(3):590–601. doi: 10.1162/jocn.2009.21199. [aCB]

Millar P. R., Balota D. A., Bishara A. J. & Jacoby L. L. (2018) Multinomial models reveal deficits of two distinct controlled retrieval processes in aging and very mild Alzheimer disease. *Memory & Cognition* **46**(7):1058–75. doi: 10.3758/s13421-018-0821-9. [CMK, rCB]

Miller J. K., Lloyd M. E. & Westerman D. L. (2008) When does modality matter? Perceptual versus conceptual fluency-based illusions in recognition memory. *Journal of Memory and Language* **58**(4):1080–94. Available at: http://dx.doi.org/10.1016/j.jml.2007.12.006. [aCB]

Mishkin M., Ungerleider L. G. & Macko K. A. (1983) Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences* **6**:414–17. Available at: https://doi.org/10.1016/0166-2236(83)90190-X. [OH]

Mitchell A. S., Czajkowski R., Zhang N., Jeffery K. & Nelson A. J. D. (2018) Retrosplenial cortex and its role in spatial cognition. *Brain and Neuroscience Advances* **2**: e2398212818757098. doi: 10.1177/2398212818757098. [rCB]

Mitchell K. J. & Hill E. M. (2019) The impact of focusing on different features during encoding on young and older adults' source memory. *Open Psychology* **1**(1):106–18. doi: 10.1515/psych-2018-0008. [rCB]

Montaldi D. & Mayes A. R. (2010) The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. *Hippocampus* **20**(11):1291–314. [arCB]

Montefinese M., Zannino G. D. & Ambrosini E. (2015) Semantic similarity between old and new items produces false alarms in recognition memory. *Psychological Research* **79**(5):785–94. Available at: https://doi.org/10.1007/s00426-014-0615-z. [HY]

Mormann F., Kornblith S., Quiroga R. Q., Kraskov A., Cerf M., Fried I. & Koch C. (2008) Latency and Selectivity of Single Neurons Indicate Hierarchical Processing in the Human medial temporal Lobe. *Journal of Neuroscience* **28**(36):8865–72. Available at: https://doi.org/10.1523/JNEUROSCI.1640-08.2008. [JC]

Moscovitch M., Nadel L., Winocur G., Gilboa A. & Rosenbaum R. S. (2006) The cognitive neuroscience of remote episodic, semantic and spatial memory. *Current Opinion in Neurobiology* **16**(2):179–90. Available at: https://doi.org/10.1016/j.conb.2006.03.013. [CS-B]

Moulin C. J. A., James N., Perfect T. J. & Jones R. W. (2003) Knowing what you cannot recognise: Further evidence for intact metacognition in Alzheimer's disease. *Aging, Neuropsychology, and Cognition* **10**(1):74–82. doi:10.1076/anec.10.1.74.13456. [BCN]

Mutlu J., Landeau B., Tomadesso C., de Flores R., Mezenge F., de La Sayette V., Eustache F. & Chételat G. (2016) Connectivity disruption, atrophy, and hypometabolism within posterior cingulate networks in Alzheimer's disease. *Frontiers in Neuroscience* **10**: article 582. doi: 10.3389/fnins.2016.00582. [aCB]

Nadel L., Samsonovich A., Ryan L. & Moscovitch M. (2000) Multiple trace theory of human memory: Computational, neuroimaging, and neuropsychological results. *Hippocampus* **10**(4):352–68. doi:10.1002/1098-1063(2000)10:4. [GR]

Neher T., Azizi A. H. & Cheng S. (2017) From grid cells to place cells with realistic field sizes. *PLoS One* **12**(7):e0181618. Available at: https://doi.org/10.1371/journal.pone.0181618. [OH]

Nestor P. J., Fryer T. D., Ikeda M. & Hodges J. R. (2003) Retrosplenial cortex (BA 29/30) hypometabolism in mild cognitive impairment (prodromal Alzheimer's disease). *European Journal of Neuroscience* **18**(9):2663–67. [aCB]

Newell B. R. & Dunn J. C. (2008) Dimensions in data: Testing psychological models using state-trace analysis. *Trends in Cognitive Sciences* **12**(8):285–90. [AFO]

Newsome R. N., Trelle A. N., Fidalgo C., Hong B., Smith V. M., Jacob A., Ryan J. D., Rosenbaum R. S., Cowell R. A. & Barense M. D. (2018) Dissociable contributions of thalamic nuclei to recognition memory: Novel evidence from a case of medial dorsal thalamic damage. *Learning and Memory* **25**(1):31–44. doi: 10.1101/lm.045484.117. [aCB]

Nigro G. & Neisser U. (1983) Point of view in personal memories. *Cognitive Psychology* **15**(4):467–82. Available at: http://dx.doi.org/10.1016/0010-0285(83)90016-6. [DK, NA]

Norman K. A. (2010) How hippocampus and cortex contribute to recognition memory: Revisiting the complementary learning systems model. *Hippocampus* **20**(11):1217–27. doi: 10.1002/hipo.20855. [HY, rCB]

Norman K. A. & O'Reilly R. C. (2003) Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review* **110**(4):611–46. Available at: https://doi.org/10.1037/0033-295X.110.4.611. [aCB, HY, OH]

Northoff G., Heinzel A., de Greck M., Bermpohl F., Dobrowolny H. & Panksepp J. (2006) Self-referential processing in our brain: A meta-analysis of imaing studies on the self. *NeuroImage* **31**:440–57. [aCB]

O'Keefe J. & Dostrovsky J. (1971) The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. *Brain research* **34**:171–75. doi:10.1016/0006-8993(71)90358-1. [GR]

O'Keefe J. & Nadel L. (1978) *The hippocampus as a cognitive map*. Clarendon Press. [GR]

Olds J. M. & Westerman D. L. (2012) Can fluency be interpreted as novelty? Retraining the interpretation of fluency in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **38**(3):653–64. doi: 10.1037/a0026784. [aCB]

Oppenheimer D. M. (2008) The secret life of fluency. *Trends in Cognitive Sciences* **12** (6):237–41. doi: 10.1016/j.tics.2008.02.014. [arCB, CFI]

Osth A. F., Bora B., Dennis S. & Heathcote A. (2017) Diffusion vs. linear ballistic accumulation: Different models, different conclusions about the slope of the zROC in recognition memory. *Journal of Memory and Language* **96**:36–61. [AFO]

Osth A. F., Jansson A., Dennis S. & Heathcote A. (2018) Modeling the dynamics of recognition memory testing with an integrated model of retrieval and decision making. *Cognitive Psychology* **104**:106–42. [AFO]

Oyebode F. & Sargeant R. (1996) Delusional misidentification syndromes: A descriptive study. *Psychopathology* **29**(4):209–14. doi: 10.1159/000284994. [JP]

Ozubko J. D. & Yonelinas A. P. (2014) The disruptive effects of processing fluency on familiarity-based recognition in amnesia. *Neuropsychologia* **54**:59–67. doi: 10.1016/j.neuropsychologia.2013.12.008. [arCB, W-CW]

Pacheco D., Sánchez-Fibla M., Duff A., Principe A., Rocamora R., Zhang H., Axmacher N. & Verschure P. F. M. J. (2019) Coordinated representational reinstatement in the human hippocampus and lateral temporal cortex during episodic memory retrieval. *Nature Communications* **10**: article no. 2255. doi: 10.1038/s41467-019-09569-0. [NA]

