Fast Mapping: A Rapid and Direct Route to the Integration of Novel Associations Into Semantic Memory Networks

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Ann-Kathrin Zaiser
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Dekan:	Prof. Dr. Stefan Strohmeier, Universität des Saarlandes
Berichterstatter:	Dr. Regine Bader, Universität des Saarlandes Prof. Dr. Dirk Wentura, Universität des Saarlandes
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Abstract

Contrary to traditional theories of declarative memory, there is evidence that novel, arbitrary associations can be rapidly and directly incorporated into cortical networks through an encoding paradigm called *fast mapping* (FM), possibly bypassing time-consuming hippocampal-neocortical consolidation processes. Yet, contradictory findings have been reported and factors driving learning by means of FM are still under debate. In the FM paradigm, a picture of a previously unknown item (e.g., a blue-footed bird) is presented next to a previously known item (e.g., a flamingo) and participants are asked to answer a question referring to an unfamiliar label (e.g., *Does the satellote have blue feet?*). By recognizing and rejecting the known item, they implicitly infer that the label must belong to the unknown item. Thereby, the unknown item and the label can be bound to an association, which is ultimately incorporated into cortical semantic networks. One critical operation required to solve the FM encoding task is the discrimination between items, which typically recruits the perirhinal cortex (PrC), especially if the items share many features. Here, feature overlap between the unknown and the known item was systematically manipulated, with the idea that, if the PrC contributes to FM learning, increasing the demands on perirhinal processing by increasing feature overlap might be beneficial. In a next step, increased PrC involvement might also drive the binding of the unknown item and the label. As expected, rapid semantic integration (i.e., a semantic priming effect) was only found for associations encoded within an FM paradigm in which the items shared many features. Moreover, a learning intention, which might trigger hippocampal rather than perirhinal binding processes, was disadvantageous for FM learning. Supportive evidence was obtained within an fMRI experiment, revealing that the PrC and other structures of an anterior temporal system (i.e., anterior temporal and anterior hippocampal regions) contribute to learning through FM only if feature overlap is high. Due to its functional characteristics, the PrC as part of an anterior temporal system might be especially qualified to discriminate between the unknown and known item, to bind the unknown item and the label to a unit, and thus to support their rapid incorporation into cortical networks.

Zusammenfassung

Im Gegensatz zu traditionellen Theorien des deklarativen Gedächtnisses gibt es Evidenz, dass neue, arbiträre Assoziationen mittels eines Enkodierparadigmas namens *Fast Mapping* (FM) schnell und direkt in kortikale Netzwerke integriert werden können, was die Umgehung zeitaufwändiger hippokampal-neokortikaler Konsolidierungsprozesse ermöglicht. Jedoch wurden viele widersprüchliche Befunde berichtet und Faktoren, die das Lernen mittels FM steuern, werden noch immer diskutiert. Im FM-Paradigma wird ein Bild eines zuvor unbekannten Objekts (z.B. ein blaufüßiger Vogel) neben einem zuvor bekannten Objekt (z.B. ein Flamingo) dargeboten und es soll eine Frage bezüglich eines unvertrauten Namens beantwortet werden (z.B. *Hat der Satellot blaue Füße?*). Durch das Erkennen und Zurückweisen des bekannten Objekts ist es möglich zu erschließen, dass der Name zum unbekannten Objekt gehört. Dadurch können das unbekannte Objekt und der Name zu einer Assoziation gebunden werden, die letztlich in kortikale semantische Netzwerke integriert wird. Eine kritische Operation, die erforderlich ist um die FM-Enkodieraufgabe zu lösen, ist die Diskrimination zwischen Objekten, welche typischerweise den perirhinalen Kortex (PrC) rekrutiert, vor allem, wenn die Objekte viele Merkmale gemein haben. In dieser Arbeit wurde die Merkmalsüberlappung zwischen dem unbekannten und dem bekannten Objekt systematisch manipuliert mit der Idee, dass, wenn der PrC zum Lernen durch FM beiträgt, eine Erhöhung der Anforderungen an den PrC in Form einer stärkeren Merkmalsüberlappung günstig sein könnte. In einem nächsten Schritt könnte eine stärkere PrC-Beteiligung auch das Binden des unbekannten Objekts und des Namens antreiben. Wie erwartet wurde eine semantische Integration (d.h. ein semantischer Priming-Effekt) nur gefunden, wenn die Assoziationen innerhalb eines FM-Paradigmas enkodiert wurden, in dem die Objekte viele Merkmale gemein hatten. Zudem erwies sich eine Lernintention, welche eher hippokampale als perirhinale Bindungsprozesse hervorrufen könnte, als unvorteilhaft für das Lernen durch FM. Stützende Evidenz wurde innerhalb eines fMRT-Experiments gewonnen, welches zeigte, dass der PrC und andere Strukturen eines anterior-temporalen Systems (d.h. anterior-temporale und anterior-hippokampale

Regionen) zum Lernen mittels FM nur dann beitragen, wenn die Merkmalsüberlappung hoch ist. Aufgrund seiner funktionellen Charakteristika könnte der PrC als Teil eines anterior-temporalen Systems speziell qualifiziert sein um zwischen dem unbekannten und bekannten Objekt zu diskriminieren, das unbekannte Objekt und den Namen zu einer Einheit zu binden und dadurch deren schnelle Integration in kortikale Netzwerke zu fördern.

Acknowledgments

First and foremost, I would like to thank my supervisors within this PhD project, Regine Bader and Patric Meyer. Thank you for the opportunity to (literally) enjoy research training in a project like this, which could not have fit any better and is very much appreciated. Thank you for your great support and many fruitful discussions, for always having an open door, for your trust in me to realize my research ideas, and for letting me grow professionally and personally. Thank you to Dirk Wentura for your interest in this project, for eye-opening discussions on negative priming effects, and for reading and reviewing this thesis. Many thanks go to Axel Mecklinger and my current and former colleagues of the Experimental Neuropsychology Unit at Saarland University, for greatly supporting me in and beyond research, which I both very much appreciate. Thank you for the daily collective lunch time, for several life-saving coffee sessions, and for countless outbursts of laughter that still make me laugh even now that I am writing these lines.

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List of Studies

This doctoral thesis is based on five experiments and one rating study that are reported within three manuscripts, of which one is currently under review. I am the first author of these manuscripts and the authors listed below contributed to the work. In oder to keep with the practice of the manuscripts, I consistently employ ”we” instead of ”I” whenever applicable in the main text.

Chapter 5 – Experiments 1 and 2:
The Role of Feature Overlap in Rapid Semantic and Lexical Integration by Means of Fast Mapping

Zaiser, A.-K., Meyer, P., & Bader, R. (under review). *Feature overlap modulates rapid semantic but not lexical integration of novel associations by means of fast mapping.* Manuscript submitted for publication.

Chapter 6 – Experiment 3:
The Neural Underpinnings of Learning by Means of Fast Mapping

Zaiser, A.-K., Bader, R., & Meyer, P. (in preparation). *High feature overlap reveals the importance of anterior and medial temporal lobe structures for learning by means of fast mapping.*

Chapter 7 – Experiments 4 and 5:
Further Determinants of Rapid Semantic Integration by Means of Fast Mapping

Zaiser, A.-K., Meyer, P., & Bader, R. (in preparation). *Incidental encoding and object discrimination are prerequisites for rapid semantic integration of novel associations by means of fast mapping.*

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Abbreviations

α	alpha, rate of type I error
$^{\circ}$	degree
η_p^2	effect size partial eta squared
€	euro
%	percent
ANOVA	analysis of variance
AT	anterior temporal
ATL	anterior temporal lobe
BA	Brodmann area
BIC	binding of items and context
CA	cornu ammonis
cf.	*confer* (compare)
CLS	complementary learning systems
cm	centimeter
d	effect size *d*
EE	explicit encoding
e.g.	*exempli gratia* (for example)
ErC	entorhinal cortex
et al.	*et alii / et aliae* (and others)
FM	fast mapping
FMHO	fast mapping, high overlap
FMLO	fast mapping, low overlap
fMRI	functional magnetic resonance imaging
FoV	field of view
i.e.	*id est* (that is)
IE	incidental encoding
intFMHO	intentional fast mapping, high overlap
M	mean

mm	millimeter
MNI	Montréal Neurological Institute
mPFC	medial prefrontal cortex
ms	millisecond
MTL	medial temporal lobe
MTT	multiple-trace theory
PhC	parahippocampal cortex
PM	posterior medial
PrC	perirhinal cortex
RsC	retrosplenial cortex
SAM	Survey of Autobiographical Memory
rTMS	repetitive transcranial magnetic stimulation
SD	standard deviation
SLIMM	schema-linked interactions between medial prefrontal and medial temporal regions
SPI	serial–parallel–independent
TE	echo time
TR	repetition time
vmPFC	ventromedial prefrontal cortex
vs.	versus

Introduction

Human memory has fascinated society ever since. Our memory is the personal record that stores all our experiences and essentially affects our personality, our perception, our behavior. Our current knowledge is built on our memories and thus, is the result of previous experiences. Many fundamental questions have been raised, such as how experiences are transformed into new knowledge. For instance, we recognize a quacking animal with a yellow bill, feathers, and orange feet as a duck. But when did we acquire the association between these visual and auditory features and the label *duck*? And how did the duck obtain its semantic meaning and assignment to the bird category instead of being stored as a loose conglomerate of perceptual features? These and other questions will be addressed in this thesis, which takes a neurocognitive perspective on the formation of new semantic memory representations.

