CORTEX 146 (2022) 74–88

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research Report

High feature overlap reveals the importance of anterior and medial temporal lobe structures for learning by means of fast mapping

Ann-Kathrin Zaiser [a,b,*], *Regine Bader* [a] *and Patric Meyer* [b,c]

[a] *Experimental Neuropsychology Unit, Department of Psychology, Saarland University, Saarbrücken, Germany*
[b] *Department of Applied Psychology, SRH University Heidelberg, Germany*
[c] *Network Aging Research (NAR), Heidelberg University, Heidelberg, Germany*

ARTICLE INFO

Article history:
Received 31 March 2021
Reviewed 16 May 2021
Revised 15 July 2021
Accepted 18 July 2021
Action editor Asaf Gilboa
Published online 21 October 2021

Keywords:
Fast mapping
Feature overlap
Perirhinal cortex
Medial temporal lobe
Anterior temporal lobe

ABSTRACT

Contrary to traditional theories of declarative memory, it has recently been shown that novel, arbitrary associations can rapidly and directly be integrated into cortical memory networks by means of a learning procedure called *fast mapping* (FM), possibly bypassing time-consuming hippocampal-neocortical consolidation processes. In the typical FM paradigm, a picture of a previously unknown item is presented next to a picture of a previously known item and participants answer a question referring to an unfamiliar label, thereby incidentally creating associations between the unknown item and the label. However, contradictory findings have been reported and factors moderating rapid cortical integration through FM yet need to be identified. Previous behavioral results showed that rapid semantic integration through FM was boosted if the unknown and the known item shared many features. In light of this, we propose that the perirhinal cortex might be especially qualified to support the rapid incorporation of these associations into cortical memory networks within the FM paradigm, due to its computational mechanisms during the processing of complex and particularly highly similar objects. We therefore expected that a high degree of feature overlap between the unknown and the known item would trigger strong engagement of the perirhinal cortex at encoding, which in turn might enhance rapid cortical integration of the novel picture-label associations. Within an fMRI experiment, we observed greater subsequent memory effects (i.e., stronger activation for subsequent hits than misses) during encoding in the perirhinal cortex and an associated anterior temporal network if the items shared many features than if they shared few features. This indicates that the perirhinal cortex indeed contributes to the acquisition of novel associations by means of FM if feature overlap is high.

* *Corresponding author*. Neurocognitive Psychology Unit, Department of Applied Psychology, SRH University Heidelberg, Maria-Probst-St. 3, 69123, Heidelberg, Germany.
E-mail address: annkathrin.zaiser@gmail.com (A.-K. Zaiser).
https://doi.org/10.1016/j.cortex.2021.07.017
0010-9452/

1. Introduction

Traditional theories of declarative memory assume that learning of novel, arbitrary associations depends on a time-consuming consolidation process, typically based on hippocampal-neocortical interplay (e.g., Frankland & Bontempi, 2005; McClelland, McNaughton, & O'Reilly, 1995). However, there is evidence that rapid and direct cortical integration of novel picture-label associations is possible by means of an encoding procedure called *fast mapping* (FM; e.g., Himmer, Müller, Gais, & Schönauer, 2017; Merhav, Karni, & Gilboa, 2014, 2015; Sharon, Moscovitch, & Gilboa, 2011; Zaiser, Meyer, & Bader, 2021). Sharon et al. (2011) reported a clear benefit from encoding within the FM paradigm in patients with severe lesions predominantly to the hippocampus. These patients did not recognize novel picture-label associations above chance level after encoding within a standard explicit encoding (EE) condition, which is typically expected to rely on hippocampal processing. Strikingly, however, their recognition performance was as good as that of healthy controls if the associations had been encoded by means of FM. In the typical FM paradigm, learning is incidental, that is, participants do not expect a subsequent memory test at encoding. They are presented with a picture of a previously unknown item (e.g., an exotic blue-footed bird) together with a picture of a previously known item that is already represented in semantic networks (e.g., a flamingo), and are asked to answer a question referring to an unfamiliar label (e.g., *Does the satellote have blue feet?*). Participants can answer this question by recognizing and rejecting the previously known item, thereby actively discovering the link between the picture of the unknown item and the unfamiliar label. It is assumed that this procedure enables the binding of the picture of the unknown item and the label to a new association that can be rapidly integrated into semantic memory networks (Sharon et al., 2011).

Yet, there are studies that revealed contradictory findings (cf. Smith, Urgolites, Hopkins, & Squire, 2014; Warren & Duff, 2014; Warren, Tranel, & Duff, 2016). However, it is unclear to what extent conclusions should be drawn on rapid cortical integration through FM from some of these studies as, for example, the experimental designs and procedures deviated from the original paradigm, such that learning was intentional (e.g., Warren & Duff, 2014; for effects of a learning intention in FM see Zaiser et al., 2021) or the associations had been repeatedly recalled before the recognition memory test (e.g., Warren & Duff, 2014; Warren et al., 2016). Moreover, rapid cortical integration through FM was not only investigated in patients with lesions confined to the hippocampus but also in patients with extended lesions to extra-hippocampal structures or with complete left-temporal lobectomies (Warren et al., 2016). In addition, there are studies that used behavioral recognition memory tests to assess retrieval from cortical networks in healthy young adults (e.g., Cooper, Greve, & Henson, 2019). It is difficult to draw conclusions from these findings on rapid cortical integration as these explicit tests alone do not allow for the dissociation between retrieval of hippocampal and cortical memory representations in such samples. A recent debate has underpinned the necessity to clarify more systematically if and under which conditions rapid cortical integration of novel associations through FM is possible (see Cooper, Greve, & Henson, 2018, and the respective commentaries), for example by identifying factors potentially moderating FM learning success (see Zaiser, Meyer, & Bader, 2019). Here, we approached this issue from a neurocognitive perspective, asking which underlying mechanisms and corresponding brain structures are likely to contribute to successful rapid cortical integration through FM.

Sharon et al. (2011) did not only show a benefit of encoding through FM for patients with lesions predominantly to the hippocampus. They also found that two additional patients who exhibited extended lesions to other temporal lobe structures, such as the perirhinal cortex (PrC) and the anterior temporal lobe (ATL), did not benefit from encoding through FM. There is a large body of evidence that the PrC as the key component of an anterior temporal system (see Ranganath & Ritchey, 2012) is involved in the processing and discrimination between complex objects, especially if they share many features (e.g., Bussey, Saksida, & Murray, 2005; Cowell, Bussey, & Saksida, 2010). For example, Barense, Gaffan, and Graham (2007) found that, in contrast to patients with lesions confined to the hippocampus, patients with lesions extending to the PrC could not discriminate between highly similar objects despite normal performance in the discrimination between less similar objects (see also Barense et al., 2005). Correspondingly, Mundy, Downing, and Graham (2012) reported increased PrC activation during a perceptual task in which participants watched sequences of highly similar objects compared to sequences of less similar objects.

In addition to its perceptual role, the PrC is involved in semantic processing (e.g., Meyer et al., 2005; Meyer et al., 2013; Meyer, Mecklinger, & Friederici, 2010; Wang et al., 2014; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010) and familiarity-based item recognition memory (e.g., Bowles et al., 2007; Bowles et al., 2010; see Brown & Aggleton, 2001, for a review). Moreover, it may bind the association of a written concrete word with its corresponding object concept (Bruffaerts et al., 2013; Liuzzi et al., 2019; Martin, Douglas, Newsome, Man, & Barense, 2018). Also, familiarity-based memory for newly built associations between items was found to be accompanied with enhanced PrC contribution to learning if the associations were encoded as integrated units (Haskins, Yonelinas, Quamme, & Ranganath, 2008). A representational-hierarchical view of the medial temporal lobe suggests that the PrC generally processes complex conjunctions of elemental features as single units, irrespective of the domain (i.e., on a perceptual as well as a semantic and mnemonic level; Cowell, Barense, & Sadil, 2019; Cowell, Bussey, & Saksida, 2006; O'Neil, Barkley, & Köhler, 2013). This cross-domain role of the PrC suggests that discriminative and mnemonic factors might interact during encoding. In line with this assumption, Chen, Zhou, and Yang (2019) found increased activation of the PrC during the discrimination between two highly similar items at encoding, compared to the discrimination between items from different categories. Importantly, this activation was predictive of later item recognition memory. Supportive evidence comes from an eye-tracking study by Zhou, Chen, and Yang (2018), who found

that more saccades between similar items were also predictive of subsequent item memory.

As the discrimination between complex objects (i.e., the previously known and the unknown item) is one of the most central cognitive operations required in the FM encoding task, one could assume that this triggers PrC involvement and that this involvement should increase with enhanced similarity between the items. Interestingly, in the study by Sharon et al. (2011), the two pictures in the FM encoding screen were highly similar in order to make the task more demanding and thereby allow for deeper encoding (see also Sharon, 2010). Such a high feature overlap between the previously unknown and the known item might have triggered PrC-mediated processes during FM encoding, from which selectively patients with hippocampal but not with additional perirhinal lesions might have benefitted. This assumption was supported by a recent study from our lab (Zaiser et al., 2021). By systematically manipulating feature overlap, we found rapid semantic integration of novel associations through FM if the previously unknown and the known item shared many features. In particular, the labels of the previously unknown items primed semantically related compared to unrelated targets immediately after encoding. Interestingly, this semantic priming effect was larger in a condition in which the unknown and the known item shared many features than when they shared few features. Here, we set out to directly test if it is indeed the PrC that supports memory processes in learning of associations through FM. We proposed that stronger PrC recruitment at encoding through increased demands on object discrimination would support the binding of the novel association to a unit, thereby potentially facilitating their rapid incorporation into cortical networks.