Pai M. C. & Yang Y. C. (2013) Impaired translation of spatial representation in young onset Alzheimer's disease patients. *Current Alzheimer Research* **10**(1):95–103. [rCB]

Pandis C. & Poole N. (2017) 15 Capgras delusion: A meta-analysis of case reports in the English language. *Journal of Neurology, Neurosurgery and Psychiatry* **88**(8):A18.2–A19. doi: 10.1136/jnnp-2017-bnpa.39. [JP]

Pannu J. K. & Kaszniak A. W. (2005) Metamemory experiments in neurological populations: A review. *Neuropsychology Review* **15**(3):105–30. [aCB]

Parks C. M. & Yonelinas A. P. (2007) Moving beyond pure signal-detection models: Comment on Wixted (2007) *Psychological Review* **114**(1):188–202. [aCB]

Parks C. M. & Yonelinas A. P. (2015) The importance of unitization for familiarity-based learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **41**(3):881–903. doi: 10.1037/xlm0000068. [aCB]

Parvizi J., Van Hoesen G. W., Buckwalter J. & Damasio A. (2006) Neural connections of the posteromedial cortex in the macaque. *Proceedings of the National Academy of Sciences USA* **103**(5):1563–68. doi: 10.1073/pnas.0507729103. [aCB]

Paynter C. A., Reder L. M. & Kieffaber P. D. (2009) Knowing we know before we know: ERP correlates of initial feeling-of-knowing. *Neuropsychologia* **47**(3):796–803. Available at: https://doi.org/10.1016/j.neuropsychologia.2008.12.009. [TS]

Pazzaglia A. M., Dube C. & Rotello C. M. (2013) A critical comparison of discrete-state and continuous models of recognition memory: Implications for recognition and beyond. *Psychological Bulletin* **139**(6):1173–203. [AFO]

Pengas G., Hodges J. R., Watson P. & Nestor P. J. (2010) Focal posterior cingulate atrophy in incipient Alzheimer's disease. *Neurobiology of Aging* **31**(1):25–33. doi: 10.1016/j.neurobiolaging.2008.03.014. [aCB]

Pergola G., Danet L., Pitel A. L., Carlesimo G. A., Segobin S., Pariente J., Suchan B., Mitchell A. S. & Barbeau E. J. (2018) The regulatory role of the human mediodorsal thalamus. *Trends in Cognitive Sciences* **22**(11):1011–25. doi: 10.1016/j.tics.2018.08.006. [aCB]

Pessoa L. (2008) On the relationship between emotion and cognition. *Nature Reviews Neuroscience* **9**:148–58. [AS]

Petersen R. C., Parisi J. E., Dickson D. W., Johnson K. A., Knopman D. S., Boeve B. F., Jicha G. A., Ivnik R. J., Smith G. E., Tangalos E. G., Braak H. & Kokmen E. (2006) Neuropathologic features of amnestic mild cognitive impairment. *Archives of Neurology* **63**(5):665–72. doi: 10.1001/archneur.63.5.665. [aCB]

Piirainen S., Youssef A., Song C., Kalueff A. V., Landreth G. E., Malm T. & Tian L. (2017) Psychosocial stress on neuroinflammation and cognitive dysfunctions in Alzheimer's disease: The emerging role for microglia? *Neuroscience & Biobehavioral Reviews* **77**:148–64. doi:10.1016/j.neubiorev.2017.01.046. [BCN]

Piolino P., Desgranges B., Belliard S., Matuszewski V., Lalevée C., De La Sayette V. & Eustache F. (2003) Autobiographical memory and autonoetic consciousness: Triple dissociation in neurodegenerative diseases. *Brain* **126**(10):2203–19. [CS-B]

Piolino P., Desgranges B. & Eustache F. (2009) Episodic autobiographical memories over the course of time: Cognitive, neuropsychological and neuroimaging findings. *Neuropsychologia* **47**:2314–29. [AS]

Pooley J. P., Lee M. D. & Shankle W. R. (2011) Understanding memory impairment with memory models and hierarchical Bayesian analysis. *Journal of Mathematical Psychology* **55**:47–56. [AFO]

Preston A. R., Bornstein A. M., Hutchinson J. B., Gaare M. E., Glover G. H. & Wagner A. D. (2010) High-resolution fMRI of content-sensitive subsequent memory responses in human medial temporal lobe. *Journal of Cognitive Neuroscience* **22**(1):156–73. doi: 10.1162/jocn.2009.21195. [arCB]

Price A. R., Bonner M. F., Peelle J. E. & Grossman M. (2017) Neural coding of fine-grained object knowledge in perirhinal cortex. *bioRxiv*. Available at: https://www.biorxiv.org/content/10.1101/194829v1.abstract. (Online preprint publication). doi: 10.1101/194829. [aCB]

Qin S., van Marle H. J., Hermans E. J. & Fernandez G. (2011) Subjective sense of memory strength and the objective amount of information accurately remembered are related to distinct neural correlates at encoding. *Journal of Neuroscience* **31**(24):8920–27. doi: 10.1523/JNEUROSCI.2587-10.2011. [rCB, RT]

Rajaram S. (1993) Remembering and knowing: Two means of access to the personal past. *Memory & Cognition* **21**(1):89–102. DOI: 10.3758/BF03211168. [CFI]

Ramakers I. H. G. B., Verhey F. R. J., Scheltens P., Hampel H., Soininen H., Aalten P., Rikkert M. O., Verbeek M. M., Spiru L., Blennow K., Trojanowski J. Q., Shaw L. M. & Visser P. J. (2012) Anxiety is related to Alzheimer cerebrospinal fluid markers in subjects with mild cognitive impairment. *Psychological Medicine* **43**(5):911–20. doi:10.1017/S0033291712001870. [BCN]

Ramanan S., Piguet O. & Irish M. (2018) Rethinking the role of the angular gyrus in remembering the past and imagining the future: The contextual integration model. *The Neuroscientist* **24**(4):342–52. doi:10.1177/1073858417735514. [CS-B]

Ranganath C. (2010) A unified framework for the functional organization of the medial temporal lobes and the phenomenology of episodic memory. *Hippocampus* **20** (11):1263–90. doi: 10.1002/hipo.20852. [aCB]

Ranganath C. & Hsieh L. T. (2016) The hippocampus: A special place for time. *Annals of the New York Academy of Sciences* **1369**(1):93–110. Available at: https://doi.org/10.1111/nyas.13043. [JC]

Ranganath C. & Ritchey M. (2012) Two cortical systems for memory-guided behaviour. *Nature Reviews: Neuroscience* **13**:1–15. [arCB, JFK]

Ranganath C., Yonelinas A. P., Cohen M. X., Dy C. J., Tom S. M. & D'Esposito M. (2004) Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia* **42**(1):2–13. [aCB]

Ratcliff R. (1978) A theory of memory retrieval. *Psychological Review* **85**(2):59–108. Available at: https://doi.org/10.1037/0033-295X.85.2.59. [AFO, HY]

Ratcliff R. & McKoon G. (1995) Bias in the priming of object decisions. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **21**(3):754–67. [rCB]