Chapter 1 provides an overview of significant theoretical frameworks of the transfer of a new experience to semantic long-term memory and embeds them into general principles of neurocognition of memory. Many traditional approaches agree upon the rapid initial acquisition of new information by a system within the hippocampus, a brain structure located in the medial temporal lobe (MTL). During hippocampal processing, single episodic representations are kept separate from each other in order to prevent interference (see Yassa & Stark, 2011, for a review). These distinct episodic memory traces are then slowly and gradually transferred to a neocortical system (e.g., Frankland & Bontempi, 2005; McClelland, McNaughton, & O'Reilly, 1995). They become incorporated into cortical semantic networks, where newly acquired information is closely linked to semantically related memory representations, allowing for the creation of abstracted concepts from many episodic experiences (but see Tulving & Markowitsch, 1998, for the reverse view that episodic memory builds on semantic memory). In other words, the episode of a quacking animal swimming in a pond is not only stored as a distinct memory trace representing the autobiographical experience but also contributes to the creation of the concept *duck*, is semantically related to previously stored birds, and provides the opportunity for future duck encounters to be integrated into conceptually similar network structures. Despite theoretical differences between frameworks, there is agreement that such system-level consolidation is a time-consuming process that strongly relies on hippocampal-neocortical interplay.

Interestingly, there is evidence that *rapid* cortical integration of novel, arbitrary associations is possible by means of an encoding paradigm called *fast mapping* (FM; e.g., Merhav, Karni, & Gilboa, 2014, 2015; Sharon, Moscovitch, & Gilboa, 2011). In a typical FM task, a picture of a previously unknown item (e.g., a blue-footed bird) is presented together with a known item (e.g., a flamingo) and a question referring to an unfamiliar label (e.g., *Does the satellote have blue feet?*). Answering this question requires the recognition and rejection of the known item and the inferential conclusion that the label refers to the unknown item. Thereby, participants are assumed to create a link between the picture of the unknown item and the label. This picture-label association is then transferred to cortical networks, which would typically involve slow hippocampal-neocortical consolidation processes. Strikingly, declarative memory of associations acquired through FM has been found shortly after encoding even in people who cannot rely on hippocampal functioning due to severe hippocampal lesions (Merhav et al., 2014; Sharon et al., 2011). It is thus reasonable to assume that FM provides a fast and direct pathway to cortical integration of novel associations, potentially bypassing time-consuming hippocampal-neocortical consolidation processes. However, contradictory findings have been reported (e.g., Greve, Cooper, & Henson, 2014; Smith, Urgolites, Hopkins, & Squire, 2014; Warren & Duff, 2014; Warren, Tranel, & Duff, 2016), which have been extensively discussed in a recent debate on the existence of the "phenomenon" of FM as a special form of learning (Cooper, Greve, & Henson, 2018; see also Coutanche, 2019; Elward, Dzieciol, & Vargha-Khadem, 2019; Gaskell & Lindsay, 2019; Gernsbacher & Morson, 2019; Gilboa, 2019; Koutstaal, 2019; Mak, 2019; O'Connor, Lindsay, Mather, & Riggs, 2019; Warren & Duff, 2019; Zaiser, Meyer, & Bader, 2019, for commentaries).

In Chapter 2, an overview and discussion of the previous literature on FM will be given and suggestions will be made on how putative contradictions can be resolved. Within five experiments reported in this thesis, factors moderating rapid semantic integration of novel associations through FM were identified (Chapter 5, Experiments 1 and 2; Chapter 7, Experiments 4 and 5) and the neurofunctional underpinnings of learning by means of FM were investigated (Chapter 6; Experiment 3). In order to do so, new stimulus material needed to be created that had been validated in a rating study prior to the experiments and is introduced in Chapter 4. In Chapter 8, the reported findings and their implications will be discussed.

This thesis provides insights on the conditions under which time-consuming consolidation processes can be bypassed in learning by means of FM, paving the way for a direct, rapid incorporation of novel, arbitrary associations into cortical networks – thereby challenging well-established, traditional theories of memory.

Chapter 1

Long-Term Memory and Its Neural Underpinnings

Is there *one* memory? Today, certainly no one would claim that memory can be considered one perfectly homogeneous construct. For example, there is broad consensus that, on a coarse-grained level, short-term and long-term memory can be differentiated with respect to capacity and the permanence of memory representations (Atkinson & Shiffrin, 1968; Cowan, 2008; but see Ranganath & Blumenfeld, 2005). A common way to further subcategorize long-term memory goes back to a taxonomy suggested by Squire (1986, 1992, see Figure 1.1 for a slightly modified version). According to his mainly retrieval-oriented categorization, long-term memory consists of two broader subsystems which are distinguishable by the degree of consciousness of retrieval: Whereas *non-declarative memory* is described as implicitly accessible memory, *declarative memory* comprises memory representations of facts and events that are consciously accessible (see also Squire, 2004; Tulving, 1985). On a more fine-grained level of the taxonomy, non-declarative memory is subdivided into procedural and automatic types of memory such as priming, conditioning, and skill learning (see Figure 1.1), whereas declarative memory is split into *semantic memory* and *episodic memory* (Tulving, 1972; Tulving & Markowitsch, 1998). This segregation seems intuitively straightforward: Whereas episodic memory comprises memories for single autobiographic episodes within the context in which they have been experienced, semantic memory has been dubbed a "mental thesaurus" (Tulving, 1972, p. 386), providing more gist-like, general memories for facts and world knowledge that has been gained through an accumulation and abstraction of many experiences (e.g., Squire, 1992; Squire & Zola, 1998; but see Irish & Piguet, 2013; Waidergoren, Segalowicz, & Gilboa, 2012). Other approaches categorize declarative memory with regard to retrieval processes in recognition memory (i.e., the

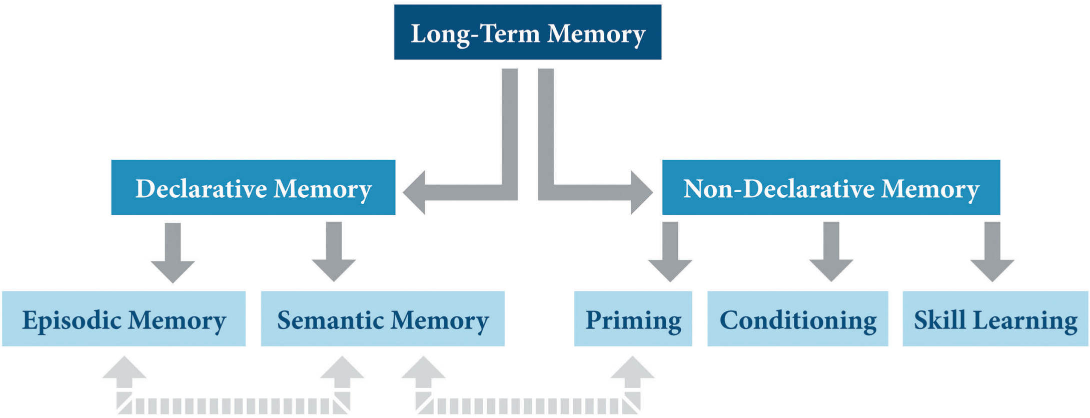

Figure 1.1 Taxonomy of long-term memory systems. Based on the original taxonomy by Squire (1986) and modified according to the text. Dashed arrows represent the permeable boundaries between episodic memory, semantic memory, and (semantic) priming.

exact *recollection* of a memory in all contextual details vs. a feeling of *familiarity*; Brown & Aggleton, 2001; Yonelinas, 2002; but see Squire, Wixted, & Clark, 2007). Lastly, there are approaches to categorize memory with regard to the required binding mechanisms (e.g., *relational* binding of item-context associations vs. *representational* binding of common information shared by multiple episodes; Opitz, 2010) or processing modes (e.g., rapid encoding of associations vs. slow encoding of items, leading to flexible vs. stable representations, respectively; Henke, 2010).

However, both behavioral and neural evidence indicate that the boundaries between memory systems are often permeable, for example, between episodic and semantic memory (see e.g., Irish & Piguet, 2013; Waidergoren et al., 2012) and even on a higher level between declarative and non-declarative memory (Squire, 1992), as “there are phenomena that do not seem to fit readily into such a taxonomy” (Tulving, Schacter, & Stark, 1982, p. 336). This is an important note for this thesis as it merges several perspectives. It has its focus on the binding of items (i.e., a picture and a word) to novel, arbitrary inter-item associations and their incorporation into semantic long-term memory networks already after having experienced them only once in a single episode. Phenomena of non-declarative memory, such as semantic priming, are used in order to access semantic memory, which would typically be subsumed under declarative memory. Due to the greatly varying comprehension of the dissection of memory and the fluent boundaries between systems (see Figure 1.1), the concepts that are most relevant for this work and their neural underpinnings shall be defined in the following and a perspective that overcomes rigid memory categorization will be introduced.