Hence, we explicitly manipulated the demands on the discrimination between the previously known and the unknown item (as in Zaiser et al., 2021) in an fMRI experiment. Specifically, we contrasted an FM encoding condition in which the previously unknown and the known item shared many features (*fast mapping, high feature overlap*; FMHO) with an FM encoding condition in which they shared few features (*fast mapping, low feature overlap*; FMLO). We expected that PrC engagement at encoding should be greater if the demands on perirhinal processing (i.e., the discrimination between complex objects) are higher (as in the FMHO condition) than if they are lower (as in the FMLO condition). We assumed that this should also be reflected in differential PrC contribution to learning. In particular, stronger PrC involvement was expected at encoding of items that were subsequently remembered in a forced-choice recognition test than at encoding of items that were subsequently forgotten. These subsequent memory effects should be greater in the FMHO condition than in the FMLO condition.

2. Method

2.1. Participants

Data were collected until 48 complete datasets of healthy participants that showed above-chance recognition performance were obtained, aiming to reach a reasonable sample size based on previous studies investigating effects that are close to the effects we expected (Atir-Sharon et al., 2015; Merhav et al., 2015). Participants were pseudo-randomly assigned to an FMHO and an FMLO group until both groups contained 24 participants (FMHO: $M_{age} = 24.1$ years, age range: 19–30; FMLO: $M_{age} = 22.1$ years, age range: 18–26) and gender distribution was the same in both groups (14 female each). All participants were native German speakers and right-handed in accordance with the Edinburgh Handedness Inventory (Oldfield, 1971). Of the total sample of $N = 97$ participants, 13 were excluded due to arachnoid and pineal cysts, one participant due to a panic attack in the scanner, and one participant as he had already taken part in another experiment using the same materials. Further three participants were excluded (and replaced) as not enough trials (<10) remained per memory condition (subsequently remembered, subsequently forgotten) after exclusion of trials based on a post-experimental rating of prior knowledge (see 2.3 Design and procedure). Of the remaining 79 participants, further 31 participants were excluded from the analyses as they did not show above-chance recognition accuracy ($p > .05$, binomial test; $n_{FMHO} = 23$; $n_{FMLO} = 8$)[1]. Participants gave written informed consent prior to the experiment and were compensated for their participation with 8€ per hour. The experiment was approved by the ethics committee of the Faculty of Human and Business Sciences at Saarland University in accordance with the declaration of Helsinki.

2.2. Materials

All pictures were drawn from the internet, belonged to one of seven categories (mammals, birds, insects, fish, fruit, vegetables, plants), and were arranged in pairs of one putatively known and one putatively unknown item each. In a previously conducted rating study, a different sample of 46 participants had rated these items for familiarity (5-point Likert scale; 1 = *not at all familiar*, 5 = *very familiar*) and previous knowledge (*known vs unknown*). Item pairs had been rated for feature overlap, which was defined as the number of features the two pictures have in common (e.g., the presence and nature of fur, a tail, legs, the similarity of colors, etc.) and was rated on a 5-point Likert scale (1 = *not at all similar*, 5 = *very similar*). For the present experiment, 48 item triplets, consisting of one unknown item, its highly similar known item, and its less similar known item (see Fig. 1), were drawn from the stimulus material of the rating study. The counterpart of a triplet, that is, the triplet in which the putatively known items appeared in the respective other overlap condition, was also included. Hence, each unknown item was assigned a highly similar known item (for usage in the FMHO condition) and a less similar known item (for usage in the FMLO condition; see Fig. 1). Analogously, each known item could appear together with one highly similar and one less similar

[1] Please note that this apparently unequal exclusion rate does not seem to be systematic as we did not observe similar patterns in previous experiments (see Zaiser et al., 2021). Moreover, recognition test performance did not differ between groups if participants who did not perform above chance level were included in the analyses, $t(77) = -1.44$, $p = .154$.

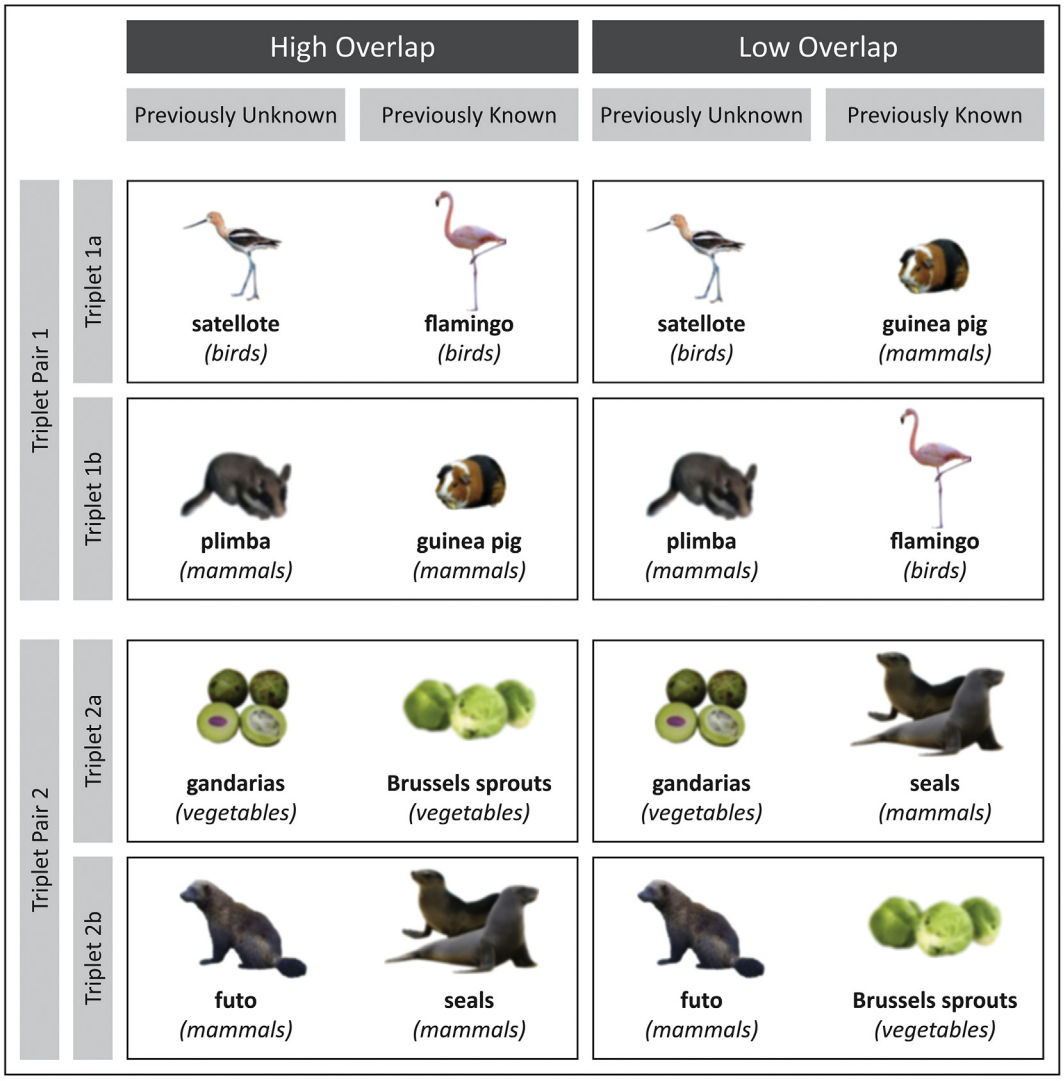

Fig. 1 – Example stimulus material. Each line depicts a picture triplet, consisting of one previously unknown item and two previously known items. Triplets were arranged in triplet pairs (e.g., Triplet Pair 1: Triplet 1a and 1b), within which overlap of the unknown and known items was counterbalanced. High-overlap item pairs were always from the same basic-level category (e.g., Triplet 1a: both birds). Low-overlap item pairs could consist of items from the same superordinate category but different basic-level categories (Triplets 1a and 1b: both animals, with birds and mammals as basic-level categories) or from different superordinate categories (Triplets 2a and 2b: plants and animals, with vegetables and mammals as basic-level categories); but note that we did not explicitly manipulate if items were of the same versus different superordinate category in the FMLO condition. Copyright © 2021 by American Psychological Association. Reproduced with permission. Zaiser, A.-K., Meyer, P., & Bader, R. (2021). High feature overlap and incidental encoding drive rapid semantic integration in the fast mapping paradigm. Journal of Experimental Psychology: General. Advance online publication. https://doi.org/10.1037/xge0001070.

unknown item. Thus, all participants were exposed to the same stimulus material but arranged in different pairs, depending on the encoding condition.