Ratcliff R., Sederberg P. B., Smith T. A. & Childers R. (2016a) A single trial analysis of EEG in recognition memory: Tracking the neural correlates of memory strength. *Neuropsychologia* **93**:128–41. [AFO]

Ratcliff R., Smith P. L., Brown S. D. & McKoon G. (2016b) Diffusion decision model: Current issues and history. *Trends in Cognitive Sciences* **20**(4):260–81. Available at: https://doi.org/10.1016/j.tics.2016.01.007. [rCB, HY]

Ratcliff R., Thapar A. & McKoon G. (2004) A diffusion model analysis of the effects of aging on recognition memory. *Journal of Memory and Language* **50**:408–24. [AFO]

Raz N., Lindenberger U., Rodrigue K. M., Kennedy K. M., Head D., Williamson A., Dahle C., Gerstorf D. & Acker J. D. (2005) Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex* **15** (11):1676–89. Available at: https://doi.org/10.1093/cercor/bhi044. [OH]

Reber P. J. (2013) The neural basis of implicit learning and memory: A review of neuropsychological and neuroimaging research. *Neuropsychologia* **51**(10):2026–42. doi: 10.1016/j.neuropsychologia.2013.06.019. [arCB]

Reber R., Schwarz N. & Winkielman P. (2004a) Processing fluency and aesthetic pleasure: Is beauty in the perceiver's processing experience? *Personality and Social Psychology Review* **8**(4):364–82. doi: 10.1207/s15327957pspr0804_3. [aCB]

Reber R., Wurtz P. & Zimmermann T. D. (2004b) Exploring "fringe" consciousness: The subjective experience of perceptual fluency and its objective bases. *Consciousness and Cognition* **13**(1):47–60. doi: 10.1016/s1053-8100(03)00049-7. [rCB]

Reder L. M. & Ritter F. E. (1992) What determines initial feeling of knowing? Familiarity with question terms, not with the answer. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **18**(3):435–51. Available at: http://dx.doi.org/10.1037/0278-7393.18.3.435. [TS]

Reitz C. (2016) Toward precision medicine in Alzheimer's disease. *Annals of Translational Medicine* **4**(6):107. doi:10.21037/atm.2016.03.05. [BCN]

Renoult L., Davidson P. S., Palombo D. J., Moscovitch M. & Levine B. (2012) Personal semantics: At the crossroads of semantic and episodic memory. *Trends in Cognitive Sciences* **16**(11):550–58. [NA]

Rice H. J. & Rubin D. C. (2011) Remembering from any angle: The flexibility of visual perspective during retrieval. *Consciousness and Cognition* **20**(3):568–77. doi: 10.1016/j.concog.2010.10.013. [DK]

Richter F. R., Cooper R. A., Bays P. M. & Simons J. S. (2016) Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. *eLife* **5**:e18260. Available at: http://doi.org/10.7554/eLife.18260. Also available at: https://elifesciences.org/articles/18260. [rCB, RT]

Rissman J. & Wagner A. D. (2012) Distributed representations in memory: Insights from functional brain imaging. *Annual Review of Psychology* **63**:101–28. doi: 10.1146/annurev-psych-120710-100344. [aCB]

Ritchey M., Libby L. A. & Ranganath C. (2015) Cortico-hippocampal systems involved in memory and cognition: The PMAT framework. In: *Progress in brain research, vol. 219*, ed. S. O'Mara & M. Tsanov, pp. 45–64. Elsevier. [aCB]

Ritchey M., McCullough A. M., Ranganath C. & Yonelinas A. P. (2017) Stress as a mnemonic filter: Interactions between medial temporal lobe encoding processes and post-encoding stress. *Hippocampus* **27**(1):77–88. doi: 10.1002/hipo.22674. [rCB]

Ritchey M., Wang S. F., Yonelinas A. P. & Ranganath C. (2019) Dissociable medial temporal pathways for encoding emotional item and context information. *Neuropsychologia* **124**:66–78. doi: 10.1016/j.neuropsychologia.2018.12.015. [rCB]

Robin J. & Moscovitch M. (2017) Familiar real-world spatial cues provide memory benefits in older and younger adults. *Psychology of Aging* **32**(3):210–19. doi: 10.1037/pag0000162. [rCB]

Roediger H. L. (1996) Memory illusions. *Journal of Memory and Language* **35**:76–100. [JFK]

Roediger III H. L. & McDermott K. B. (1995) Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **21**:803–14. [GEB, JFK]

Rubin D. C. & Berntsen D. (2003) Life scripts help to maintain autobiographical memories of highly positive, but not highly negative, events. *Memory & Cognition* **31**:1–14. [AS]

Rudy J. W. (2009) Context representations, context functions, and the parahippocampal-hippocampal system. *Learning and Memory* **16**:573–85. [VS]

Rugg M. D. & Curran T. (2007) Event-related potentials and recognition memory. *Trends in Cognitive Sciences* **11**:251–57. [AFO]

Rugg M. D., Fletcher P. C., Chua P. M. L. & Dolan R. J. (1999) The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage* **10** (5):520–29. Available at: https://doi.org/10.1006/nimg.1999.0488. [CS-B]

Rugg M. D. & King D. R. (2018) Ventral lateral parietal cortex and episodic memory retrieval. *Cortex* **107**:238–50. doi: 10.1016/j.cortex.2017.07.012. [rCB, RT]

Rugg M. D. & Vilberg K. L. (2013) Brain networks underlying episodic memory retrieval. *Current Opinion in Neurobiology* **23**(2):255–60. doi:10.1016/j.conb.2012.11.005. [aCB, CS-B]

Ruggiero G., Iavarone A. & Iachini T. (2018) Allocentric to egocentric spatial switching: Impairment in aMCI and Alzheimer's Disease patients? *Current Alzheimer Research* **15**(3):229–36. doi: 10.2174/1567205014666171030114821. [rCB]

Russell-Williams J., Jaroudi W., Perich T., Hoscheidt S., El Haj M. & Moustafa Ahmed A. (2018) Mindfulness and meditation: Treating cognitive impairment and reducing stress in dementia. *Reviews in the Neurosciences* **29**(7):791–804. [BCN]

Ryu S.-Y., Kwon M. J., Lee S.-B., Yang D. W., Kim T.-W., Song I. U., Yang P. S., Kim H.-J. & Lee A. Y. (2010) Measurement of the precuneus and hippocampal volumes using magnetic resonance volumetry in Alzheimer's disease. *Journal of Clinical Neurology* **6** (4):196–203. doi: 10.3988.jcn.2010.6.4.196. [rCB]

Saksida L. M. & Bussey T. J. (2010) The representational-hierarchical view of amnesia: Translation from animal to human. *Neuropsychologia* **48**(8):2370–84. doi: 10.1016/j.neuropsychologia.2010.02.026. [aCB]

Salat D. H., Kaye J. A. & Janowsky J. S. (2001) Selective preservation and degeneration within the prefrontal cortex in aging and Alzheimer disease. *Archives of Neurology* **58**(9):1403–408. [aCB]

Salmon E., Lekeu F., Garraux G., Guillaume B., Magis D., Luxen A., Moonen G. & Collette F. (2008) Metabolic correlates of clinical heterogeneity in questionable Alzheimer's disease. *Neurobiology of Aging* **29**:1823–29. [aCB]