Pioneering work on the neural underpinnings of long-term memory was conducted by Scoville and Milner (1957). They investigated memory in Henry Molaison (H. M.), who underwent a resection of large parts of the MTL and especially the hippocampus (see Figure 1.2) due to intractable epilepsy (see Augustinack et al., 2014; and Corkin, Amaral, González, Johnson, & Hyman, 1997, for more detailed lesion overviews). Despite the success of the surgery with regard to his seizures, he unexpectedly suffered from severe anterograde and temporally graded retrograde amnesia (see Corkin, 2002, for a review). H. M. was unable to create new declarative memories for experiences following the surgery and to retrieve events he had experienced only recently before the surgery. In contrast, memories that had been created more than 11 years prior to the surgery were preserved (Sagar, Cohen, Corkin, & Growdon, 1985), and also non-declarative implicit memory remained unimpaired (Corkin, 1968; Gabrieli, Corkin, Mickel, & Growdon, 1993; see Corkin, 2002, for a review). This led to the assumption that the MTL and especially the hippocampus has a crucial role in declarative memory (see Eichenbaum, Yonelinas, & Ranganath, 2007, for a review). Since then, the MTL has been in the spotlight of memory research.

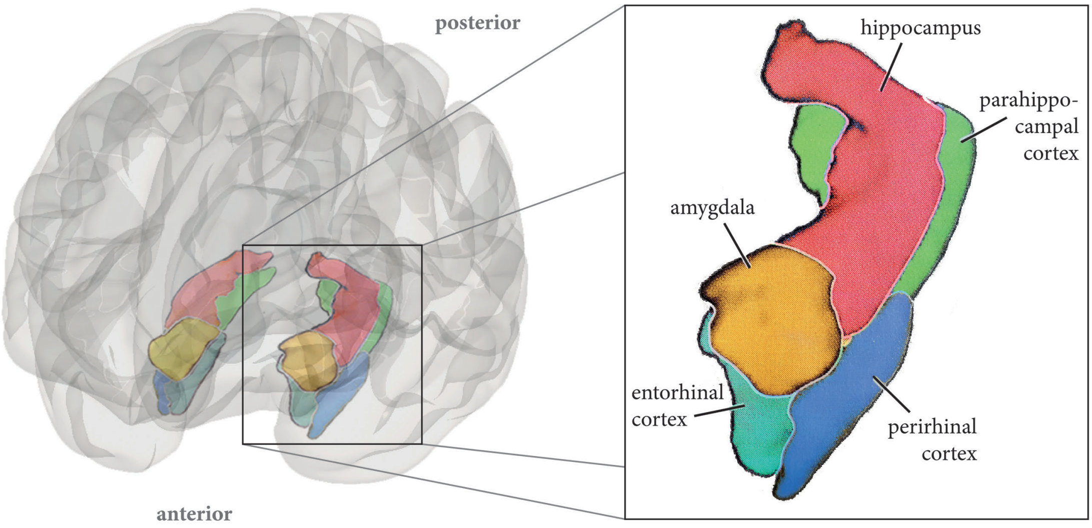

Figure 1.2 Three-dimensional view of the medial temporal lobe (MTL) subregions. Within-brain view for the purpose of rough localization only; proportions and position to be seen as an approximation. Please note that the amygdala is often not defined as part of the MTL (e.g., Squire, Stark, & Clark, 2004). Color figure of the MTL adapted from Purves et al. (2013, p. 286), with permission from Oxford University Press. Colors changed in accordance with Figure 1.3 and Figure 1.4. Whole-brain template extracted from MATLAB Conn toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012, www.nitrc.org/projects/conn).

Within declarative memory, patients with lesions predominantly to the hippocampus showed a deterioration of episodic memory (Zola-Morgan, Squire, & Amaral, 1986) but spared semantic memory (e.g., Hirano, Noguchi, Hosokawa, & Takayama, 2002; Vargha-Khadem, 1997; Vargha-Khadem, Gadian, & Mishkin, 2001), whereas patients with reduced volume of especially the anterior temporal lobe (ATL) and adjacent MTL structures, such as in semantic dementia (e.g., Hodges & Patterson, 2007), showed the reverse pattern (e.g., Adlam, Patterson, & Hodges, 2009; Irish et al., 2016; Irish et al., 2011). This double dissociation seems to provide support for the episodic–semantic distinction and suggests that episodic memory typically relies especially on the hippocampus, whereas semantic memory depends more on anterior temporal and extra-hippocampal MTL structures. Furthermore, there is also evidence for a selective impairment of recollection- but not familiarity-based retrieval in patients with lesions predominantly to the hippocampus (e.g., Aggleton et al., 2005; Vargha-Khadem, 1997; Vargha-Khadem et al., 2001), whereas patients with lesions to cortical MTL structures such as the perirhinal cortex (PrC; see Figure 1.2) exhibit specific deterioration in familiarity-based but not recollection-based retrieval (e.g., Bowles et al., 2007; Bowles et al., 2010).

Lesion-related double dissociations with regard to *memory systems* (e.g., episodic vs. semantic memory, according to Squire, 1986) or *retrieval processes* (i.e., recollection vs. familiarity) are informative on a system or process level, respectively, since the memory impairments are assessed using tasks that aim at the distinction of interest, irrespective of the underlying mechanisms. For example, the inability to exactly remember items together with a detailed context leads to the assumption of an impaired recollection process, which is a complex process based on a complex combination of mechanisms, in the way it has been defined (see Yonelinas, 2002). Even though some memory subsystems and retrieval processes are more closely related (e.g., episodic memory and recollection) and can be better ascribed to specific brain regions (e.g., the hippocampus) than others, Waidergoren et al. (2012) point out that recollection-based retrieval can appear in both semantic and episodic memory, that the interpretation of familiarity as one homogeneous process might be oversimplified, and that recollection- and familiarity-based retrieval are at least not restricted to the hippocampus or cortical regions of the MTL (see also Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012; Renoult et al., 2016; Suzuki & Naya, 2014). Describing memory on a system or process level might thus possibly not be the most efficient approach towards a full understanding of memory. The mechanistic components underlying these levels, such as the *representational content* and *cognitive operations*, are often conflated and their specific interaction is left unspecified. A cognitive operation could be, for example, *pattern separation*, which orthogonalizes memory representations in order to keep them distinct and thus, to prevent interference through overlapping information (see Yassa & Stark, 2011; and Rolls, 2013, for reviews). A further cognitive operation would be *pattern completion*, that is, recalling detailed, unique memory representations through the reinstantiation of the complete representation when only a partial cue is provided (e.g., Hunsaker & Kesner, 2013; see Rolls, 2013, for a review). Representational content, in contrast, describes the associative nature of the processed information. Binding multiple items to an inter-item association or binding items and their context to an item-context association is typically ascribed to the hippocampus (e.g., Davachi, 2006). In the hippocampus, these associations can be represented separately through their orthogonalization by pattern separation (see Yassa & Stark, 2011, for a review). In contrast, binding single features within an item (i.e., intra-item associations; e.g., the colors yellow and brown, feathers and a bill as intrinsic features of a brown duck with a yellow bill) would trigger pattern separation between single items, which can be ascribed to the PrC (Barense et al., 2005; Burke et al., 2011; Chen, Zhou, & Yang, 2019; Cowell, Bussey, & Saksida, 2010; Kent, Hvoslef-Eide, Saksida, & Bussey, 2016). Thus, it seems that many structures within the MTL may play a role in similar cognitive operations, depending on the representational demands of the task. No matter if inter-item, item-context, or intra-item associations, the cognitive operation of pattern separation would always be the orthogonalization of information in order to make them distinct and unique. On a process level, however, cognitive operations are conflated with representational content. This results in attempts to pin the higher-level phenomenology of processes to different brain structures, ignoring the underlying mechanisms that constitute these processes.

It is important to note that there is indeed justification for the investigation of memory on a system or process level. System-, process-, representation-, and operation-oriented views are not contradictory but simply communicate on different levels. The challenge rather is to find the level with the greatest explanatory strength. I share the opinion that if we really aim to understand the neurocognitive mechanisms of long-term memory, it is inevitable to argue on a deeper level, that is, on a level of cognitive operations and representational content, which in return can explain the systems and processes on a higher level (Cowell, Barense, & Sadil, 2019; see also Bussey, Saksida, & Murray, 2005; Cowell et al., 2010, 2011; Saksida & Bussey, 2010). This can constitute a more elegant way to find a model of memory that is most parsimonious but still has a great explanatory strength as it acknowledges that the same operation (e.g., pattern completion) can contribute to different processes in different systems (e.g., recollection and priming), which is also reflected in the fluent boundaries between the memory subsystems suggested by Squire (1986, see Figure 1.1). Therefore, much of the derivation of the hypotheses in this thesis will be built on this perspective. There are cytoarchitectonically and functionally distinguishable brain structures that can be better related to certain combinations of operations and representational contents than others (e.g., Lavenex & Amaral, 2000). In the following, the brain structures most relevant for this thesis and their neurofunctional characteristics will be introduced and finally be embedded into a broader framework of memory-guided behavior.