Of the triplets included in the present study, the previously unknown item had been classified as unknown by most participants in the rating study (on average, by 90%, $SD = 12\%$) and had been rated with the lowest familiarity ($M = 2.08$, $SD = .43$). The previously known items had been rated as known by most participants (on average, by 85%, $SD = 12\%$) and with the highest familiarity ($M = 4.42$, $SD = .40$). Moreover, only triplets with the highest difference between the overlap rating of the high-overlap and the low-overlap item pair were included ($M_{FMHO} = 3.59$, $SD_{FMHO} = .51$; $M_{FMLO} = 1.42$, $SD_{FMLO} = .37$; $M_{diff} = 2.17$, $SD_{diff} = .62$). In the final item set, significantly more participants of the rating study had rated the previously known items as known than the previously unknown items. Moreover, familiarity ratings for the previously unknown items were significantly lower than for the previously known items and overlap of the high feature overlap pairs was higher than overlap of the low feature overlap pairs (all $ps < .001$). In addition, the lowest overlap rating of the high-overlap pairs was still higher than the highest overlap rating of the low-overlap pairs.

Further 12 trials were added as filler trials, in which the question referred to the previously known item, which was supposed to prevent participants from developing strategies such as always referring to the unknown item without paying attention to the known item. Filler trials matched the participants' encoding condition with regard to feature overlap and were excluded from all analyses.

Half of the questions at encoding required a positive response, half a negative response, and questions were identical for both overlap conditions. The items' actual names were substituted with their botanical or zoological name (sometimes slightly modified) or with a pseudo-word if these labels might have triggered expectations about an item's category or features (e.g., if the name contained information on the item, such that *giraffe gazelle* would indicate a hoofed animal and was thus given its zoological name *gerenuk*). Word length of all labels was between 4 and 10 letters ($M = 6.88$, $SD = 1.84$).

2.3. Design and procedure

Stimulus presentation and timing were controlled using the experimental software PsychoPy (Peirce, 2009; http://www.psychopy.org/). All stimuli throughout the experiment were presented against a white background, projected onto a screen behind the magnet, which was visible through a mirror attached to the head coil. All tasks except for the post-experimental stimulus rating were conducted in the scanner; the encoding and recognition phase were recorded. Responses were collected via two 2-button response grips (one in each hand), with which participants could respond by pressing one of two buttons on either side (thumb and index finger).

2.3.1. Encoding

In order to ensure incidental learning, participants were told that visual perception would be investigated. All participants encoded the same picture-label associations by means of FM and feature overlap was manipulated between subjects. They first completed six practice trials (including two filler trials), matching their individual overlap condition. In the actual encoding phase, 60 experimental trials (including 12 filler trials) were presented in random order with the constraint that one of the filler trials was presented at the beginning and one at the end of the encoding phase in order to reduce primacy and recency effects. Each trial started with a fixation cross that was horizontally centered and slightly below the center of the screen, at the same height as the question would subsequently appear. The duration of this inter-stimulus interval was jittered between 1000 and 8000 msec in equally distributed steps of 500 msec. After the fixation cross had disappeared, the question was displayed separately for the first 2000 msec in Arial 27 point font and together with the pictures for further 3500 msec (see Fig. 2). The label within the question was presented in the horizontal center of the screen in bold font. Participants were instructed to read the question thoroughly and, as soon as the pictures would appear, to identify the item to which the question refers and how it is thus to be answered. After both the pictures and the question had disappeared, the words *yes* and *no* were displayed on the left and right side of the screen in orange and blue color (position and color counterbalanced between subjects). Participants could respond by pressing the keys with the left or right index finger. After 3000 msec, participants received written feedback and moved on to the next trial. If they had not responded within this time, they were encouraged to respond faster. In contrast to most previous FM studies, we decided against the repetition of encoding trials as repeating the associations would have prevented from capturing the effects of one-shot learning. Moreover, if the novel associations had been encoded repeatedly, it would not have been possible to disentangle which fMRI signal at encoding is associated with subsequent recognition accuracy. Consequently, we would not have been able to determine subsequent memory effects.

2.3.2. Recognition

After a 4-min filler task, in which participants had solved simple mathematical equations, a three-alternative forced-choice recognition test was administered in which participants were tested for all 48 picture-label associations. A fixation cross was displayed in the center of the screen for a jittered interval between 1000 and 8000 msec in equally distributed steps of 500 msec (with 1000 msec, 4500 msec, and 8000 msec appearing four times), before it was replaced by the recognition test label (see Fig. 2). The target picture and the two foil pictures were arranged around the label, with their positions on the screen randomly assigned (top-left, top-right, bottom-center). Participants were instructed to indicate which of the three pictures belonged to the test label by pressing the respective button on the response grips (left thumb, right thumb, right index finger). All three pictures had appeared in the encoding phase and were always from the same superordinate category (i.e., all animals or all plants) in order to control for item familiarity. Responses could not be given before 3000 msec of stimulus presentation, indicated by a verbal prompt at the bottom of the screen, in order to ensure sufficient exposure time to all pictures. The next trial started after 6000 msec of overall stimulus presentation. No feedback was provided. Prior to the actual recognition test, participants had completed a practice phase of four trials in which the four novel associations of the encoding practice phase were tested. After completion of the recognition task, an unrelated perceptual task was administered.

2.3.3. Rating of previous knowledge

Outside the scanner, participants' individual prior knowledge of all items was assessed. Participants were seated in front of a 17-inch laptop at a viewing distance of approximately 50 cm, where they were informed that the main aim of the experiment was to investigate memory and it was necessary to assess which items they had already known prior to their participation. We also informed them that the stimuli had been renamed and they were asked to indicate prior knowledge irrespective of an item's label in the experiment. The participants then were sequentially presented with all pictures in random order and were instructed to rate how well they had known each item prior to the experiment on a 5-point Likert scale (1 = *had not known the item at all before the experiment*; 5 = *had known the item very well before the experiment*). After ratings of ≥ 4, they were asked to type in the item's name at the lowest category level possible (e.g., *hawk* instead of *bird*).

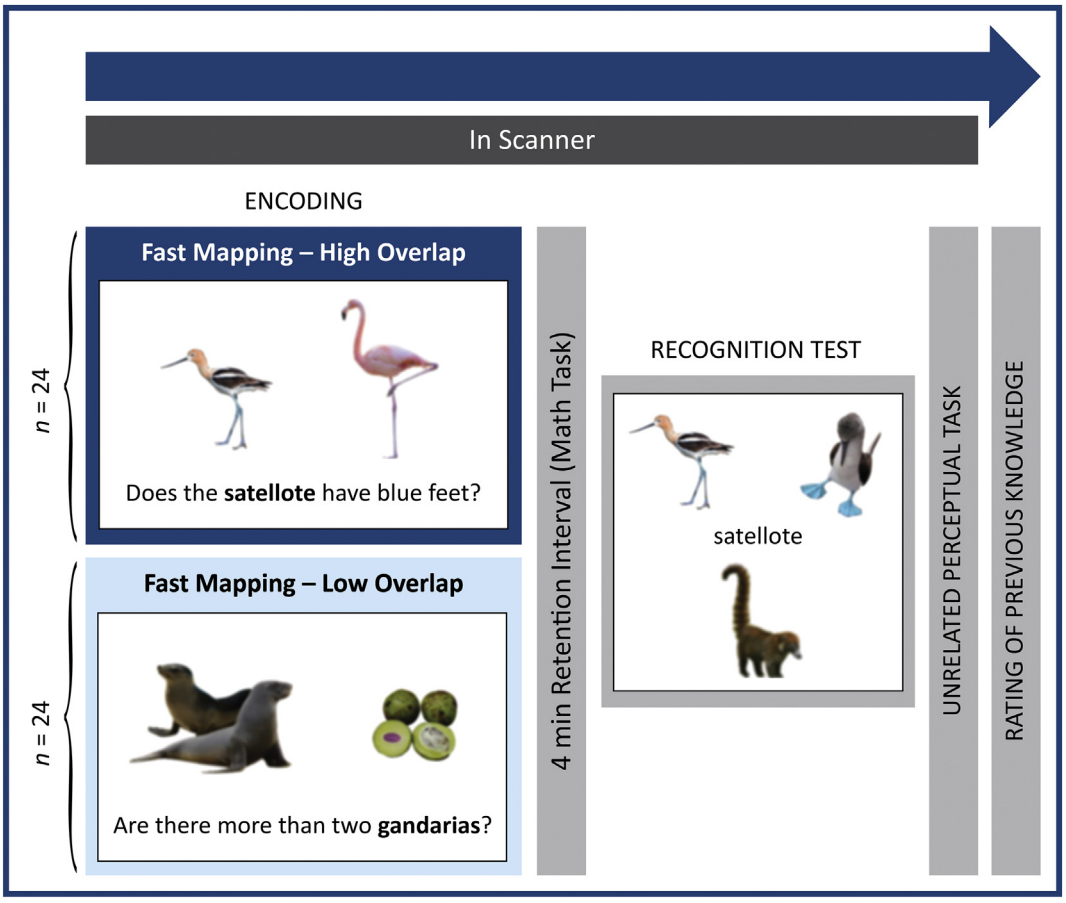

Fig. 2 – Experimental design and procedure. Encoding condition was manipulated between subjects. The plain question was presented for 2000 msec and then together with the pictures for further 3500 msec. After the pictures and the question had disappeared, response options (*yes/no*) were displayed and feedback was given after a response had been made. At recognition, the target and two foil pictures within one display always belonged to the same superordinate category (i.e., all animals or all plants) and had all been presented in the encoding phase.