Salvatore P., Bhuvaneswar C., Tohen M., Khalsa H., Maggini C. & Baldessarini R. (2014) Capgras' syndrome in first-episode psychotic disorders. *Psychopathology* **47**(4):261–69. doi: 10.1159/000357813. [JP]

Sarter M. & Markowitsch H. J. (1985a) The amygdala's role in human mnemonic processing. *Cortex* **21**:7–24. [AS]

Sarter M. & Markowitsch H. J. (1985b) The involvement of the amygdala in learning and memory: A critical review with emphasis on anatomical relations. *Behavioral Neuroscience* **99**:342–80. [AS]

Scahill R. I., Schott J. M., Stevens J. M., Rossor M. N. & Fox N. C. (2002) Mapping the evolution of regional atrophy in Alzheimer's disease: Unbiaised analysis of fluid-registered serial MRI. *Proceedings of the National Academy of Sciences USA* **99** (7):4703–707. [aCB]

Schacter D. L. (1997) False recognition and the brain. *Current Directions in Psychological Science* **6**(3):65–70. [aCB]

Schauer M., Neuner F. & Elbert T. (2011) *Narrative exposure therapy. A short-term intervention for traumatic stress disorders after war, terror or torture*, 2nd, expanded edition. Hogrefe & Huber Publishers. [NA]

Schoemaker D., Gauthier S. & Pruessner J. C. (2014) Recollection and familiarity in aging individuals with mild cognitive impairment and Alzheimer's disease: A literature review. *Neuropsychology Review* **24**(3):313–31. doi: 10.1007/s11065-014-9265-6. [aCB]

Schultz H., Sommer T. & Peters J. (2012) Direct evidence for domain-sensitive functional subregions in human entorhinal cortex. *Journal of Neuroscience* **32**(14):4716–23. doi: 10.1523/jneurosci.5126-11.2012. [aCB]

Schurgin M. W. & Flombaum J. I. (2018) Visual working memory is more tolerant than visual long-term memory. *Journal of Experimental Psychology: Human Perception and Performance*, **44**(8):1216–27. [TFB]

Schwarz A. J., Yu P., Miller B. B., Shcherbinin S., Dickson J., Navitsky M., Joshi A. D., Devous M. D. & Mintun M. S. (2016) Regional profiles of the candidate tau PET ligand 18F-AV-1451 recapitulate key features of Braak histopathological stages. *Brain* **139**(Pt 5):1539–50. doi: 10.1093/brain/aww023. [aCB]

Schwarz N. (2004) Metacognitive experiences in consumer judgment and decision making. *Journal of Consumer Psychology* **14**(4):332–48. Available at: https://doi.org/10.1207/s15327663jcp1404_2. [aCB]

Schwarz N. & Winkielman P. (2004) Processing fluency and aesthetic pleasure: Is beauty in the perceiver's processing experience? *Personality and Social Psychology Review* **8** (4):364–82. DOI: 10.1207/s15327957pspr0804_3. [CFI]

Scoboria A., Wade K. A., Lindsay D. S., Azad T., Strange D., Ost J. & Hyman I. E. (2017) A mega-analysis of memory reports from eight peer reviewed false memory implantation studies. *Memory* **25**:146–63. [GEB]

Scoville W. B. & Milner B. (1957) Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery and Psychiatry* **20**(1):11–21. [aCB]

Segobin S., Laniepce A., Ritz L., Lannuzel C., Boudehent C., Cabe N., Urso L., Vabret F., Eustache F., Beaunieux H. & Pitel A. L. (2019) Dissociating thalamic alterations in alcohol use disorder defines specificity of Korsakoff syndrome. *Brain* **142** (5):1458–70. doi.org/10.1093/brain/awz056. [JPA]

Serino S., Morganti F., Di Stefano F. & Riva G. (2015) Detecting early egocentric and allocentric impairments deficits in Alzheimer's disease: An experimental study with virtual reality. *Frontiers in Aging Neuroscience* **7**: article 88. (Online publication). doi: 10.3389/fnagi.2015.00088. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4438252/ [rCB, GR]

Serino S., Pedroli E., Tuena C., De Leo G., Stramba-Badiale M., Goulene K., Mariotti N. G. & Riva G. (2017) A novel Virtual Reality-based training protocol for the enhancement of the "mental frame syncing" in individuals with Alzheimer's Disease: A development-of-concept trial. *Frontiers in Aging Neuroscience* **9**: article no. 240. doi:10.3389/fnagi.2017.00240. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5529401/. [GR]

Serino S. & Riva G. (2013) Getting lost in Alzheimer's disease: A break in the mental frame syncing. *Medical Hypotheses* **80**(4):416–21. doi:10.1016/j.mehy.2012.12.031. [GR]

Serino S. & Riva G. (2017) The proactive self in space: How egocentric and allocentric spatial impairments contribute to anosognosia in Alzheimer's disease. *Journal of Alzheimer's disease: JAD* **55**(3):881–92. doi:10.3233/JAD-160676. [GR]

Sestieri C., Shulman G. L. & Corbetta M. (2017) The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews: Neuroscience* **18**(3):183–92. Available at: http://doi.org/10.1038/nrn.2017.6. [RT]

Shadlen M. N. & Newsome W. T. (2001) Neural Basis of a Perceptual Decision in the Parietal Cortex (Area LIP) of the Rhesus Monkey. *Journal of Neurophysiology* **86** (4):1916–36. Available at: https://doi.org/10.1152/jn.2001.86.4.1916. [HY]

Shimamura A. P. (2011) Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective and Behavioral Neuroscience* **11**(3):277–91. Available at: http://doi.org/10.3758/s13415-011-0031-4. [RT]

Siebert M., Markowitsch H. J. & Bartel P. (2003) Amygdala, affect, and cognition: Evidence from ten patients with Urbach-Wiethe disease. *Brain* **126**:2627–37. [AS]

Siegel M., Buschman T. J. & Miller E. K. (2015) Cortical information flow during flexible sensorimotor decisions. *Science* **348**(6241):1352–55. [VS]

Signer S. (1994) Localization and Lateralization in the Delusion of Substitution. *Psychopathology* **27**(3–5):168–76. doi: 10.1159/000284866. [JP]

Simmons-Stern N. R., Deason R. G., Brandler B. J., Frustace B. S., O'Connor M. K., Ally B. A. & Budson A. E. (2012) Music-based memory enhancement in Alzheimer's disease: Promise and limitations. *Neuropsychologia* **50**(14):3295–303. doi: 10.1016/j.neuropsychologia.2012.09.019. [rCB]

Simons J. S., Graham K. S. & Hodges J. R. (2002a) Perceptual and semantic contributions to episodic memory: Evidence from semantic dementia and Alzheimer's disease. *Journal of Memory and Language* **47**(2):197–213. Available at: https://doi.org/10.1016/S0749-596X(02)00003-7. [rCB, CS-B]

Simons J. S., Peers P. V., Mazuy Y. S., Berryhill M. E. & Olson I. R. (2010) Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex* **20**(2):479–85. Available at: http://doi.org/10.1093/cercor/bhp116. [rCB, RT]

Simons J. S., Verfaellie M., Galton C. J., Miller B. L., Hodges J. R. & Graham K. S. (2002b) Recollection-based memory in frontotemporal dementia: Implications for theories of long-term memory. *Brain* **125**(11):2523–36. [CS-B]