1.1 The Functional Characteristics of the Medial Temporal Lobe

Although many regions all over the brain are involved in memory, probably no other brain structure has been linked to long-term memory as strongly as the MTL, with the hippocampus as most prominent component especially in the early literature. The hippocampus comprises the dentate gyrus, the cornu ammonis (CA) hippocampal subfields, and the subiculum (see Figure 1.3; Squire & Zola-Morgan, 1991). Together with the entorhinal cortex (ErC) and the parahippocampal gyrus, consisting of the perirhinal cortex (PrC) and the parahippocampal cortex (PhC), it creates the MTL (Squire, Stark, & Clark, 2004, see also Figure 1.2 and Figure 1.3). For a better overview, the functional characteristics of the MTL will be outlined separately for encoding and retrieval processes.

1.1.1 Medial Temporal Lobe: Encoding

Information flow in the MTL is assumed to have a hierarchic structure with the hippocampus at the top of the hierarchy, both at encoding (Davachi, 2006) and retrieval (Diana, Yonelinas, & Ranganath, 2007; see also Montaldi & Mayes, 2010). At encoding, novel information is projected from modality-specific cortical association

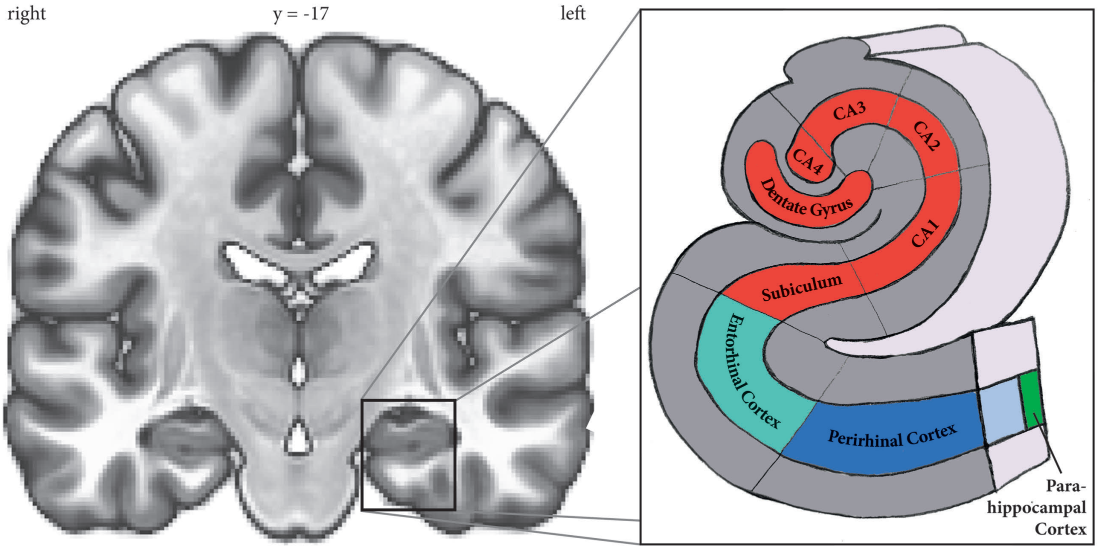

Figure 1.3 Schematic coronal view of the medial temporal lobe (MTL), illustrating relative locations of MTL components. Proportions and localizations to be seen as a rough approximation only. Note that CA4 is often not defined as separate hippocampal subfield but is subsumed under the CA3 part that inserts within the dentate gyrus. Template of the coronal slice on the left extracted from the MATLAB Conn toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012, www.nitrc.org/projects/conn).

areas to the parahippocampal gyrus and then further transferred to the hippocampus via the ErC (e.g., Davachi, 2006; Lavenex & Amaral, 2000). The PrC as anterior part of the parahippocampal gyrus receives input from visual association areas along the ventral visual stream, whereas the PhC as posterior part receives input from the dorsal stream. The hierarchy at encoding will be described upwards, starting with the parahippocampal gyrus (i.e., PhC and PrC).

The PhC has been especially found involved in the processing of visuo-spatial information (e.g., Davachi, Mitchell, & Wagner, 2003), such as in navigational tasks (Aguirre, Detre, Alsop, & D'Esposito, 1996; Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Epstein, 2008) or general scene processing (Bohbot et al., 2015; Hodgetts, Shine, Lawrence, Downing, & Graham, 2016; Robin & Olsen, 2019; see Robin, 2018, for a review). Apart from spatial processing, PhC function also includes the processing of contextual associations in general (Bar, 2004; Düzel et al., 2003; see Aminoff, Kveraga, & Bar, 2013, for a review; but see Robin & Olsen, 2019, for the view of a more modality-specific PhC processing of scenes), with stronger activation during encoding leading to better memory for associations (e.g., Ranganath et al., 2003). It is further engaged in the binding of contextual details (Aminoff et al., 2013) not only for visual but also multi-modal information such as auditory (e.g., Arnott, Cant, Dutton,

& Goodale, 2008) or odor stimuli (e.g., Kjelvik, Evensmoen, Brezova, & Håberg, 2012). PhC involvement has not only been found for the processing of associations but also in item memory (Gold et al., 2006; Kirwan & Stark, 2004; Köhler, Danckert, Gati, & Menon, 2005; Pihlajamaki et al., 2004). One reason for this heterogeneity with regard to the representational content could be the anatomical variability along its longitudinal axis. Pihlajamaki et al. (2004) reported especially posterior PhC regions to be involved in memory for spatial relations *within* a familiar spatial arrangement, whereas more anterior PhC parts are involved in memory for familiar spatial arrangements as such (i.e., the change of *contents* of a familiar context), which might be processed in a more holistic way that is closer to the representation of a unit. Interestingly, Aminoff et al. (2013) suggested that, just like item features can be bound to coherent feature conjunctions that are processed as a unit, context features can be bound to contextual feature conjunctions that are represented within a single "context frame".

In contrast to the PhC, the PrC operates on a representational level of complex, holistically processed intra-item feature conjunctions. It is assumed that the PrC supports the resolution of ambiguitiy between items by binding an item's elemental features (e.g., color, shapes, sounds, etc.) to multi-modal feature conjunctions or intra-item associations, which represent all item features in an exact, unique constellation (Barense et al., 2005; Barense, Gaffan, & Graham, 2007; Cowell et al., 2010; Diana et al., 2007; Fernandez & Tendolkar, 2006; Suzuki & Amaral, 2004). For example, the colors green, brown, yellow, orange, and the presence of feathers, a pointed shape in the upper part, two eyes – all of these placed upon two stilts – are merged to a holistically processed, distinct feature conjunction of a green-headed item with brown feathers, a yellow bill, standing on two orange feet. This feature conjunction would be represented separately from a yellow body carrying green feet with an orange head and a feathered bill, even though the same elemental features appear in both items. Thus, this perirhinal function supports the creation of pattern-separated unique item representations (Burke et al., 2011; Kent et al., 2016; Saksida, Bussey, Buckmaster, & Murray, 2006). In memory, the creation of separate memory traces reduces overlap between memory representations and thereby prevents new and old memory representations from pro- and retroactive interference, respectively (McClelland et al., 1995; Norman & O'Reilly, 2003; Yassa & Stark, 2011). In perceptual tasks, the same cognitive operation enables us to discriminate on-line between highly similar items. The cognitive operations of perirhinal intra-item feature binding and the resulting item-level pattern separation are not restricted to picture material but have also been found for polymodal associations (Fernandez & Tendolkar, 2006), such as picture-sound conjunctions (Taylor, Moss, Stamatakis, & Tyler, 2006) or associations between pictures and tactile stimuli (Holdstock, Hocking, Notley, Devlin, & Price, 2009), as long as the features were processed as intrinsic features within the same item. Based on Mayes et al. (2004), Mayes, Montaldi, and Migo (2007) suggested a domain-dichotomy view, which assumes that the PrC is also essentially involved in inter-item binding if the items belong to the same domain (e.g., are both faces), whereas between-domain associations are ascribed to the hippocampus. However, contradictory findings have been reported, such that patients with circumscribed hippocampal lesions were equally impaired in learning of within-domain and between-domain associations (Turriziani, 2004). In support of that, Bastin and Van der Linden (2006) found an equal selective decline of associative memory for both within- and between-domain associations in old age and Park and Rugg (2011) reported corresponding fMRI evidence for similar PrC involvement in learning of within- and between-domain associations. Irrespective of the validity of the domain-dichotomy view, the binding of arbitrary between-domain inter-item associations, such as two previously independent, unrelated words of different categories, is typically not ascribed to the PrC. However, PrC processing can also support between-domain binding of arbitrary inter-item associations but only if unitization of the items is encouraged, that is, if the task requires to integrate single items into a holistically processed compound, which can be processed as a single unit. In other words, the PrC contributes to the conversion of inter-item to intra-item associations (see e.g., Haskins, Yonelinas, Quamme, & Ranganath, 2008; Quamme, Yonelinas, & Norman, 2007, for word-word associations; see also Diana, Yonelinas, & Ranganath, 2010; Staresina & Davachi, 2006, for word-color associations). On a system level, the PrC is not only involved in declarative memory as such but is also observed in general semantic processing (Bruffaerts et al., 2013), such as the understanding of the semantic meaning of a sentence (Meyer, Mecklinger, & Friederici, 2010), in judgments of an item's conceptual properties (Martin, Douglas, Newsome, Man, & Barense, 2018), and in semantic priming (Heusser, Awipi, & Davachi, 2013; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010; Wang, Ranganath, & Yonelinas, 2014), which again underscores the fluent boundaries between declarative and non-declarative memory (see Figure 1.1).