2.4. *Data acquisition and processing*

A 3T Siemens Magnetom Skyra scanner with a 20-channel head coil was used for structural and functional data acquisition. Structural data were acquired prior to the experiment, using a T1-weighted three-dimensional magnetization-prepared rapid gradient-echo sequence (TR = 1900 msec; TE = 2.13 msec; sagittal orientation; flip angle = 9°; voxel size = .9 mm isotropic, distance factor = 50%; 192 slices; FoV = 240 mm). For the functional scans, a T2*-weighted two-dimensional gradient-echo planar imaging sequence (TR = 2000 msec; TE = 30 msec; flip angle = 90°; voxel size = 3 mm isotropic; distance factor = 25%; matrix = 64 × 64; FoV = 192 mm; right-left phase encoding direction) was used for both runs (one at encoding, one at recognition). Thirty-six transversal slices were acquired (interleaved, ascending), with a −30° axial-to-coronal rotation relative to the anterior-posterior commissure plane (anterior upward) in order to reduce susceptibility artifacts in anterior and medial temporal lobe structures (see e.g., Weiskopf, Hutton, Josephs, & Deichmann, 2006). Before scanning, we made sure that the FoV covered all regions of interest. In order to allow for signal equilibrium, the first four volumes of each functional run were discarded.

Imaging data were processed using SPM 12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). The 398 volumes of the encoding phase and 260 volumes of the recognition test phase were corrected for slice acquisition time using the first slice of each volume as reference image. They were motion-corrected by realignment of all images of a run to its first image and then co-registered to each participant's anatomical T1 image. After segmentation into gray and white matter, cerebrospinal fluid, bone, soft tissue, and air, they were spatially normalized to the Montréal Neurological Institute (MNI) standard T1 template with interpolation to 2-mm isotropic voxels and then smoothed using a Gaussian 7-mm full-width half-maximum kernel. Images were visually inspected for artifacts and adequacy of motion correction and transformation into standard space.

2.5. *Analyses*

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org/) and SPM 12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/) for imaging data. For all analyses, trials were only included if the individual rating of prior knowledge was congruent with what was expected at

stimulus creation, that is, if the putatively unknown item was classified as unknown by a participant (i.e., a rating of prior knowledge of ≤ 3) and if the putatively known item was classified as known (i.e., a rating of ≥ 4). Neither the number of remaining subsequently remembered trials ($M = 21.75$; range: 17–29) differed between overlap groups, $t(46) = -1.99$, $p = .278$, nor the number of subsequently forgotten trials ($M = 17.13$; range: 10–23), $t < 1$. Participants with less than 10 remaining knowledge-congruent trials for at least one subsequent-memory condition (subsequently remembered, subsequently forgotten) were removed from the sample and replaced by new participants ($n = 3$). All inclusion and exclusion criteria were established prior to data analyses.

2.5.1. *Behavioral analyses*

Encoding and recognition accuracy represents the percentage of correct responses. All t tests comparing performance between groups were two-tailed and significance level of all tests was set to $\alpha = .05$.

2.5.2. *fMRI analyses*

Individual time series were modeled with separate regressors for subsequently remembered and subsequently forgotten trials in the encoding phase and for correct and incorrect trials in the recognition test phase. For each run, six motion parameters were added as regressors of no interest and a high-pass filter with a 128-s cutoff was applied. The regressors were created by convolving the stimulus function related to event onset (i.e., time of picture onset for both the encoding and the recognition run) with a canonical hemodynamic response function. One contrast image was computed for each subject and phase (encoding: subsequently remembered > subsequently forgotten; recognition: correct > incorrect). The contrast of subsequently remembered > subsequently forgotten trials at encoding will be referred to as *subsequent memory effect*. In order to investigate differential subsequent memory effects between the FMHO and FMLO group, we tested the second-level difference between FMHO subsequent memory effects and FMLO subsequent memory effects, that is, the *interaction contrast* of subsequent memory and encoding condition. The interaction contrast of recognition success and encoding condition for the recognition test data reflects the group difference in the correct > incorrect contrast. An explicit mask was applied covering the whole brain, and for PrC ROI analyses, a specific PrC mask was created, comprising left and right BA36, dilated by 2 (both constructed from the WFU Pickatlas toolbox 3.0.5; Maldjian, Laurienti, Kraft, & Burdette, 2003). Based on previous literature (e.g., Davachi & Wagner, 2002; Dobbins et al., 2003; Staresina & Davachi, 2006), the general p-value threshold for the whole-brain analyses was a priori determined as $p < .001$, uncorrected, and a minimum cluster size of 10 contiguous voxels was used for the analyses (see also Lieberman & Cunningham, 2009). Due to the lower signal-to-noise ratio in the medial temporal lobe and adjacent structures as a consequence of susceptibility artifacts, the p-value threshold for analyses within the PrC, the hippocampus, and anterior temporal structures was a priori set to $p < .005$, uncorrected, at a minimum cluster size of five contiguous voxels (see e.g., Davachi & Wagner, 2002; Dobbins et al., 2003; Ojemann et al., 1997; O'Kane, Insler, & Wagner, 2005; Schacter & Wagner, 1999; Staresina & Davachi, 2006; Strange, Otten, Josephs, Rugg, & Dolan, 2002). We defined the PrC as Brodmann area (BA) 36 (BAs according to the WFU Pickatlas 3.0.5; Maldjian et al., 2003). The ATL was defined as BA 38, plus BA 20 and 21 for clusters with peaks that were located anterior to the most posterior part of BA 38 ($y = 0$).

3. Results

3.1. *Behavioral results*

On average, 92.90% ($SD = 5.42\%$) of the questions in the encoding phase were answered correctly and the proportion of correct encoding trials did not differ between subsequently remembered and forgotten trials, $t(47) = -1.38$, $p = .174$, neither in the FMHO condition, $t < 1$, nor in the FMLO condition, $t(23) = -1.20$, $p = .241$, all two-tailed. In addition, the difference of the correctly answered encoding questions for subsequently remembered versus forgotten items was not different between the FMHO and FMLO group, $t < 1$. At recognition, participants successfully recognized $M = 56\%$ ($SD = 6\%$) of the picture-label associations and recognition accuracy was not different between the FMHO group ($M = 55\%$, $SD = 5\%$) and the FMLO group ($M = 57\%$, $SD = 6\%$), $t(46) = -1.40$, $p = .169$, two-tailed.

3.2. *Imaging results*

3.2.1. *Encoding*

In order to check if PrC activation during perception of highly similar versus dissimilar pictures was actually different, we first investigated if the PrC was generally recruited more strongly at encoding in the FMHO condition than in the FMLO condition, irrespective of subsequent memory success. This was the case in one cluster in the left PrC, $t = 3.81$ (peak: $x = -22$, $y = -10$, $z = -28$; cluster size = 32 voxels), and in one cluster in the right PrC, $t = 3.23$ (peak: $x = 24$, $y = -18$, $z = -24$; cluster size = 10 voxels).

In order to test our main hypothesis that PrC contribution to FM learning should be greater in the FMHO condition than in the FMLO condition, we compared subsequent memory effects (subsequently remembered trials > subsequently forgotten trials) for the encoding conditions (subsequent memory effect FMHO > subsequent memory effect FMLO) within PrC ROI analyses using a previously determined PrC mask (see 2.5 Analyses) as region of interest. Within the right PrC, we identified a cluster of 35 voxels, in which subsequent memory effects were greater in the FMHO condition compared to the FMLO condition, peak $t = 4.51$ ($x = 28$, $y = -12$, $z = -26$; see Fig. 3). Separate analyses for this cluster within each group showed that this interaction was driven by a positive subsequent memory effect for the FMHO condition, $t(23) = 2.71$, $p = .006$, $d = .55$, and a negative subsequent memory effect for the FMLO condition, $t(23) = -2.49$, $p = .021$, $d = -.51$, two-tailed (see Fig. 3). Moreover, engagement of the PrC in encoding of remembered items was greater in the FMHO condition than in the FMLO condition, $t(46) = 2.83$, $p = .003$, $d = .82$, whereas no differences in PrC involvement between encoding conditions were observed for subsequently forgotten items, $t < 1$ (see