Smith S. M., Ward T. B., Tindell D. R., Sifonis C. M. & Wilkenfeld M. J. (2000) Category structure and created memories. *Memory & Cognition* **28**(3):386–95. [JFK]

Snitz B. E., Weissfeld L. A., Cohen A. D., Lopez O. L., Nebes R. D., Aizenstein H. J., McDade E., Price J. C., Mathis C. A. & Klunk W. E. (2015) Subjective cognitive complaints, personality and brain amyloid-beta in cognitively normal older adults. *The American Journal of Geriatric Psychiatry* **23**(9):985–93. Available at: https://doi.org/10.1016/j.jagp.2015.01.008. [BCN]

Sohal V. S. & Hasselmo M. E. (2000) A model for experience-dependent changes in the responses of inferotemporal neurons. *Network* **11**(3):169–90. [aCB]

Solstad T., Boccara C. N., Kropff E., Moser M. B. & Moser E. I. (2008) Representation of geometric borders in the entorhinal cortex. *Science* **322**(5909):1865–68. doi:10.1126/science.1166466. [GR]

Song H. & Schwarz N. (2008a) Fluency and the detection of misleading questions: Low processing fluency attenuates the Moses illusion. *Social Cognition* **26**(6):791–99. doi:10.1521/soco.2008.26.6.791. [TS]

Song H. & Schwarz N. (2008b) If it's hard to read, it's hard to do: Processing fluency affects effort prediction and motivation. *Psychological Science* **19**(10):986–88. doi:10.1111/j.1467-9280.2008.02189.x. [TS]

Song Z., Wixted J. T., Smith C. N. & Squire L. R. (2011) Different nonlinear functions in hippocampus and perirhinal cortex relating functional MRI activity to memory strength. *Proceedings of the National Academy of Sciences USA* **108**:5783–88. [AFO]

Squire L. R. & Dede A. J. (2015) Conscious and unconscious memory systems. *Cold Spring Harbor: Perspectives in Biology* **7**(3): article 021667. doi: 10.1101/cshperspect.a021667. Available at: https://cshperspectives.cshlp.org/. [rCB]

Squire L. R., Wixted J. T. & Clark R. E. (2007) Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews: Neuroscience* **8**(11):872–83. doi: 10.1038/nrn2154. [aCB, AFO]

Sreekumar V. (2015) Context in the wild: Environment, behavior, and the brain (Unpublished doctoral dissertation). Department of Psychology, The Ohio State University. [VS]

Stamenova V., Gao F., Black S. E., Schwartz M. L., Kovacevic N., Alexander M. P. & Levine B. (2017) The effect of focal cortical frontal and posterior lesions on recollection and familiarity in recognition memory. *Cortex* **91**:316–26. doi: 10.1016/j.cortex.2017.04.003. [aCB]

Staniloiu A. & Markowitsch H. J. (2014) Dissociative amnesia. *Lancet Psychiatry* **1**(3):226–41. doi: 10.1016/s2215-0366(14)70279-2. [AS, rCB]

Stanley M. L., Parikh N., Stewart G. W. & De Brigard F. (2017) Emotional intensity in episodic autobiographical memory and counterfactual thinking. *Consciousness and Cognition* **48**:283–91. [AS]

Staresina B. P., Cooper E. & Henson R. N. (2013) Reversible information flow across the medial temporal lobe: The hippocampus links cortical modules during memory retrieval. *Journal of Neuroscience* **33**(35):14184–92. doi: 10.1523/jneurosci.1987-13.2013. [aCB, JC]

Staresina B. P., Duncan K. D. & Davachi L. (2011) Perirhinal and parahippocampal cortices differentially contribute to later recollection of object- and scene-related event details. *Journal of Neuroscience* **31**(24):8739–47. doi: 10.1523/jneurosci.4978-10.2011. [aCB]

Staresina B. P., Henson R. N., Kriegeskorte N. & Alink A. (2012) Episodic reinstatement in the medial temporal lobe. *Journal of Neuroscience* **32**(50):18150–56. doi: 10.1523/jneurosci.4156-12.2012. [aCB]

Staresina B. P., Reber T. P., Niediek J., Boström J., Elger C. E. & Mormann F. (2019) Recollection in the human hippocampal-entorhinal cell circuitry. *Nature Communications* **10**(1):1–11. Available at: https://doi.org/10.1038/s41467-019-09558-3. [JC]

Stark S. M., Yassa M. A., Lacy J. W. & Stark C. E. L. (2013) A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment. *Neuropsychologia* **51**(12):2442–49. Available at: https://doi.org/10.1016/j.neuropsychologia.2012.12.014. [OH]

Starkstein S. E. (2014) Anosognosia in Alzheimer's disease: Diagnosis, frequency, mechanism and clinical correlates. *Cortex* **61**:64–73. doi: 10.1016/j.cortex.2014.07.019. [aCB]

Steinvorth S., Wang C., Ulbert I., Schomer D. & Halgren E. (2010) Human entorhinal gamma and theta oscillations selective for remote autobiographical memory. *Hippocampus* **173**:166–73. Available at: https://doi.org/10.1002/hipo.20597. [JC]

St. Jacques P. L., Szpunar K. K. & Schacter D. L. (2017) Shifting visual perspective during retrieval shapes autobiographical memories. *NeuroImage* **148**:103–14. doi: 10.1016/j.neuroimage.2016.12.028. [rCB]

Stone A. & Valentine T. (2005) Strength of visual percept generated by famous faces perceived without awareness: Effects of affective valence, response latency and visual field. *Consciousness and Cognition* **14**:548–64. Available at: https://doi.org/ 10.1016/j.concog.2005.01.009. [GG]

Strikwerda-Brown C., Grilli M. D., Andrews-Hanna J. R. & Irish M. (2019) "All is not lost" – Rethinking the nature of the self in dementia. *Ageing Research Reviews* **54**: e100932. Available at: https://doi.org/10.1016/j.arr.2019.100932. [CS-B]

Suddendorf T. & Corballis M. C. (1997) Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs* **123**(2):133–67. [OH]

Suzuki W. A. & Amaral D. G. (1994) Perirhinal and parahippocampal cortices of the macaque monkey: Cortical afferents. *Journal of Comparative Neurology* **350**(4):497–533. doi: 10.1002/cne.903500402. [aCB]

Suzuki W. A. & Naya Y. (2014) The perirhinal cortex. *Annual Review of Neuroscience* **37** (1):39–53. Available at: https://doi.org/10.1146/annurev-neuro-071013-014207. [HY, rCB]

Taube J. S., Muller R. U. & Ranck Jr. J. B. (1990) Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience* **10**(2):420–35. [GR]

Taylor J. R., Buratto L. G. & Henson R. N. (2013) Behavioral and neural evidence for masked conceptual priming of recollection. *Cortex* **49**(6):1511–25. [CFI]

Taylor J. R. & Henson R. N. (2012a) Could masked conceptual primes increase recollection? The subtleties of measuring recollection and familiarity in recognition memory. *Neuropsychologia* **50**(13):3027–40. [CFI]

Taylor J. R. & Henson R. N. (2012b) You can feel it all over: Many signals potentially contribute to feelings of familiarity. *Cognitive Neuroscience* **3**(3–4):209–10. doi: 10.1080/17588928.2012.689966. [aCB]