At encoding, both item information from the PrC and context information from the PhC are then further transferred to the ErC (Davachi, 2006). The ErC extends along the longitudinal axis of the hippocampus, medial to the parahippocampal gyrus, with its medial parts more distal and its lateral regions more proximal to the PrC and PhC (see Figure 1.2). Whereas the PrC projects to proximal entorhinal areas, the PhC projects to more distal regions of the ErC (Eichenbaum et al., 2007; Ranganath & Ritchey, 2012), in which input from PrC and PhC still remains in separate pathways (Eichenbaum et al., 2007; Suzuki & Amaral, 2004; Witter et al., 2000, see also Figure 1.4 for a similar separation at retrieval). This is supported by findings that the antero-lateral (i.e., anterior proximal) ErC is more involved in the holistic processing of items, whereas postero-medial (i.e., posterior distal) ErC regions seem to be specialized on spatial information (see Robin, Rai, Valli, & Olsen, 2019, for a review). The ErC then transfers this information to the hippocampus and, in particular, to the hippocampal subfield CA3 (in adults mainly via the dentate gyrus; see Figure 1.3). In CA3, information from the PrC and PhC converge to one domain-general memory trace on which all information of an episode is coded, creating a unique, hippocampally pattern-separated combination of an item within its specific context. This is supported by a large body of evidence showing that learning of associations between items or between items and their context essentially depends on hippocampal engagement at encoding (Davachi & Wagner, 2002; Park & Rugg, 2011; Sperling et al., 2003). For example, hippocampal involvement is frequently found in tasks, in which items and contexts need to be bound to item-context associations, such as source memory tasks (Kensinger, 2006; Ranganath et al., 2003; Staresina & Davachi, 2008) and tasks in which the spatial location of a previously presented item shall be remembered (Uncapher, Otten, & Rugg, 2006). On a system level, hippocampal engagement has mainly been observed in declarative memory and intentional encoding (Corkin, 2002; Eichenbaum et al., 2007; Tulving & Markowitsch, 1998) but also in non-declarative memory (Ross, Sadil, Wilson, & Cowell, 2018; Schendan, Searl, Melrose, & Stern, 2003). Olsen, Moses, Riggs, and Ryan (2012) resolve this putative contradiction by pointing out the level of representational content. They state that the hippocampus is especially involved whenever the relational binding between multiple different stimuli is required, irrespective of whether one is consciously aware of the use of relational binding. Correspondingly, Wang and Giovanello (2016) suggest that subregions of the MTL are not specialized in either incidental or intentional retrieval but within the hippocampus, distinct roles for anterior and posterior hippocampal regions have been identified with regard to the representational content. In large parts of the literature, no differentiation of hippocampal function was made along its longitudinal axis. More recent work showed that anterior parts of the hippocampus are functionally related to anterior cortical parts of the MTL, such as the PrC, and other components of an anterior temporal network (see Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Ranganath & Ritchey, 2012, see also Section 1.3), whereas posterior parts of the hippocampus are connected and functionally similar to the PhC and other structures of a posterior medial network, such as the retrosplenial cortex (RsC; Brunec et al., 2018; Brunec et al., 2019; Ranganath & Ritchey, 2012; see Poppenk et al., 2013, for a review). It is thus important to keep in mind that anterior parts of the hippocampus might possibly be more involved in object processing and the representation of intra-item feature conjunctions. In contrast, posterior parts might rather contribute to relational binding and represent context-related information (see e.g., Kensinger, 2006, for such a pattern in a source- vs. item-memory task; see also Wang & Giovanello, 2016).

1.1.2 Medial Temporal Lobe: Retrieval

Analogously to the approach Davachi (2006) suggested for hippocampal processing at encoding, Diana et al. (2007) based their "binding of items and context" (BIC) model (see Figure 1.4) on the assumption that also at retrieval, the hippocampus operates at the top level of a hierarchy. In order to successfully retrieve an experience from memory, the distinct memory representations that have been created and orthogonalized through pattern separation in the dentate gyrus and the hippocampal subfield CA3 (Bakker, Kirwan, Miller, & Stark, 2008) need to be conveyed to subfield CA1, from which information is projected back to the ErC, thereby closing the so-called trisynaptic circuit (Rolls, 2013; Yassa & Stark, 2011, see also Figure 1.3). Whenever a cue of a previously acquired, pattern-separated episode is provided, the complete original memory trace can be reactivated in CA3 and reinstatiated in CA1 until it is projected downwards to the MTL cortex, pattern-completing the cued memory representation (Bein, Duncan, & Davachi, 2019; Hunsaker & Kesner, 2013; Rolls, 2013).

In line with that, hippocampal involvement has been reported in recall tasks, in which retrieval relies on pattern completion (McClelland et al., 1995; Rolls, 2013; but see Ross et al., 2018, for content-specific hippocampal involvement in recall). In recognition memory, recollection-based retrieval, by which contextual details are reactivated (Yonelinas, 2002), has been ascribed to hippocampal engagement (e.g., Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Ford, Verfaellie, & Giovanello, 2010; Ranganath et al., 2003; Rugg et al., 2012; Wang et al., 2014; Yonelinas, 2005). In patients with hippocampal lesions, the recollection component of recognition memory was found impaired by using estimates from behavioral data (e.g., Aggleton et al., 2005; Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998) or by means of the electrophysiological correlate of recollection-based retrieval (i.e., a late parietal old/new effect; Addante, Ranganath, Olichney, & Yonelinas, 2012; Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001). On the representational level, the hippocampus is specialized in the domain-independent retrieval of items within their context (Diana et al., 2007). In support of the BIC model, there is evidence that the hippocampus contributes to explicit retrieval of arbitrary item-context associations, such as in source memory (Cansino, 2002), and retrieval of inter-item associations, such as word pairs (Ford et al., 2010; Giovanello, Verfaellie, & Keane, 2003; Giovanello, Schnyer, & Verfaellie, 2004) or face-name pairs (Turriziani, 2004).

The PhC is involved in retrieval of spatial relationships (Malkova & Mishkin, 2003) and automatic reinstatement of context if only single objects of an episode are presented (Hayes, Nadel, & Ryan, 2007). In a similar vein, Diana, Yonelinas, and Ranganath (2013) presented an item's encoding context prior to the item at test and found

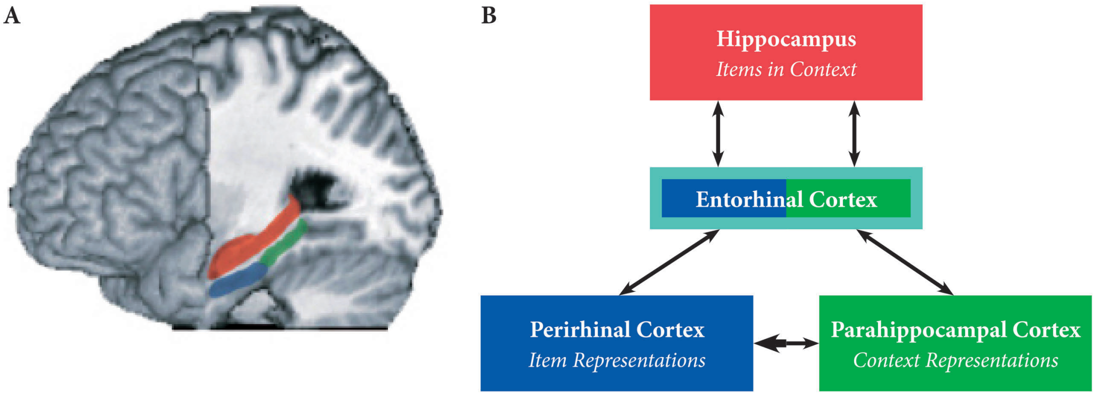

Figure 1.4 **A**. Relative locations of the perirhinal cortex (blue), parahippocampal cortex (green), and hippocampus (red). The entorhinal cortex would be located more medially, parallel to the axis of perirhinal and parahippocampal cortices (see Figure 1.2 and Figure 1.3). **B**. Schematic illustration of the "binding of items and context" (BIC) model (with pathways from perirhinal and parahippocampal cortex remaining separate in the entorhinal cortex, as indicated in blue and green colors). Black lines depict the most significant anatomical connections. Italic letters indicate the proposed roles of each region. Colors of entorhinal cortex changed in accordance with Figure 1.2 and Figure 1.3. Adapted from Ranganath (2010, p. 1265), with permission from John Wiley and Sons.

that PhC activation at context presentation was predictive for subsequent recollection of the item. Martin, McLean, O'Neil, and Köhler (2013) found PhC involvement in familiarity-based retrieval but only for buildings and not for faces or chairs.