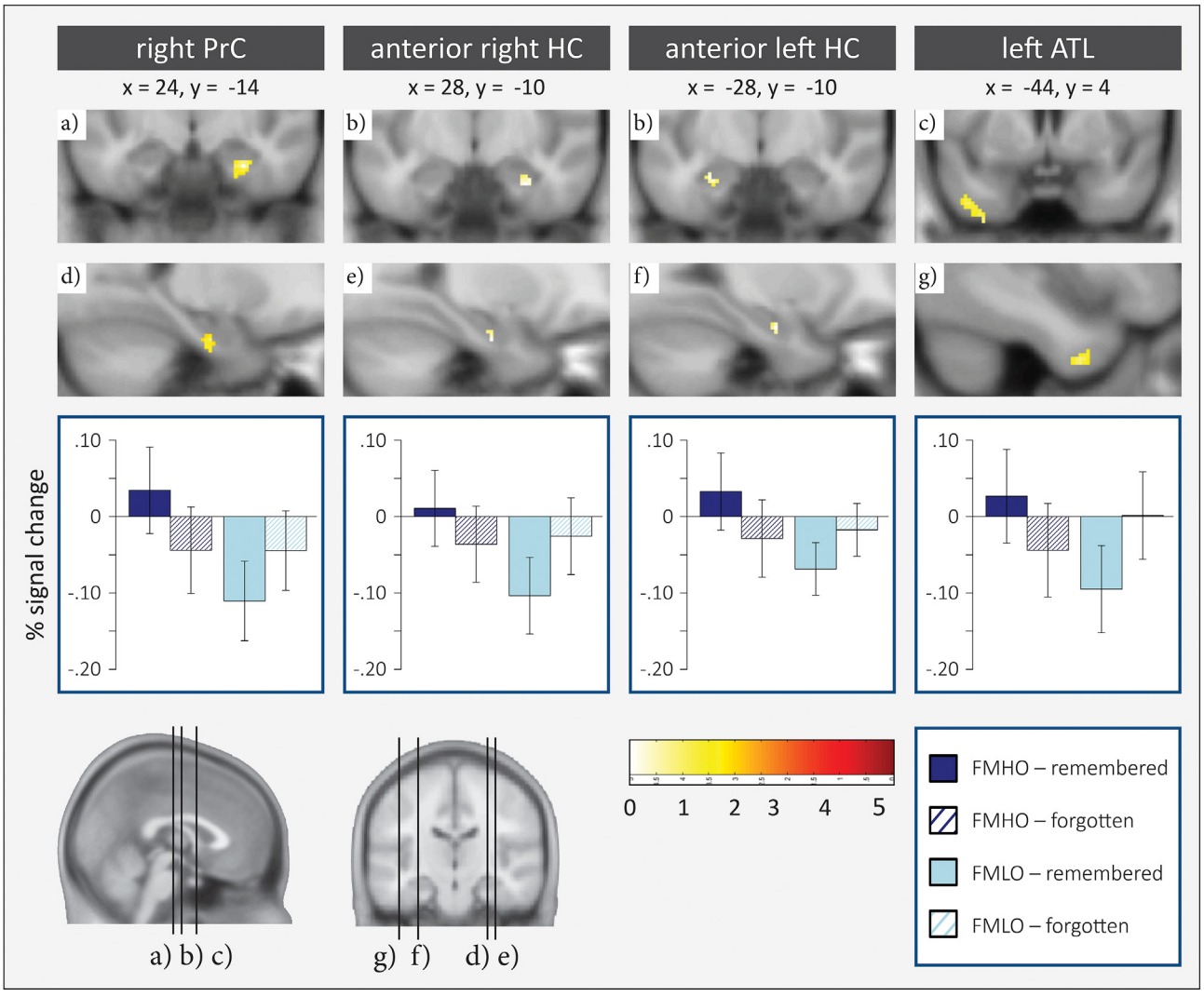

Fig. 3 – Selected clusters in which subsequent memory effects were observed to be greater for the FMHO condition compared to the FMLO condition. Error bars represent the two-tailed within-subjects confidence intervals of the difference between percent signal change at encoding of subsequently remembered compared to subsequently forgotten trials. PrC = perirhinal cortex, HC = hippocampus, ATL = anterior temporal lobe; FMHO = fast mapping, high overlap, FMLO = fast mapping, low overlap.

Fig. 3). In the left PrC ROI, no such supra-threshold interaction cluster was found.

Next, we conducted whole-brain analyses, investigating areas in which subsequent memory effects in the FMHO condition were greater than in the FMLO condition. These analyses revealed that the right PrC cluster reported above further extended to parts of the anterior right hippocampus (see Table 1 and Fig. 3). In addition to the contribution of this right perirhinal/anterior hippocampal cluster to learning, the analyses revealed further clusters showing the interaction effect in, amongst others, the ATL and the left anterior hippocampus, the medial prefrontal cortex (mPFC), and the left orbitofrontal cortex (see Table 1). Notably, the patterns of signal change underlying the interaction effects in the regions named above are remarkably similar, that is, positive subsequent memory effects in the FMHO condition and negative subsequent memory effects in the FMLO condition (see Fig. 3).

3.2.2. *Recognition*

Further analyses comparing involvement for correct versus incorrect recognition trials at retrieval revealed that a cluster in the right PrC and right anterior hippocampus, $t = 3.57$ (peak: $x = 22$, $y = -8$, $z = -28$), cluster size = 24, seems to contribute to retrieval success (i.e., correct > incorrect) more in the FMHO condition than in the FMLO condition. The same interaction was identified in the ATL and in particular the right temporal pole, $t = 4.21$ (peak: $x = 36$, $y = 6$, $z = -44$), cluster size = 45, and the left temporal pole, $t = 3.06$ (peak: $x = -36$, $y = 4$, $z = -42$), cluster size = 24. The reverse interaction contrast, indicating larger effects for the FMLO compared to the FMHO group, was

Table 1 – Local Maxima of Clusters Showing Differential Subsequent Memory Effects Between Encoding Conditions, at $p < .001$, Uncorrected.

Lobe	Region	Hemisphere	BA	x	y	z	Cluster size	t value
FMHO > FMLO								
Frontal	Medial prefrontal cortex	left	10	−4	54	−10	44	4.59
	Medial prefrontal cortex	right	10	6	54	0	21	4.03
	Premotor cortex	left	6	−34	−14	36	13	3.94
	Orbitofrontal cortex	left	11	−10	36	−24	11	3.62
Temporal	Perirhinal cortex/Anterior hippocampus	right	36	28	−12	−26	65	4.51*
	Transverse temporal gyrus	left	41	−36	−32	12	52	4.36
	Middle temporal gyrus/Inferior temporal gyrus	right	20/21	60	−14	−24	28	4.29
	Anterior hippocampus/Amygdala	left		−28	−8	−22	40	4.03*
	Middle temporal gyrus/Inferior temporal gyrus/Temporal poles	left	20/38	−46	2	−38	100	3.59*
	Middle temporal gyrus	left	39	−46	−62	12	10	3.48
Parietal	Angular gyrus	right	39	52	−68	42	44	4.98
	Cuneus/Precuneus/Calcarine cortex	right	31/17/18	8	−60	24	54	4.12
Occipital	Middle occipital gyrus	right	19	44	−84	26	22	4.92
	Cuneus	right	18	6	−78	26	18	4.01
	Lingual gyrus	left	18	−10	−76	−12	12	3.76
Other	Putamen	right	49/11	26	12	−8	152	4.97
	Brainstem	right		6	−40	−50	26	4.82
	Insula	left	13	−32	12	0	20	4.18
	Cerebral white matter	right		22	−38	40	10	3.66
FMHO < FMLO								
no suprathreshold clusters								

Note. *$p < .005$, uncorrected, minimum cluster size of 5 contiguous voxels. Please note that within all of these three clusters, suprathreshold clusters also remain at a threshold of $p < .001$, uncorrected, minimum cluster size of 10 contiguous voxels. BA = Brodmann area.

found in the left entorhinal cortex, $t = 2.98$ (peak: $x = -18$, $y = -2$, $z = -34$), cluster size = 8.

4. Discussion

There has been an extensive debate on the phenomenon of FM, questioning if FM enables rapid, direct cortical integration of novel associations, potentially bypassing the slow hippocampus-dependent consolidation processes that would typically be expected in memory for associations (e.g., Frankland & Bontempi, 2005; McClelland et al., 1995). We used a neurocognitive approach in order to identify factors that could potentially moderate learning within the FM paradigm and its underlying neurofunctional processes. We argued that high demands on the discrimination between the unknown and the known item in the FM paradigm might be associated with stronger PrC engagement, which might support the binding of the label to the unknown item. We manipulated feature overlap between the unknown and the known item with the idea that the demands on perirhinal processing are especially high in the FMHO condition. We expected that this should recruit the PrC more strongly and lead to a stronger contribution of the PrC to learning in the FMHO condition compared to the FMLO condition. This was confirmed by the present experiment, revealing subsequent memory effects within the right PrC in the FMHO condition, which were greater for the FMHO condition than for the FMLO condition.

There is complementary behavioral evidence that rapid semantic integration (as measured by means of semantic priming effects) through FM benefits from a high similarity between the objects that need to be discriminated at encoding (Zaiser et al., 2021). However, despite this evidence for feature overlap as a moderating factor, it has not yet been investigated which underlying neurocognitive mechanisms and neurofunctional correlates are associated with learning by means of FM. Many previous FM studies point to the ATL as key candidate for rapid semantic integration through FM (e.g., Atir-Sharon et al., 2015; Merhav et al., 2015; Sharon et al., 2011). This is reasonable insofar as the ATL has repeatedly been identified as a semantic hub, receiving input information from multiple modality-specific sensory areas which are then integrated into a coherent concept in the ATL (see e.g., Lambon Ralph, Jefferies, Patterson, & Rogers, 2017, and Patterson, Nestor, & Rogers, 2007, for reviews). Atir-Sharon et al. (2015) observed that the ATL specifically contributes to learning by means of FM but not EE, and Merhav et al. (2015) reported the engagement of the ATL and ATL-related networks at retrieval of associations shortly after they had been acquired through FM (but not EE). These findings implicate that the ATL potentially plays an important role in affording a direct route to cortical integration of the associations. Furthermore, the pattern of residual ATL volumes in the patients reported by Sharon et al. (2011) clearly distinguishes between the four amnesic patients who benefitted from FM and two other patients who did not show a learning benefit. Ranganath and Ritchey (2012) suggested that the ATL is part of an anterior temporal system, one of two systems in their model for memory-guided behavior. Apart from anterior parts of the ATL, this anterior temporal system encompasses the lateral orbitofrontal cortex, the amygdala, anterior regions of the hippocampus, and, as a key component, the PrC. In contrast to the ATL, the role of the PrC in rapid cortical integration through FM has not been investigated explicitly, although in the study by Sharon et al. (2011), PrC volume seems to correlate with recognition accuracy in the FM condition. Factors leading to differential PrC engagement during FM learning (e.g., feature overlap) have not been manipulated or controlled in previous studies. Moreover, as the PrC is prone to susceptibility artifacts in fMRI (see e.g., Weiskopf et al., 2006), the identification of PrC activation in some studies might have been impeded.

