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<RH>**Authors' Response**

<RT>Interactions with the Integrative Memory model

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<R-AB>**Abstract:** The Integrative Memory model formalizes a new conceptualisation 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 recognises previously encountered information.

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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 (section R1), the attribution system (section R2) and the subjective experiences of memory (section R3).

<A>**R1. Representation core systems**

The idea that the content of past experiences are encoded in core systems which 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.

<B>***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. 2002). 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 organised 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 (Besson et al., unpublished data). 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 2018). 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.

<B>***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. 2009). 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 visualised 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 synchronisation (El Haj et al. 2019; **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).

<B>*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, Dumont & Warburton 2011; Eichenbaum, Yonelinas & Ranganath 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 in 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).

<B>*R1.4. Self and emotion*

A few commentators deplored that we did not take into account the emotional flavour 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 flavour 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, favouring 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**).

<A>**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.

<B>***R2.1. Fluency cues***

In the target article, we argue that fluency cues are important signals for familiarity when recognising 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. 2004; 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 section 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 re-interpretation 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 recognise (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 analyse 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 favoured 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. 2005; Millar et al. 2018).

<B>*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 section 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, favouring 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, Ciaramelli & Moscovitch 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 judgements (Wang et al. 2016), vividness ratings (Richter et al. 2016; Tibon et al. 2019) or confidence judgements (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. 2016) 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 favour 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.

<B>***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 towards similar lures with no increase towards 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 neuro-architecture 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 from childhood to 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.

<A>**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.

<B>***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 judgements 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 (section 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 usual 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.

<B>*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 recognises 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.

<B>***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 section 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.

<A>**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.

<RFT>**References** [Bastin et al. Response] [rCB]

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