In the same study, Martin et al. (2013) observed involvement of the PrC for faces and chairs but not for buildings. They concluded that this supports the view that familiarity is not restricted to the PrC but depends on object categories. One could go one step further and speculate that this can be explained on a representational level. For example, buildings might have been processed more scene-like, containing more specific details that are contextually related, whereas faces and chairs are processed more holistically. This would be in line with the the frequently reported involvement of the PrC in retrieval of single items (see e.g., Diana et al., 2007, for a review). On a process level, the PrC has been associated with familiarity-based recognition (see also Diana et al., 2007; Montaldi & Mayes, 2010, for a review). For example, Wang et al. (2014) found a decrease in perirhinal involvement with increasing familiarity-based recognition strength for items that had been learned within the experiment. This region was overlapping with a PrC cluster that showed decreased activity for successfully primed words in the same experiment (see also Duke, Martin, Bowles, McRae, & Köhler, 2017, for similar results on recent-exposure familarity; but note that an increase of PrC activity was found for cumulative lifetime familiarity). In line with this, patients with selective lesions to the PrC have been found specifically impaired in familiarity-based but not recollection-based retrieval (Bowles et al., 2007; Bowles et al., 2010; see also Köhler & Martin, 2019, for a review of evidence from an individual with lesions to perirhinal and anterior temporal regions sparing the hippocampus). On a system level, the PrC seems to be involved in retrieval of conceptual information from semantic networks. Kivisaari et al. (2019) reported that when their participants processed three cues of the same semantic concept (e.g., *is a fruit*, *is peeled*, *monkeys eat it*), a brain decoding model that includes semantically richer representations of the respective concept (e.g., *banana*) fits better with the participants' fMRI activation pattern than a model based on the three cues alone. This pattern was found in the PrC and widespread cortical regions. Carefully speaking, such a completion of cues to a full conceptual representation by inserting semantic richness from memory might possibly be a pattern-completion-like process for conceptual information.

Interim Summary

Processing in the MTL has a hierarchical structure, with the hippocampus at the top of the hierarchy, receiving input from and projecting back to MTL cortex. The PrC is involved in the binding of single features to unique, distinct feature conjunctions that are processed as single units. In contrast, the PhC is more engaged in the processing of contextual details and their relation. The hippocampus at the top of the hierarchy creates distinct episodic memory traces, coding items within their contexts. Thus, the representational content that is processed within these regions seems to determine their involvement in processes that are more related to memory for items, contexts, or the relation between them. Although the PrC has frequently been found involved in the processing of items, there is evidence that the PrC also contributes to associative memory if two arbitrarily matched items are processed as a single unit, that is, if inter-item associations have been converted to intra-item associations. Montaldi and Mayes (2010) assume that representational content might potentially be a continuum, that is, arbitrary associations can get closer to an item level with an increasing extent to which they are unitized. They further state that such a degree to which associations are processed as a single unit is hard to determine. This makes it difficult to assign MTL structures to rigid categories with regard to the representational content. However, it seems that the more some content is processed as a coherent whole or single unit, the more likely it is that this information is processed in anterior MTL regions such as the PrC.

1.2 A Representational-Hierarchical View

The representational-hierarchical view (see e.g., Cowell et al., 2010, 2011; Kent et al., 2016; O'Neil, Barkley, & Köhler, 2013; Saksida et al., 2006) is built on the assumption of a hierarchical processing structure along the ventral visual stream with regard to representational content, from the processing of more elemental, simple features such as colors and shapes in more posterior visual association areas to highly complex feature conjunctions in the PrC as the apex of the ventral stream. Built on this view, the perceptual-mnemonic feature-conjunction model suggested by Bussey et al. (2005; see also Bussey, Saksida, & Murray, 2003; Murray & Bussey, 1999) holds that the representational gradient is what equally guides memory and perception. For example, the PrC is not only involved in item memory and the perception of single objects but in the processing on an item level in general. From a representational-hierarchical perspective, it is essentially assumed that no brain region within the ventral visual stream is pinned to one cognitive operation and no cognitive operation can be mapped to a specific brain region. For example, even though cognitive operations such as pattern separation have most often been investigated in the hippocampus in a mnemonic context (e.g., Bakker et al., 2008; Kirwan et al., 2012; Yassa & Stark, 2011), the computational principles per se are found throughout the brain and across domains (Gilbert & Kesner, 2002; Wilson, 2009). Pattern separation, that is, the orthogonalization of representations in order to reduce overlap, has also been associated with the PrC and not only with mnemonic but also perceptual tasks (e.g., Burke et al., 2011; Kent et al., 2016) – it just differs with regard to the representational level (Cowell et al., 2019). Moreover, perceptual perirhinal pattern separation at encoding (as induced by a discriminative encoding task) seems to predict subsequent item memory (Chen et al., 2019). The extent to which a component within the ventral stream is involved depends on the representational requirements of a task: Whereas the discrimination between items that differ already in their elemental features can be conducted in early posterior regions, the discrimination between items that are only distinguishable by their specific feature conjunction would typically recruit the PrC. For example, perirhinal pattern separation would support the discrimination between the feature conjunction of a green-headed duck with orange feet from an orange-headed duck with green feet, even if the single features are exactly the same. The discrimination between feature conjunctions that share fewer features, such as a green-headed duck with orange feet and a blue car with black wheels, does not pose such high demands on perirhinal processing since the discrimination between elemental features, which are represented in more posterior areas of the ventral stream, would be sufficient. This also indicates that task demands are decisive, that is, the higher the demands on a cognitive operation, the more engagement of the responsible region in the ventral stream can be observed.

In support of that, Mundy, Downing, and Graham (2012) found increased PrC involvement in a task in which highly similar objects were presented compared to a set of objects that shared only few features. In addition, it has been found that lesions to the PrC especially lead to impairments in the discrimination of objects that share many features but not objects that share few features (Barense et al., 2005; Barense et al., 2007; Barense et al., 2012; Bussey et al., 2003). The PrC is also involved in the recall of objects that generally share many features with other exemplars from the same category but have only few distinct features. For instance, Moss, Tyler, and Jennings (1997) found that patients with perirhinal lesions have difficulties in the recall of conceptual knowledge on specific animals since most animals have legs, eyes, a mouth, and so forth, whereas artifacts can be reproduced more easily as they are more distinct. This might indicate that the PrC also plays a role in pattern completion on a semantic, gist-like item level – in contrast to hippocampal pattern completion, in which a complete episode is reinstantiated from a cue (see also Amano, Shibata, Kawato, Sasaki, & Watanabe, 2016; Ross et al., 2018). This would be in line with the assumption that the same cognitive operations can occur widely along the ventral visual stream but the representational complexity increases from posterior to anterior regions.

It is conceivable that this approach can be extended to other regions beyond the ventral visual stream, which might be reflected in the findings by Mundy et al. (2012). They showed that, just like the PrC is more involved in the processing of highly similar objects, the posterior hippocampus is also recruited more strongly in the processing of items that share many features. Interestingly, this was only the case for scene stimuli, which can be considered complex item-context conjunctions (Konkel, 2009). Saksida and Bussey (2010) suggest to consider the hippocampus as an additional level of the representational hierarchy reaching beyond the ventral stream, which processes episodic conjunctions consisting of inter-item and item-context associations. Kent et al. (2016) added to this that the general principles of a representational approach can be extended to other modalities than vision.

1.3 The Medial Temporal Lobe and Beyond

Building on the BIC model by Diana et al. (2007; see also Davachi, 2006, and Montaldi & Mayes, 2010), Ranganath and Ritchey (2012) proposed a comprehensive framework that wraps up research on memory functions within and outside the MTL by embedding previous findings into two broader systems for memory-guided behavior, that is, an anterior temporal (AT) system and a posterior medial (PM) system (see Figure 1.5). In contrast to previous models, the AT-PM framework explicitly stresses interactions of the MTL with anterior temporal, prefrontal, and parietal regions. Generally speaking, the AT-PM framework suggests that the AT system contributes more strongly to item memory and holistic processing of objects whereas the PM system is more involved in memory for relational context information. The components within the two systems are strongly interconnected but, if at all, only weakly connected with the respective other system. Importantly, the AT-PM framework accounts for differential processing along the longitudinal axis of the hippocampus, with its anterior regions being part of the AT network and its posterior regions belonging to the PM network. This is in line with recent literature, showing a gradient within the hippocampus regarding the representational level (e.g., Brunec et al., 2018; Giovanello, Schnyer, & Verfaellie, 2009; see Poppenk et al., 2013, for a review) and spatial navigation (Brunec et al., 2019; Duarte, Ferreira, Marques, & Castelo-Branco, 2014). The anterior hippocampus has been found to be more associated with item memory whereas the processing of relational information has been ascribed to the posterior hippocampus (Wang & Giovanello, 2016). Moreover, the anterior hippocampus is more involved in semantic processing (i.e., the identification of semantic novelty; Poppenk et al., 2008) and Poppenk and Moscovitch (2011) found that a greater posterior/anterior hippocampal volume ratio is associated with better recollection-based memory accuracy whereas overall hippocampal volume is not predictive for recollective memory. In line with previous literature (Eichenbaum et al., 2007; Suzuki & Amaral, 2004; Witter et al., 2000, see also Section 1.1.1), Ranganath and Ritchey (2012) propose that the AT and PM pathways and their connections to the hippocampus are also largely segregated, with the perirhinal pathway to the anterior hippocampus contributing to memory formation on an item level and projections from the PhC to the posterior hippocampus being responsible for the consolidation of context representations. In line with Davachi (2006), they suggest that the hippocampus has an integrative role as information of both systems might finally converge in the dentate gyrus and CA3 regions, where full episodes are represented.