The present fMRI experiment showed that both ATL and PrC contribution to learning was increased in the FMHO condition. We suggest that this ATL and PrC involvement might be relevant for different cognitive operations within the FM paradigm. We consider FM as an encoding paradigm that comprises multiple mechanisms that contribute to rapid cortical integration of arbitrary associations. In particular, rapid cortical integration through FM includes the *discrimination* between pictures of complex objects, *binding* the visual features of an unknown item and an unfamiliar label to a coherent unit, and the *integration* of this unit into cortical memory networks. Our approach was to increase the demands on the *discrimination* between the unknown and the known item, which should especially recruit the PrC. Although it is yet unclear if it is an increase in perceptual or semantic overlap that drives the subsequent memory effects in the FMHO condition, we suggest that it might be both. Recent findings by Martin et al. (2018) underpin this idea. They showed that feature conjunctions are processed by the PrC not only on a purely perceptual or a purely semantic level but that the PrC uniquely processes complete specifications of items, with perceptual and semantic information represented in combination. It is thus conceivable that an increase in both perceptual and semantic overlap could lead to increased engagement of the PrC in object *discrimination*. This might automatically trigger PrC-mediated *binding* mechanisms, thereby merging the picture and the label to a unit. One explanation for stronger ATL contribution to learning in the FMHO condition could be that eventually, the *integration* of these newly bound units into semantic memory networks might be supported by ATL engagement, which would be in line with current models of the ATL as a semantic hub (e.g., Lambon Ralph et al., 2017). In particular, the availability of a highly similar known item at FMHO encoding could make the respective semantic networks better accessible and thereby, facilitate semantic integration once the picture and label have been bound to a unit. An alternative approach could be that the ATL also supports semantic integration more directly, possibly at an earlier stage in the FM paradigm and in addition to the pathway via PrC-mediated binding processes. In particular, it has previously been suggested that linking semantic item information to lexical information (i.e., a label) could be mediated by language-related networks that are strongly connected to the ATL, including the inferior frontal gyrus (see Davis & Yee, 2018). These networks could promote access to an item's label and thereby support the binding of a label to item information. This might make the

representation of an item more distinct since the label is additional information that is not shared with other items. Making items more distinct is especially beneficial in the FMHO condition. In that way, anterior temporal structures could additionally be supportive beyond the ATL integration processes that might follow PrC-mediated unitization in the FM paradigm. However, we cannot finally say in what way exactly the PrC and the ATL contribute to learning in the FM paradigm.[2]

It has been reported previously that fast and direct consolidation of new information is also possible if this information is congruent with a certain schema (e.g., Tse et al., 2007; Van Kesteren et al., 2013; see van Kesteren, Ruiter, Fernández, & Henson, 2012, for a review). Schemas can be understood as higher-level structures of prior knowledge that is conceptually related (e.g., a bird schema would comprise different birds, nests, the ability to fly, etc.). The embedding of new information into an existing schema can be facilitated if this information is congruent with the schema (see Gilboa & Marlatte, 2017, for a review). The benefit of schema congruency has been associated with mPFC involvement (van Kesteren et al., 2012, 2013). In the present study, we also observed greater mPFC subsequent memory effects in the FMHO condition compared to the FMLO condition. Although the mPFC has been associated with many cognitive functions other than schema learning, the stronger mPFC memory contribution in the FMHO condition may reasonably reflect a stronger pre-activation of the relevant schema by the highly similar known item at encoding. For example, during encoding of the bird *satellote*, an accompanying flamingo likely has triggered the facilitating bird schema more strongly than a guinea pig. However, it is not yet clear if mPFC recruitment incrementally contributes to rapid cortical integration through FM or if it is rather a by-product of PrC- and ATL-mediated learning, which might already be sufficient. More importantly, even though schema-based learning might foster the *integration* of the picture of the unknown item, which is schema-congruent with the known item in the FMHO condition due to their strong semantic relation, it is unclear how schema-based learning alone could account for the *binding* of the picture of the unknown item and the arbitrarily matched (i.e., schema-incongruent) label.

We suggest that enhancing the demands on PrC involvement, operationalized by increasing feature overlap (as in the FMHO condition), supports learning by means of FM. ATL involvement may comparably foster learning in the FMHO condition, which we attribute to a stronger integration process. Furthermore, the potentially greater schema-congruency in the FMHO condition might have additionally contributed to the FM learning process, although current models of schema learning have difficulties to explain the binding of the unknown item to the label (see e.g., Van Kesteren et al., 2012). The exact contribution of different cognitive operations and the underlying neurofunctional mechanisms driving rapid cortical integration in the highly complex FM paradigm yet needs to be further investigated.

So far, the most striking finding about the phenomenon of FM was that learning by means of FM can be hippocampus-independent (e.g., Sharon et al., 2011). However, others reported contradictory findings. For example, no memory benefit from FM was observed for older adults with reduced hippocampal volume as a result of healthy aging (Greve, Cooper, & Henson, 2014).[3] Moreover, hippocampal contribution to learning through FM in healthy young adults has been reported by Atir-Sharon et al. (2015) or at least could not finally be ruled out by Merhav et al. (2015). As already proposed previously (e.g., Atir-Sharon et al., 2015; Merhav et al., 2014, 2015; Zaiser et al., 2019, 2021), it might be over-simplified to claim that FM encoding is necessarily hippocampus-independent and hippocampal contribution to FM learning should be discussed in a more differentiated manner. First, recent research suggests that the hippocampus should not be considered a functionally homogeneous structure but might rather exhibit differences in functionality along its longitudinal axis. Whereas fine-grained recollection-like and navigational processes are allocated to more posterior parts of the hippocampus, the anterior hippocampus is associated with more coarse, gist-like representations, receiving schematic information from the ATL and object information from the PrC (e.g., Brunec et al., 2018; Brunec et al., 2019; Poppenk & Moscovitch, 2011; see Poppenk, Evensmoen, Moscovitch, & Nadel, 2013, for a review). This fits with the model of two cortical systems for memory-guided behavior by Ranganath and Ritchey (2012), which suggests that anterior parts of the hippocampus belong to the same anterior temporal system as the PrC and the ATL, and thus are associated with semantic representations of objects. Notably, in the current findings, specifically anterior parts of the hippocampus contributed to learning by means of FM, especially when feature overlap was high. This suggests that the anterior hippocampus indeed plays a role in learning through FM, which might have been neglected so far. In previous discussions on the contribution of the hippocampus to learning within the FM paradigm, the definition of the hippocampus as a functionally homogeneous structure might not have been precise enough. Hence, we suggest that lesions of patients in studies on FM learning should especially be controlled for gradients along the longitudinal axis of the hippocampus.

The second important issue in the debate on hippocampal contribution to learning through FM is that the observed benefit for patients who cannot rely on hippocampal processing (see Sharon et al., 2011) does not allow for the reverse conclusion that FM is necessarily always independent of the hippocampus. In patients who are unable to functionally rely on the hippocampus, an alternative route triggered by FM encoding might make it possible to completely bypass

[2] Please note that subsequent generalized context-dependent psycho–physiological interaction analyses with the functionally identified right PrC cluster as seed region did not reveal any differential functional connectivity patterns between encoding conditions or subsequent memory. However, this does not necessarily mean that there are no PrC-ATL connectivity differences between the FMHO and FMLO conditions but the effects might simply be too small to be detected within this experiment.

[3] Please note that in Greve et al. (2014), hippocampal volume of healthy elderly participants was, on average, still 88% of the young control group. Thus, an FM benefit comparable to Sharon et al. (2011) is not likely to be detected in this group (see also Coutanche, 2019; Zaiser et al., 2019).

hippocampal processing. However, this does not necessarily equally apply for other samples such as healthy young participants. For healthy older participants the conditions are also less clear. The typically observed hippocampal degradation in healthy aging is associated with a decline in learning of arbitrary associations compared to item memory (e.g., Naveh-Benjamin, 2000; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003). Yet, it is unclear to what extent a non-hippocampal route is triggered by FM encoding in healthy older individuals as it can be assumed that hippocampal learning is not completely dysfunctional and thus, learning of associations does not necessarily need to be hippocampus-independent. Thus, if a non-hippocampal route is not explicitly triggered (e.g., by increasing feature overlap) and rapid cortical integration is measured using an explicit recognition test in a behavioral experiment, it cannot necessarily be expected that an FM benefit in healthy elderly is found. Greve et al. (2014) reported no learning benefit from FM in healthy elderly as measured by explicit recognition accuracy and even a positive relationship between the individual hippocampal grey-matter volume and recognition accuracy (in both the FM and EE condition). Given that this older sample could still functionally rely on their hippocampus, this is in line with the notion that hippocampal processing might indeed play a role in learning through FM whenever the hippocampal route is accessible. However, Greve et al. (2014) did not further analyze their data separately for anterior and posterior parts of the hippocampus. Moreover, it is conceivable that even if healthy elderly are impaired in hippocampal learning of associations, the route by which hippocampal processing could be bypassed was also not sufficiently triggered in Greve et al. (2014) as it was not controlled for feature overlap.