Taylor K. I., Devereux B. J. & Tyler L. K. (2011) Conceptual structure: Towards an integrated neuro-cognitive account. *Language and Cognitive Processes* **26**(9):1368–401. doi: 10.1080/01690965.2011.568227. [aCB]

Taylor K. I. & Probst A. (2008) Anatomic localization of the transentorhinal region of the perirhinal cortex. *Neurobiology of Aging* **29**(10):1591–96. doi: 10.1016/j.neurobiolaging.2007.03.024. [aCB]

Teyler T. J. & DiScenna P. (1986) The hippocampal memory indexing theory. *Behavioral Neuroscience* **100**(2):147–54. [OH]

Teyler T. J. & Rudy J. W. (2007) The hippocampal indexing theory and episodic memory: Updating the index. *Hippocampus* **17**(12):1158–69. doi: 10.1002/hipo.20350. [NA, aCB, OH]

Tian J., Huang R., Cohen J. Y., Osakada F., Kobak D., Machens C. K., Callaway E. M., Uchida N. & Watabe-Uchida M. (2016) Distributed and mixed information in monosynaptic inputs to dopamine neurons. *Neuron* **91**(6):1374–89. [VS]

Tibon R., Fuhrmann D., Levy D. A., Simons J. S. & Henson R. N. (2019) Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. *Journal of Neuroscience* **39**(22):4365–74. Available at: https://doi.org/10.1523/JNEUROSCI.2102-18.2018. [rCB, RT]

Topolinski S. (2012) The sensorimotor contributions to implicit memory, familiarity, and recollection. *Journal of Experimental Psychology: General* **141**(2):260–81. doi: 10.1037/a0025658. [aCB]

Trautner P., Dietl T., Staedtgen M., Mecklinger A., Grunwald T., Elger C. E. & Kurthen M. (2004) Recognition of famous faces in the medial temporal lobe: An invasive ERP study. *Neurology* **63**(7):1203–208. Available at: https://doi.org/10.1212/01.WNL.0000140487.55973.D7. [JC]

Trebaul L., Deman P., Tuyisenge V., Jedynak M., Hugues E., Rudrauf D., Bhattacharjee M., Tadel F., Chanteloup-Foret B., Saubat C., Reyes Mejia G. C., Adam C., Nica A., Pail M., Dubeau F., Rheims S., Trébuchon A., Wang H., Liu S., Blauwblomme T., Garcés M., De Palma L., Valentin A., Metsähonkala E.-L., Petrescu A. M., Landré E., Szurhaj W., Hirsch E., Valton L., Rocamora R., Schulze-Bonhage A., Mindruta I., Francione S., Maillard L., Taussig D., Kahane P. & David O. (2018) Probabilistic functional tractography of the human cortex revisited. *NeuroImage* **181**:414–29. Available at: https://doi.org/10.1016/j.neuroimage.2018.07.039. [JC]

Tsao A., Moser M.-B. & Moser E. I. (2013) Traces of Experience in the Lateral Entorhinal Cortex. *Current Biology* **23**(5):399–405. [VS]

Tsao A., Sugar J., Lu L., Wang C., Knierim J. J., Moser M.-B. & Moser E. I. (2018) Integrating time from experience in the lateral entorhinal cortex. *Nature* **561** (7721):57–62. [VS]

Tsivilis D., Vann S. D., Denby C., Roberts N., Mayes A. R., Montaldi D. & Aggleton J. P. (2008) A disproportionate role for the fornix and mammillary bodies in recall versus recognition memory. *Nature Neuroscience* **11**(7):834–42. doi: 10.1038/nn.2149. [JPA]

Tulving E. (1985) Memory and consciousness. *Canadian Psychology* **26**(1):1–12. [aCB, JFK]

Tulving E. (1999) On the uniqueness of episodic memory. In: *Cognitive neuroscience of memory*, ed. L. G. Nilsson & H. J. Markowitsch, pp. 11–42. Hogrefe & Huber. [aCB]

Tulving E. (2002) Episodic memory: From mind to brain. *Annual Review of Psychology* **53**:1–25. doi: 10.1146/annurev.psych.53.100901.135114. [DK, rCB]

Turkiewicz G., Zanetti M., Zung S. & Cordeiro Q. (2009) Coexistência das síndromes de Capgras e Frégoli associadas à redução de volume frontotemporal e hiperintensidades em substância branca cerebral [Coexistence of Capgras and Fregoli syndromes associated to frontotemporal volume reduction and cerebral white matter hyperintensities]. *Archives Of Clinical Psychiatry (São Paulo)* **36**(6):240–43. doi: 10.1590/s0101-60832009000600004. [JP]

Unkelbach C. & Greifeneder R. (2013) *The experience of thinking: How the fluency of mental processes influences cognition and behavior*. Psychology Press. [aCB]

Utochkin I. S. & Brady T. F. (2019) Independent storage of different features of real-world objects in long-term memory. *Journal of Experimental Psychology: General*. (Advance online publication). doi: 10.1037/xge0000664. [rCB, TFB]

Valenstein E., Bowers D., Verfaellie M., Heilman K. M., Day A. & Watson R. T. (1987) Retrosplenial amnesia. *Brain* **110** (Pt 6):1631–46. [aCB]

van den Heuvel M. P. & Sporns O. (2013) Network hubs in the human brain. *Trends in Cognitive Sciences* **17**(12):683–96. doi: 10.1016/j.tics.2013.09.012. [aCB]

Vann S. D. (2010) Re-evaluating the role of the mammillary bodies in memory. *Neuropsychologia* **48**(8):2316–27. doi: 10.1016/j.neuropsychologia.2009.10.019. [rCB]

Vann S. D., Aggleton J. P. & Maguire E. A. (2009a) What does the retrosplenial cortex do? *Nature Reviews: Neuroscience* **10**(11):792–802. doi: 10.1038/nrn2733. [arCB]

Vann S. D., Tsivilis D., Denby C. E., Quamme J. R., Yonelinas A. P., Aggleton J. P., Montaldi D. & Mayes A. R. (2009b) Impaired recollection but spared familiarity in patients with extended hippocampal system damage revealed by 3 convergent methods. *Proceedings of the National Academy of Sciences* **106** (13):5442–47. [JPA]

Vatansever D., Menon D. K., Manktelow A. E., Sahakian B. J. & Stamatakis E. A. (2015) Default mode dynamics for global functional integration. *Journal of Neuroscience* **35** (46):15254–62. doi: 10.1523/JNEUROSCI.2135-15.2015. [aCB]

Verfaellie M. & Cermak L. S. (1999) Perceptual fluency as a cue for recognition judgments in amnesia. *Neuropsychology* **13**(2):198–205. [aCB]

Vilberg K. L. & Rugg M. D. (2008) Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia* **46**(7):1787–99. Available at: http://doi.org/10.1016/j.neuropsychologia.2008.01.004. [RT]

Villain N., Desgranges B., Viader F., de la Sayette V., Mezenge F., Landeau B., Baron J. C., Eustache F. & Chételat G. (2008) Relationships between hippocampal atrophy, white matter disruption, and gray matter hypometabolism in Alzheimer's disease. *Journal of Neuroscience* **28**(24):6174–81. doi: 10.1523/jneurosci.1392-08.2008. [aCB]