The PrC as key component of the AT system is strongly connected with the anterior hippocampus, the amygdala, the ventral temporal poles, and the lateral orbitofrontal cortex. These AT system components also show functional similarities with the PrC. The amygdala seems to have a bias for familiarity- compared to recollection-based retrieval (Farovik, Place, Miller, & Eichenbaum, 2011) and the lateral orbitofrontal cortex is involved in object recognition (Xiang & Brown, 2004). According to Ranganath and Ritchey (2012), the PrC and the temporopolar cortex are highly interwo-

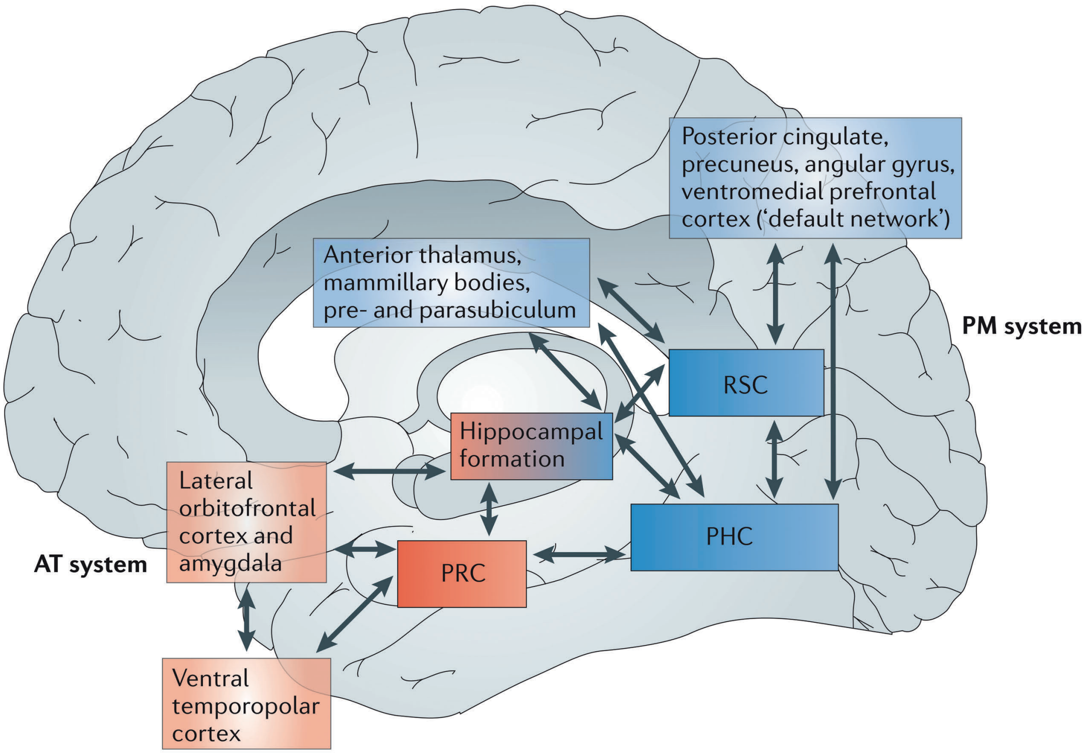

Figure 1.5 Two cortical systems for memory-guided behavior as suggested by Ranganath and Ritchey (2012). Components depicted in red are assigned to the anterior temporal (AT) system, components depicted in blue belong to the posterior medial (PM) system. Arrows denote relatively strong anatomical connections between the respective components. PRC = perirhinal cortex, PHC = parahippocampal cortex, RSC = retrosplenial cortex. Reprinted from Ranganath and Ritchey (2012, p. 719), with permission from Springer Nature.

ven at object processing but the discrimination between the perirhinal binding process and the temporopolar integration process is not yet completely understood. Even the anatomical borders between the PrC and the temporal poles seem to be unclear (see also Olson, Plotzker, & Ezzyat, 2007). Martin et al. (2018) found that the PrC not only represents perceptual information but rather fully specified object concepts, integrating their perceptual and conceptual features to a coherent whole. ATL regions seem to distinctively represent conceptual features, potentially merging information from modality-specific cortical structures. In line with that, the hub-and-spoke model (Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004, see also Figure 1.6) suggests that modality-specific information is stored in the respective modality-specific regions distributed across the neocortex (i.e., "spokes") and the ATL acts as a transmodal hub, in which all unimodal information of the spoke regions converge. Analogously to the increase in complexity along the ventral visual stream with the PrC as convergence zone, the more fine-grained graded-hub-and-spoke model by Plaut (2002) adds that the contribution to conceptual processing of regions within the ATL depends on the distance to the respective spoke, such that more abstract concepts and words are semantically represented in the superior temporal gyrus (i.e., more closely connected to auditory systems) while pictures and concrete objects are better represented in the medial ATL (i.e., more closely connected to visual systems; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017). The idea of the ATL as a semantic hub has been supported by findings revealing ATL recruitment for crossmodal semantic processing. For example, ATL engagement has been found in perceptual and conceptual processing of words and pictures (e.g., Bright, Moss, & Tyler, 2004; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Visser, Jefferies, Embleton, & Lambon Ralph, 2012) and pictures and sounds or voices (Abel et al., 2015; Tranel, Grabowski, Lyon, & Damasio, 2005; see Visser, Jefferies, & Lambon Ralph, 2010, for a meta analysis). Repetitive transcranial magnetic stimulation (rTMS) studies of healthy individuals identified the ATL as crucial for semantic but not perceptual (Pobric, Jefferies, & Lambon Ralph, 2010a) or numeric processing (Lambon Ralph, Pobric, & Jefferies, 2009), a pattern that is also reflected in semantic dementia, in which typically a severe degradation of the ATL is observed (see Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010, for a comparison between semantic dementia and rTMS findings). Furthermore, Pobric, Jefferies, and Lambon Ralph (2010b) found that the inhibition of ATL regions produced slowed responses for category-general semantic tasks whereas the inhibition of spoke regions, which is supposed to impair modality-specific sensory processing, produced category-specific impairments. Moreover, anatomically constrained magnetoencephalography showed that visual and auditory processing in a semantic judgment task provoked an activation spread from modality-specific sensory areas to a convergence zone in the ATL (Marinkovic et al., 2003).

At a first glance, the PrC and ATL seem to have contradictory cognitive functions. Perirhinal processing supports the binding of single features to distinct intra-item feature conjunctions in order to *prevent* overlap between representations. In contrast, the temporal poles are involved in the abstraction of elements that are shared between different feature conjunctions, thereby *creating* overlap between representations (Chadwick et al., 2016). With reference to the duck example, PrC processing would support the creation of a different, unique feature conjunction for each out of many mallard ducks (by binding elemental features to intra-item feature conjunctions). However, although represented as distinct units in the PrC, all ducks would abstract to

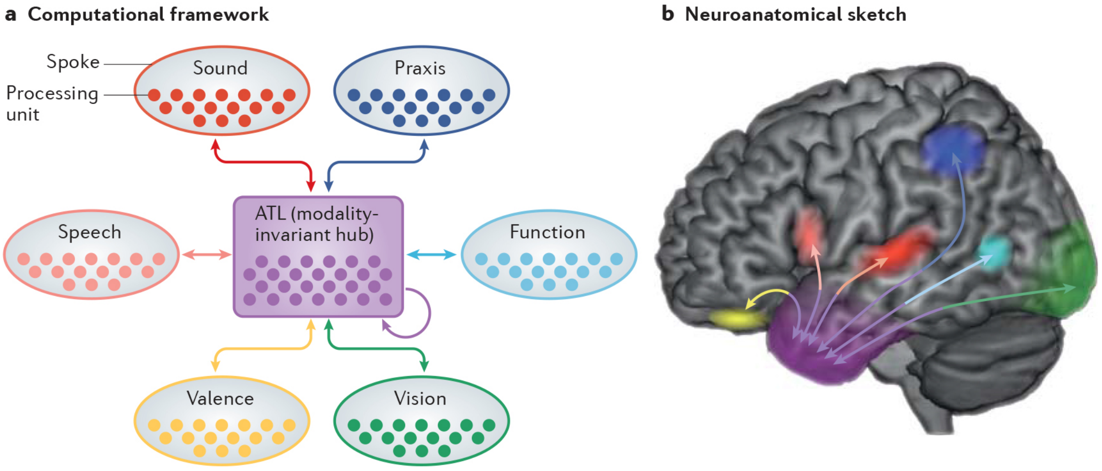

Figure 1.6 The hub-and-spoke model according to Lambon Ralph, Jefferies, Patterson, and Rogers (2017). **A**. Computational structure of the hub-and-spoke model. Each modality-specific spoke is bidirectionally connected to a single transmodal hub in the anterior temporal lobe (ATL). According to this model, the input of each of the spokes can be used in order to reinstantiate the information of the other spokes via the hub, thereby forming generalizable semantic representations. **B**. Neuroanatomical sketch of the location of the hub and spokes. The hub is located within the ATL region (purple), whereas the modality-specific spokes are distributed across different neocortical regions (the same colour coding is used as for the computational model in A). Reprinted from Lambon Ralph, Jefferies, Patterson, and Rogers (2017, p. 43), with permission from Springer Nature.