Apart from the finding that anterior and medial temporal lobe structures seem to contribute to learning especially within the FMHO condition, it is unclear which processes drove learning in the FMLO condition. One could assume that analogously to anterior hippocampal contribution in the FMHO condition, posterior parts of the hippocampus might have been involved more strongly in learning in the FMLO condition. Importantly, one should be aware that not finding the posterior hippocampus to be engaged in learning or retrieval in the FMLO condition does not allow for the conclusion that it has not been involved but might as well result from a lack of power. The role of the hippocampus in rapid cortical integration through FMHO in contrast to FMLO could be examined in further fMRI experiments, possibly comparing both with a complementary EE condition, in which hippocampal contribution is expected. However, this was beyond the scope of the present experiment. In this experiment, we wanted to focus on the role of object discrimination, potentially triggering PrC processing and, consequently, enabling a rapid and direct route to cortical integration. Contrasting an FMHO with an FMLO condition, which solely differed in the degree of feature overlap, made it possible to control for any other aspects that might differ between encoding processes. This would not have been possible if we had compared an FM(HO) condition with the typical EE condition, as they strongly differ in several elements of the encoding paradigms. First, learning in the EE condition is intentional. Moreover, in contrast to the FMHO condition, only one picture is presented in the EE condition and thus, these conditions differ in object discrimination and the requirement to exclude a known item in order to infer that the label belongs to the unknown item. In addition, in the EE condition as it is typically administered (but see Atir-Sharon et al., 2015, and Zaiser et al., 2021), participants get different instructions (i.e., they are asked to remember an item without making a decision whereas FM encoding typically requires a choice between two options). It certainly would have been more likely to find differential subsequent memory effects comparing the FMHO condition with an EE condition. However, we would not have known to which underlying processes these could be attributed. One possibility to disentangle potential effects of object discrimination and learning intention could be to conduct an experiment in which these factors are crossed (see also Zaiser et al., 2021, Experiment 3, for a behavioral version revealing that both object discrimination and intentional learning affect rapid semantic integration through FM). Such an fMRI experiment would make it possible to directly compare the role of the hippocampus in conditions in which hippocampal processing would clearly be expected, which is complementary to the direct, rapid pathway that is expected to be triggered through FM(HO).

5. Conclusion

Consistent with previous findings showing that feature overlap moderates rapid semantic integration after FM encoding on a behavioral level (Zaiser et al., 2021), we conclude from the present results that differential PrC recruitment at encoding essentially influences rapid learning of novel associations within the FM paradigm. Beside the PrC, other anterior and medial temporal structures (i.e., the ATL and anterior hippocampus) were found to contribute to learning within the FM paradigm especially if the demands on object discrimination were high (operationalized by increasing feature overlap). Together with current knowledge of the functional characteristics of these brain structures, these findings pave the way to potentially hippocampus-independent learning of novel, arbitrary associations and can explain why hippocampal consolidation could be bypassed in an FM study using high feature overlap pairs (Sharon et al., 2011).

Data and materials statement

Data and analyses reported in this article can be found here: https://osf.io/r6e4c/. As copyright owners are unknown, the pictures used as stimulus materials are not openly published but available from the corresponding author [Ann-Kathrin Zaiser] upon request, on the condition that they will be used exclusively for scientific purposes and will not be openly published. Study procedures and analyses have not been preregistered prior to the research being conducted. We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Author contribution

Ann-Kathrin Zaiser: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Writing – review & editing.

Regine Bader: Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Resources, Funding acquisition.

Patric Meyer: Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Open practices

The study in this article earned an Open Data badge for transparent practices. All data reported in the manuscript are available from the corresponding author upon request.

Declaration of competing interest

None.

Acknowledgments

This work was funded by the German Research Foundation (grant numbers BA 5381/1-1 and ME 4484/1-1) in partial fulfilment of Ann-Kathrin Zaiser's doctoral dissertation. We would like to thank Luca Tarantini, Henry Schirok, and Laura Port for their help with data collection.

REFERENCES

Atir-Sharon, T., Gilboa, A., Hazan, H., Koilis, E., & Manevitz, L. M. (2015). Decoding the formation of new semantics: MVPA investigation of rapid neocortical plasticity during associative encoding through fast mapping. *Neural Plasticity, 2015*, 804385. https://doi.org/10.1155/2015/804385

Barense, M. D., Bussey, T. J., Lee, A. C. H., Rogers, T. T., Davies, R., Saksida, L. M., & Graham, K. S. (2005). Functional specialization in the human medial temporal lobe. *Journal of Neuroscience, 25*, 10239–10246. https://doi.org/10.1523/jneurosci.2704-05.2005

Barense, M. D., Gaffan, D., & Graham, K. S. (2007). The human medial temporal lobe processes online representations of complex objects. *Neuropsychologia, 45*, 2963–2974. https://doi.org/10.1016/j.neuropsychologia.2007.05.023

Bowles, B., Crupi, C., Mirsattari, S. M., Pigott, S. E., Parrent, A. G., Pruessner, J. C., & Köhler, S. (2007). Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proceedings of the National Academy of Sciences, 104*, 16382–16387. https://doi.org/10.1073/pnas.0705273104

Bowles, B., Crupi, C., Pigott, S., Parrent, A., Wiebe, S., Janzen, L., & Köhler, S. (2010). Double dissociation of selective recollection and familiarity impairments following two different surgical treatments for temporal-lobe epilepsy. *Neuropsychologia, 48*, 2640–2647. https://doi.org/10.1016/j.neuropsychologia.2010.05.010

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

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. *The Journal of Neuroscience, 33*, 18597–18607. https://doi.org/10.1523/JNEUROSCI.1548-13.2013

Brunec, I. K., Bellana, B., Ozubko, J. D., Man, V., Robin, J., Liu, Z.-X., & Moscovitch, M. (2018). Multiple scales of representation along the hippocampal anteroposterior axis in humans. *Current Biology, 28*, 2129–2135. https://doi.org/10.1016/j.cub.2018.05.016. e6.

Brunec, I. K., Robin, J., Patai, E. Z., Ozubko, J. D., Javadi, A.-H., Barense, M. D., & Moscovitch, M. (2019). Cognitive mapping style relates to posterior-anterior hippocampal volume ratio. *Hippocampus, 29*, 748–754. https://doi.org/10.1002/hipo.23072

Bussey, T. J., Saksida, L. M., & Murray, E. A. (2005). The perceptual-mnemonic/feature conjunction model of perirhinal cortex function. *The Quarterly Journal of Experimental Psychology Section B, 58*, 269–282. https://doi.org/10.1080/02724990544000004

Chen, H., Zhou, W., & Yang, J. (2019). Dissociation of the perirhinal cortex and hippocampus during discriminative learning of similar objects. *The Journal of Neuroscience, 39*, 6190–6201. https://doi.org/10.1523/jneurosci.3181-18.2019

Cooper, E., Greve, A., & Henson, R. N. (2018). Little evidence for fast mapping (FM) in adults: A review and discussion. *Cognitive Neuroscience*, 1–14. https://doi.org/10.1080/17588928.2018.1542376

Cooper, E., Greve, A., & Henson, R. N. (2019). Investigating fast mapping task components: No evidence for the role of semantic referent nor semantic inference in healthy adults. *Frontiers in Psychology, 10*, 394. https://doi.org/10.3389/fpsyg.2019.00394

Coutanche, M. N. (2019). Addressing misconceptions of fast mapping in adults. *Cognitive Neuroscience, 10*, 226–228. https://doi.org/10.1080/17588928.2019.1593955

Cowell, R. A., Barense, M. D., & Sadil, P. S. (2019). A roadmap for understanding memory: Decomposing cognitive processes into operations and representations. *eNeuro, 6*. https://doi.org/10.1523/eneuro.0122-19.2019. ENEURO.0122.