Vogt B. A. & Laureys S. (2005) Posterior cingulate, precuneal and retrosplenial cortices: Cytology and components of the neural network correlates of consciousness. *Progress in Brain Research* **150**:205–17. doi: 10.1016/s0079-6123(05)50015-3. [aCB]

Vogt B. A. & Pandya D. N. (1987) Cingulate cortex of the rhesus monkey: II. Cortical afferents. *Journal of Comparative Neurology* **262**(2):271–89. doi: 10.1002/cne.902620208. [aCB]

Vogt B. A., Pandya D. N. & Rosene D. L. (1987) Cingulate cortex of the rhesus monkey: I. Cytoarchitecture and thalamic afferents. *Journal of Comparative Neurology* **262** (2):256–70. doi: 10.1002/cne.902620207. [aCB]

Vogt B. A., Vogt L. & Laureys S. (2006) Cytology and functionally correlated circuits of human posterior cingulate areas. *NeuroImage* **29**(2):452–66. doi: 10.1016/j.neuroimage.2005.07.048. [aCB]

Voss J. L., Lucas H. D. & Paller K. A. (2012) More than a feeling: Pervasive influences of memory without awareness of retrieval. *Cognitive Neuroscience* **3**(3–4):193–207. doi: 10.1080/17588928.2012.674935. [arCB]

Wagner A. D., Shannon B. J., Kahn I. & Buckner R. L. (2005) Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences* **9**(9):445–53. Available at: http://doi.org/10.1016/j.tics.2005.07.001. [HY, rCB, RT]

Wang J. & Barbas H. (2018) Specificity of primate amygdalar pathways to hippocampus. *Journal of Neuroscience* **38**:10019–41. [AS]

Wang T. H., Johnson J. D., de Chastelaine M., Donley B. E. & Rugg M. D. (2016) The effects of age on the neural correlates of recollection success, recollection-related cortical reinstatement, and post-retrieval monitoring. Cerebral Cortex **26**(4):1698–714. doi: 10.1093/cercor/bhu333. [rCB]

Wang W.-C. & Giovanello K. S. (2016) The role of medial temporal lobe regions in incidental and intentional retrieval of item and relational information in aging. *Hippocampus* **26**(6):693–99. Available at: https://doi.org/10.1002/hipo.22578. [W-CW]

Wang W.-C. & Yonelinas A. P. (2012) Familiarity is related to conceptual implicit memory: An examination of individual differences. *Psychonomic Bulletin and Review* **19** (6):1154–64. Available at: https://doi.org/10.3758/s13423-012-0298-7. [W-CW]

Wang W. C., Yonelinas A. P. & Ranganath C. (2013) Dissociable neural correlates of item and context retrieval in the medial temporal lobes. *Behavioural Brain Research* **254**:102–107. doi: 10.1016/j.bbr.2013.05.029. [aCB]

Ward E. J., Chun M. M. & Kuhl B. A. (2013) Repetition suppression and multi-voxel pattern similarity differentially track implicit and explicit visual memory. *Journal of Neuroscience* **33**(37):14749–57. [TS]

Wells C. E., Moulin C. J., Ethridge P., Illman N. A., Davies E. & Zeman A. (2014) Persistent psychogenic déjà vu: A case report. *Journal of Medical Case Reports* **8**: article no. 414. doi: 10.1186/1752-1947-8-414. [rCB]

Werning M. & Cheng S. (2017) Taxonomy and unity of memory. In *The Routledge handbook of philosophy of memory*, ed. S. Bernecker & K. Michaelian, pp. 7–20. Routledge. [OH]

Westerberg C. E., Paller K. A., Weintraub S., Mesulam M.-M., Holdstock J. S., Mayes A. R. & Reber P. J. (2006) When memory does not fail: Familiarity-based recognition in mild cognitive impairment and Alzheimer's disease. *Neuropsychology* **20**(2):193–205. Available at: https://doi.org/10.1037/0894-4105.20.2.193. [OH]

Westerman D. L. (2008) Relative fluency and illusions of recognition memory. *Psychonomic Bulletin and Review* **15**(6):1196–200. doi: 10.3758/PBR.15.6.1196. [aCB]

Westerman D. L., Lloyd M. E. & Miller J. K. (2002) The attribution of perceptual fluency in recognition memory: The role of expectation. *Journal of Memory and Language* **47**:607–17. [arCB]

Wheeler M. A. & Stuss D. T. (2003) Remembering and knowing in patients with frontal lobe injuries. *Cortex* **39**:827–46. [aCB]

White C. N., Ratcliff R., Vasey M. W. & McKoon G. (2010) Using diffusion models to understand clinical disorders. *Journal of Mathematical Psychology* **54**:39–52. [AFO]

Whittlesea B. W. (2002) Two routes to remembering (and another to remembering not). *Journal of Experiment Psychology: General* **131**(3):325–48. [arCB]

Whittlesea B. W. & Price J. R. (2001) Implicit/explicit memory versus analytic/nonanalytic processing: Rethinking the mere exposure effect. *Memory & Cognition* **29** (2):234–46. [arCB]

Whittlesea B. W. & Williams L. D. (2000) The source of feelings of familiarity: The discrepancy-attribution hypothesis. Journal of Experimental Psychology: Learning, Memory, and Cognition **26**(3):547–65. [arCB]

Whittlesea B. W. & Williams L. D. (2001a) The discrepancy-attribution hypothesis: I. The heuristic basis of feelings of familiarity. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **27**(1):3–13. [aCB]

Whittlesea B. W. & Williams L. D. (2001b) The discrepancy-attribution hypothesis: II. Expectation, uncertainty, surprise, and feelings of familiarity. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **27**(1):14–33. [aCB]

Whittlesea B. W. A. (1997) Production, evaluation, and preservation of experiences: Constructive processing in remembering and performance tasks. In: *The psychology of learning and motivation: Advances in research and theory, vol. 37*, ed. D. L. Medin, pp. 211–64. Academic Press. [aCB, GEB]

Whittlesea B. W. A., Jacoby L. L. & Girard K. (1990) Illusions of immediate memory: Evidence of an attributional basis for feelings of familiarity and perceptual quality. *Journal of Memory and Language* **29**(6):716–32. Available at: https://doi.org/10.1016/0749-596X(90)90045-2. [aCB, TS]

Whittlesea B. W. A. & Leboe J. P. (2000) The heuristic basis of remembering and classification: Fluency, generation, and resemblance. *Journal of Experimental Psychology: General* **129**(1):84–106. [TS]

Willems S., Dedonder J. & Van der Linden M. (2010) The mere exposure effect and recognition depend on the way you look! *Experimental Psychology* **57**(3):185–92. doi: 10.1027/1618-3169/a000023. [rCB]

Willems S., Salmon E. & Van der Linden M. (2008) Implicit/explicit memory dissociation in Alzheimer's disease: The consequence of inappropriate processing? *Neuropsychology* **22**(6):710–17. [arCB]

Willems S. & Van der Linden M. (2006) Mere exposure effect: A consequence of direct and indirect fluency–preference links. *Consciousness and Cognition* **15**(2):323–41. doi: 10.1016/j.concog.2005.06.008. [arCB]

Willems S. & Van der Linden M. (2009) Experimental dissociations between memory measures: Influence of retrieval strategies. *Consciousness and Cognition* **18**(1):39–55. doi: 10.1016/j.concog.2008.10.001. [rCB]

Willems S., van der Linden M. & Bastin C. (2007) The contribution of processing fluency to preference: A comparison with familiarity-based recognition. *European Journal of Cognitive Psychology* **19**(1):119–40. doi: 10.1080/09541440600604248. [aCB]

Wixted J. T. (2007) Dual-process theory and signal-detection theory of recognition memory. *Psychological Review* **114**(1):152–76. [TS, VS]

Wixted J. T. & Mickes L. (2010) A continuous dual-process model of remember/know judgments. *Psychological Review* **117**(4):1025–54. [aCB, TS]

Wixted J. T. & Squire L. R. (2011) The medial temporal lobe and the attributes of memory. *Trends in Cognitive Sciences* **15**(5):210–17. doi: 10.1016/j.tics.2011.03.005. [aCB]

Wolk D. A., Schacter D. L., Berman A. R., Holcomb P. J., Daffner K. R. & Budson A. E. (2004) An electrophysiological investigation of the relationship between conceptual fluency and familiarity. *Neuroscience Letters* **369**(2):150–55. doi: 10.1016/j.neulet.2004.07.081. [aCB]

Wong J. T., Cramer S. J. & Gallo D. A. (2012) Age-related reduction of the confidence-accuracy relationship in episodic memory: Effects of recollection quality and retrieval monitoring. *Psychology of Aging* **27**(4):1053–65. doi: 10.1037/a0027686. [rCB]

Wong S., Irish M., Leshikar E. D., Duarte A., Bertoux M., Savage G., Hodges J. R., Piguet O. & Hornberger M. (2017) The self-reference effect in dementia: Differential involvement of cortical midline structures in Alzheimer's disease and behavioural-variant frontotemporal dementia. *Cortex* **91**:169–85. doi: 10.1016/j.cortex.2016.09.013. [aCB]

Woodruff C. C., Uncapher M. R. & Rugg M. D. (2006) Neural correlates of differential retrieval orientation: Sustained and item-related components. *Neuropsychologia* **44**:3000–10. [rCB]

Woollams A. M. & Patterson K. (2018) Cognitive consequences of the left-right asymmetry of atrophy in semantic dementia. *Cortex* **107**:64–77. Available at: https://doi.org/10.1016/j.cortex.2017.11.014. [GG]

Woollams A. M., Taylor J. R., Karayanidis F. & Henson R. N. (2008) Event-related potentials associated with masked priming of test cues reveal multiple potential contributions to recognition memory. *Journal of Cognitive Neuroscience* **20**(6):1114–29. doi: 10.1162/jocn.2008.20076. [CFI]

Wright P., Randall B., Clarke A. & Tyler L. K. (2015) The perirhinal cortex and conceptual processing: Effects of feature-based statistics following damage to the anterior temporal lobes. *Neuropsychologia* **76**:192–207. doi: 10.1016/j.neuropsychologia.2015.01.041. [arCB]

Xue G. (2018) The neural representations underlying human episodic memory. *Trends in Cognitive Sciences* **22**(6):544–61. doi: 10.1016/j.tics.2018.03.004. [rCB]

Yassa M. A. & Stark C. E. (2011) Pattern separation in the hippocampus. *Trends in Neuroscience* **34**(10):515–25. doi: 10.1016/j.tins.2011.06.006. [rCB]

Yazar Y., Bergström Z. M. & Simons J. S. (2012) What is the parietal lobe contribution to long-term memory? *Cortex* **48**(10):1381–82; discussion 1383–87. doi: 10.1016/j.cortex.2012.05.011. [rCB, RT]

Yazar Y., Bergström Z. M. & Simons J. S. (2014) Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PLOS ONE* **9**(10):e110414. Available at: http://doi.org/10.1371/journal.pone.0110414. [RT]

Yeung L.-K., Olsen R. K., Bild-Enkin H. E. P., D'Angelo M. C., Kacollja A., McQuiggan D. A., Keshabyan A., Ryan J. D. & Barense M. D. (2017) Anterolateral entorhinal cortex volume predicted by altered intra-item configural processing. *Journal of Neuroscience* **37**(22):5527–38. doi: 10.1523/JNEUROSCI.3664-16.2017. [aCB]

Yeung L.-K., Olsen R. K., Hong B., Mihajlovic V., D'Angelo M. C., Kacollja A., Ryan J. D. & Barense M. D. (2019) Object-in-place memory predicted by anterolateral entorhinal cortex and parahippocampal cortex volume in older adults. *Journal of Cognitive Neuroscience* **31**(5):711–29. doi: 10.1101/409607. [aCB]

Yeung L. K., Ryan J. D., Cowell R. A. & Barense M. D. (2013) Recognition memory impairments caused by false recognition of novel objects. *Journal of Experimental Psychology: General* **142**(4):1384–97. doi: 10.1037/a0034021. [aCB]

Yim H., Garrett P., Baker M., Sreekumar V. & Dennis S. (2019) Examining dependencies among different time scales in episodic memory – An experience sampling study. PsyArXiv Preprint. Available at: https://doi.org/10.31234/osf.io/5w94j. Also available at: https://psyarxiv.com/5w94j/. [VS]

Yonelinas A. P. (1994) Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **20**(6):1341–54. [aCB]

Yonelinas A. P. (2002) The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language* **46**(3):441–517. [AFO, JFK, TS]

Yonelinas A. P. (2013) The hippocampus supports high-resolution binding in the service of perception, working memory and long-term memory. *Behavioral Brain Research* **254**:34–44. Available at: https://doi.org/10.1016/J.BBR.2013.05.030. [arCB, W-CW]

Yonelinas A. P., Aly M., Wang W. C. & Koen J. D. (2010) Recollection and familiarity: Examining controversial assumptions and new directions. *Hippocampus* **20** (11):1178–94. doi: 10.1002/hipo.20864. [aCB]

Yonelinas A. P. & Ritchey M. (2015) The slow forgetting of emotional episodic memories: An emotional binding account. *Trends in Cognitive Sciences* **19**(5):259–67. doi: 10.1016/j.tics.2015.02.009. [rCB]

Zeidman P. & Maguire E. A. (2016) Anterior hippocampus: The anatomy of perception, imagination and episodic memory. *Nature Reviews: Neuroscience* **17**(3):173–82. doi: 10.1038/nrn.2015.24. [rCB]

Zhao Q.-F., Tan L., Wang H.-F., Jiang T., Tan M.-S., Tan L., Xu W., Li J.-Q., Wang J., Lai T.-J. & Yu J.-T. (2016) The prevalence of neuropsychiatric symptoms in Alzheimer's disease: systematic review and meta-analysis. *Journal of Affective Disorders* **190**:264–71. Available at: https://doi.org/10.1016/j.jad.2015.09.069. [BCN]

Zhao X.-H., Wang P.-J., Li C.-B., Hu Z.-H., Xi Q., Wu W.-Y. & Tang X.-W. (2007) Altered default mode network activity in patient with anxiety disorders: An fMRI study. *European Journal of Radiology* **63**(3):373–78. doi:10.1016/j.ejrad.2007.02.006. [BCN]