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*, 12186–12197. https://doi.org/10.1523/jneurosci.2818-06.2006

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*, 1245–1262. https://doi.org/10.1002/hipo.20865

Davachi, L., & Wagner, A. D. (2002). Hippocampal contributions to episodic encoding: Insights from relational and item-based learning. *Journal of Neurophysiology, 88*, 982–990. https://doi.org/10.1152/jn.2002.88.2.982

Davis, C. P., & Yee, E. (2018). Features, labels, space, and time: Factors supporting taxonomic relationships in the anterior temporal lobe an thematic relationships in the angular gyrus. *Language, Cognition, and Neuroscience, 34*, 1347–1357. https://doi.org/10.1080/23273798.2018.1479530

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia, 41*, 318–333. https://doi.org/10.1016/s0028-3932(02)00164-1

Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience, 6*, 119–130. https://doi.org/10.1038/nrn1607

Gilboa, A., & Marlatte, H. (2017). Neurobiology of schemas and schema-mediated memory. *Trends in Cognitive Sciences, 21*, 618–631. https://doi.org/10.1016/j.tics.2017.04.013

Greve, A., Cooper, E., & Henson, R. N. (2014). No evidence that 'fast-mapping' benefits novel learning in healthy older adults. *Neuropsychologia, 60*, 52–59. https://doi.org/10.1016/j.neuropsychologia.2014.05.011

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*, 554–560. https://doi.org/10.1016/j.neuron.2008.07.035

Himmer, L., Müller, E., Gais, S., & Schönauer, M. (2017). Sleep-mediated memory consolidation depends on the level of integration at encoding. *Neurobiology of Learning and Memory, 137*, 101–106. https://doi.org/10.1016/j.nlm.2016.11.019

Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience, 18*, 42–55. https://doi.org/10.1038/nrn.2016.150

Lieberman, M. D., & Cunningham, W. A. (2009). Type I and type II error concerns in fMRI research: Re-balancing the scale. *Social Cognitive and Affective Neuroscience, 4*, 423–428. https://doi.org/10.1093/scan/nsp052

Liuzzi, A. G., Dupont, P., Peeters, R., Bruffaerts, R., De Deyne, S., Storms, G., & Vandenberghe, R. (2019). Left perirhinal cortex codes for semantic similarity between written words defined from cued word association. *Neuroimage, 191*, 127–139. https://doi.org/10.1016/j.neuroimage.2019.02.011

Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage, 19*, 1233–1239. https://doi.org/10.1016/S1053-8119(03)00169-1

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

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review, 102*, 419–457. https://doi.org/10.1037/0033-295X.102.3.419

Merhav, M., Karni, A., & Gilboa, A. (2014). Neocortical catastrophic interference in healthy and amnesic adults: A paradoxical matter of time. *Hippocampus, 24*, 1653–1662. https://doi.org/10.1002/hipo.22353

Merhav, M., Karni, A., & Gilboa, A. (2015). Not all declarative memories are created equal: Fast Mapping as a direct route to cortical declarative representations. *Neuroimage, 117*, 80–92. https://doi.org/10.1016/j.neuroimage.2015.05.027

Meyer, P., Feldkamp, H., Hoppstädter, M., King, A. V., Frölich, L., Wessa, M., & Flor, H. (2013). Using voxel-based morphometry to examine the relationship between regional brain volumes and memory performance in amnestic mild cognitive impairment. *Frontiers in Behavioral Neuroscience, 7*, 89. https://doi.org/10.3389/fnbeh.2013.00089

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*, 590–601. https://doi.org/10.1162/jocn.2009.21199

Meyer, P., Mecklinger, A., Grunwald, T., Fell, J., Elger, C. E., & Friederici, A. D. (2005). Language processing within the human medial temporal lobe. *Hippocampus, 15*, 451–459. https://doi.org/10.1002/hipo.20070

Mundy, M. E., Downing, P. E., & Graham, K. S. (2012). Extrastriate cortex and medial temporal lobe regions respond differentially to visual feature overlap within preferred stimulus category. *Neuropsychologia, 50*, 3053–3061. https://doi.org/10.1016/j.neuropsychologia.2012.07.006

Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*, 1170–1187. https://doi.org/10.1037/0278-7393.26.5.1170

Naveh-Benjamin, M., Hussain, Z., Guez, J., & Bar-On, M. (2003). Adult age differences in episodic memory: Further support for an associative-deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29*, 826–837. https://doi.org/10.1037/0278-7393.29.5.826

Ojemann, J. G., Akbudak, E., Snyder, A. Z., McKinstry, R. C., Raichle, M. E., & Conturo, T. E. (1997). Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. *Neuroimage, 6*, 156–167. https://doi.org/10.1006/nimg.1997.0289

O'Kane, G., Insler, R. Z., & Wagner, A. D. (2005). Conceptual and perceptual novelty effects in human medial temporal cortex. *Hippocampus, 15*, 326–332. https://doi.org/10.1002/hipo.20053

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

O'Neil, E. B., Barkley, V. A., & Köhler, S. (2013). Representational demands modulate involvement of perirhinal cortex in face processing. *Hippocampus, 23*, 592–605. https://doi.org/10.1002/hipo.22117

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*, 976–987. https://doi.org/10.1038/nrn2277

Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics, 2*(10), 1–8. https://doi.org/10.3389/neuro.11.010.2008

Poppenk, J., Evensmoen, H. R., Moscovitch, M., & Nadel, L. (2013). Long-axis specialization of the human hippocampus. *Trends in Cognitive Sciences, 17*, 230–240. https://doi.org/10.1016/j.tics.2013.03.005

Poppenk, J., & Moscovitch, M. (2011). A hippocampal marker of recollection memory ability among healthy young adults: Contributions of posterior and anterior segments. *Neuron, 72*, 931–937. https://doi.org/10.1016/j.neuron.2011.10.014

R Core Team. (2016). R: A language and environment for statistical computing [Computer software]. Vienna, Austria: R Foundation for Statistical Computing.

Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience, 13*, 713–726. https://doi.org/10.1038/nrn3338

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus, 9*, 7–24. https://doi.org/10.1002/(sici)1098-1063(1999)9:1_7::aid-hipo2_3.0.co;2-k

Sharon, T. (2010). Bypassing the hippocampus: Rapid neocortical acquisition of long-term arbitrary associations via fast mapping. Doctoral dissertation. Haifa, Israel: University of Haifa. Retrieved from Younes & Soraya Nazarian Library. (ZE220.S537 2010).

Sharon, T., Moscovitch, M., & Gilboa, A. (2011). Rapid neocortical acquisition of long-term arbitrary associations independent of the hippocampus. *Proceedings of the National Academy of Sciences, 108*, 1146–1151. https://doi.org/10.1073/pnas.1005238108

Smith, C. N., Urgolites, Z. J., Hopkins, R. O., & Squire, L. R. (2014). Comparison of explicit and incidental learning strategies in memory-impaired patients. *Proceedings of the National Academy*

of Sciences, 111, 475–479. https://doi.org/10.1073/pnas.1322263111

Staresina, B. P., & Davachi, L. (2006). Differential encoding mechanisms for subsequent associative recognition and free recall. *Journal of Neuroscience, 26*, 9162–9172. https://doi.org/10.1523/jneurosci.2877-06.2006

Strange, B. A., Otten, L. J., Josephs, O., Rugg, M. D., & Dolan, R. J. (2002). Dissociable human perirhinal, hippocampal and parahippocampal roles during verbal encoding. *Journal of Neuroscience, 15*, 523–528. https://doi.org/10.1523/JNEUROSCI.22-02-00523.2002

Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., & Morris, R. G. M. (2007). Schemas and memory consolidation. *Science, 316*, 76–82. https://doi.org/10.1126/science.1135935

Van Kesteren, M. T. R., Beul, S. F., Takashima, A., Henson, R. N. A., Ruiter, D. J., & Fernandez, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. *Neuropsychologia, 51*, 2352–2359. https://doi.org/10.1016/j.neuropsychologia.2013.05.027

Van Kesteren, M. T. R., Ruiter, D. J., Fernández, G., & Henson, R. N. A. (2012). How schema and novelty augment memory formation. *Trends in Neurosciences, 35*, 211–219. https://doi.org/10.1016/j.tins.2012.02.001

Wang, W.-C., Lazzara, M. M., Ranganath, C., Knight, R. T., & Yonelinas, A. P. (2010). The medial temporal lobe supports conceptual implicit memory. *Neuron, 68*, 835–842. https://doi.org/10.1016/j.neuron.2010.11.009

Wang, W.-C., Ranganath, C., & Yonelinas, A. P. (2014). Activity reductions in perirhinal cortex predict conceptual priming and familiarity-based recognition. *Neuropsychologia, 52*, 19–26. https://doi.org/10.1016/j.neuropsychologia.2013.10.006

Warren, D. E., & Duff, M. C. (2014). Not so fast: Hippocampal amnesia slows word learning despite successful fast mapping. *Hippocampus, 24*, 920–933. https://doi.org/10.1002/hipo.22279

Warren, D. E., Tranel, D., & Duff, M. C. (2016). Impaired acquisition of new words after left temporal lobectomy despite normal fast-mapping behavior. *Neuropsychologia, 80*, 165–175. https://doi.org/10.1016/j.neuropsychologia.2015.11.016

Weiskopf, N., Hutton, C., Josephs, O., & Deichmann, R. (2006). Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3T and 1.5T. *Neuroimage, 33*, 493–504. https://doi.org/10.1016/j.neuroimage.2006.07.029

Zaiser, A.-K., Meyer, P., & Bader, R. (2019). Evidence for fast mapping in adults – moderating factors yet need to be identified [Commentary on the paper "Little evidence for fast mapping (FM) in adults: A review and discussion" by E. Cooper, A. Greve, & R. N. Henson]. *Cognitive Neuroscience*. https://doi.org/10.1080/17588928.2019.1605986

Zaiser, A.-K., Meyer, P., & Bader, R. (2021). High feature overlap and incidental encoding drive rapid semantic integration in the fast mapping paradigm. *Journal of Experimental Psychology: General*. https://doi.org/10.1037/xge0001070. Advance online publication.

Zhou, W., Chen, H., & Yang, J. (2018). Discriminative learning of similar objects enhances memory for the objects and contexts. *Learning & Memory, 25*(12), 601–610. https://doi.org/10.1101/lm.047514.118