the subordinate-level concept *mallard duck* and to the concept *duck* on a basic level through anterior temporal processing. Although never mentioned explicitly, this does not necessarily mean that in the ATL, only such an integrative cognitive operation can be conducted. The distinct feature conjunctions created by the PrC might also be represented as “pattern-separated” representations in the ATL, albeit on a highly generalized, conceptual level (e.g., the concept of a mallard duck would be separable from the concept of a mandarin duck). This fits with findings indicating that the ATL is especially qualified for the processing of very *specific* abstracted conceptual representations with unique feature combinations (Rogers, Patterson, Jefferies, & Lambon Ralph, 2015). For example, it has been found that in patients with semantic dementia, the identification of objects especially on a subordinate level (e.g., mallard) is impaired, whereas it is often preserved on a basic level (e.g., duck) and most often on a superordinate level (e.g., animal; Hodges, Graham, & Patterson, 1995). It is therefore conceivable that, in contrast to the PrC, the ATL might process highly abstracted concepts by an integration process but is especially involved in the processing of concepts that are most specifically defined, which could be due to a separation process on a conceptual level.

In the PM system of the AT-PM framework, the PhC and RsC as key components are strongly interconnected and are both connected to the mammillary bodies, the anterior thalamic nuclei, the pre- and parasubiculum, and the default network (including posterior cingulate, the precuneus, the lateral parietal cortex, and the medial prefrontal cortex, mPFC; Raichle et al., 2001). Contrary to the AT system, Ranganath and Ritchey (2012) suggest that the PM system is engaged in the processing of spatiotemporal context, in spatial memory (see also Mayes, Meudell, Mann, & Pickering, 1988), and spatial navigation (see also Bird & Burgess, 2008). Ranganath and Ritchey (2012) posit that the PhC might be responsible for the general representation of visuospatial contexts whereas the RsC is involved in the orientation of oneself within spatial arrangements. They further propose that the PM system might contribute to the orientation of the self in an individual's identification with certain goals or motivations. Recollection-based retrieval also depends on the PM system, which is in line with research showing involvement of the default network especially in recollection-based recognition (Vilberg & Rugg, 2008). Ranganath and Ritchey (2012) also suggest that the PM system is able to create *situation models*, which they define as "mental representation of the relationships between entities, actions, and outcomes" (Ranganath & Ritchey, 2012, p. 721; see also Zwaan & Radvansky, 1998, for an early overview of situation models). They draw the analogy to a schema, with the difference that whereas a schema comprises conceptually related associations, situation models in the PM system embody a concept of context-related spatial, temporal, and causal relationships of a situation (e.g., going to the duck pond in the north of the city by bike together with a friend after work). The (predominantly left-hemispheric) medial and lateral parietal cortices have been especially associated with recollection-based memory (Cansino, 2002; Henson, Hornberger, & Rugg, 2005; Wheeler & Buckner, 2004; Yonelinas, 2005), which has also been associated with the RsC that represents mainly context-relevant information (Daselaar, Fleck, & Cabeza, 2006). Recollection-based retrieval has also been related to the mPFC (Yonelinas, 2005) as part of the default network. However, the actual mPFC contribution to memory is potentially less direct, that is, it could as well be discussed in terms of cognitive control components that are relevant to guide the memory search processes (Dobbins, Rice, Wagner, & Schacter, 2003; Henson et al., 2005; Henson, Shallice, & Dolan, 1999), especially as the mPFC has been associated with the top-down embedding of new information into already existing schemas or networks of conceptual knowledge (see Gilboa & Marlatte, 2017, for a review; see also Section 1.4.2.1).

Summary: Long-Term Memory and Its Neural Underpinnings

According to the representational-hierarchical view, each component along the ventral visual stream contributes to memory (and cognition in general) to the extent that it represents the content to be processed. Posterior regions represent more elemental, single features and the complexity increases downstream, with the PrC representing the most complex feature conjunctions. Whenever a task cannot be solved on the basis of single features but requires the processing of complex feature conjunctions, more anterior processing is needed. Regions outside the MTL, such as the ATL, show similar graded processing. The ATL has been dubbed a semantic hub, in which unimodal information from modality-specific cortical structures converges to complex conceptual representations. The AT-PM framework suggests that the PrC is a key component of an anterior temporal (AT) system that includes, amongst others, parts of the ATL and the anterior hippocampus. Whereas the AT system is involved in the binding of intra-item associations and conceptual processing, the posterior medial (PM) system represents spatial and temporal context and is involved in relational binding and recollection-based retrieval.

Significance for This Thesis

This thesis has a focus on the rapid incorporation of arbitrary picture-label associations into semantic memory networks by means of fast mapping. While the PrC supports the binding of single features within an item to intra-item feature conjunctions, the hippocampus supports the binding of item-context or inter-item associations (e.g., the picture of a duck with the label *mallard*). Consequently, if a picture is to be bound with an arbitrary, previously unrelated word, one would typically expect the requirement of hippocampal processing. However, the incorporation of hippocampally bound associations into semantic long-term memory networks is not rapid but a rather time-consuming process that will be outlined in the following.

1.4 The Formation of New Memories

It has already been outlined how new information is encoded and orthogonalized to distinct representations, and how memory representations can ultimately be retrieved. What happens in the black box between encoding and retrieval has been left unclear. There are essentially two ways to describe memory consolidation: On a synaptic level and on a system level (see Dudai, 2004, for an overview). Memory consolidation on a synaptic level describes a process of rapid synaptic reorganization based on Hebbian learning by which neural pathways are created or strengthened through the change of firing patterns and synaptic links (e.g., via long-term potentiation). Consolidation on a system level, in contrast, describes the transfer of new information from a hippocampal system to a neorcortical system and its incorporation into neocortical networks, by which connectivity patterns between systems are altered. I will employ the term *consolidation* in the sense of system-level consolidation. It is assumed that in the neocortical system, the new information is linked to previously stored information units (i.e., nods) within neocortical networks. Such networks are to be seen as theoretical constructs that do not have a physical equivalent (i.e., there is no duck nod stored at a specific site in the brain) but have been proven to be a valid method to approximate the computational mechanisms of a cortical memory system. The links in these networks are stronger the more closely the nods are related. Relatedness can be construed with regard to different aspects. For example, in semantic networks, a newly encountered mallard duck would strongly be linked to conceptually similar nods (e.g., other ducks) and less closely linked to less similar nods (e.g., elephant). In lexical networks, the word *duck* would be closely related to its direct lexical neighbors (i.e., words that differ from the target word in only one letter), such as *luck* or *dock*, and less closely related to *door*, which only shares one letter with *duck*.

1.4.1 Traditional Approaches to Memory Consolidation

There are several approaches to describe system-level consolidation, of which only the most significant for this thesis will be introduced in the following. They broadly agree that the formation of new cortical memories through information transfer from the hippocampal to the neocortical system is a gradual and time-consuming process (e.g., Frankland & Bontempi, 2005; McClelland et al., 1995; Norman & O'Reilly, 2003). Such a slow hippocampus-mediated process is beneficial in order to prevent newly acquired information from interference with previously stored memory representations in cortical networks, by means of hippocampal binding and pattern separation (Bakker et al., 2008; Norman & O'Reilly, 2003; Lacy, Yassa, Stark, Muftuler, & Stark, 2010; Kirwan et al., 2012; Duff et al., 2011; see Yassa & Stark, 2011, for review). In addition, it has been shown that spindle-ripple events during slow-wave sleep, including hippocampal sharp-wave ripples, are particularly supportive for declarative memory consolidation (e.g., Fogel & Smith, 2011; see Diekelmann & Born, 2010, for a review), especially for the consolidation of associations (Studte, Bridger, & Mecklinger, 2015). Most theories assume an operation called *sharpening* for the incorporation process (e.g., Opitz, 2010; O'Reilly & Norman, 2002). Sharpening strengthens memory representations in cortical networks using statistical regularities, that is, the links between elements that co-occur more frequently across episodes (e.g., a duck in the context of a pond) are strengthened compared to elements that co-occur only rarely (e.g., a duck in the context of a playground). Neocortical structures extract the commonalities across several episodes, thereby creating gist-like conceptual representations, which are independent of the information that is specific for a single episode. The more often we make a certain experience, the more precise this gist gets until we can access generalized schematic knowledge without remembering every single episode (e.g., general knowledge that ducks are found in ponds). Associations that have been conceptually integrated by means of hippocampal-neocortical consolidation are assumed to be of a rigid nature. In contrast to hippocampally processed inter-item associations, which are bound less strongly and are more elemental in nature, thereby enabling flexible recall, semantically well integrated intra-item associations are processed as a coherent whole and thus, their elemental components are less flexibly accessible (see e.g., Giovanello et al., 2009). Several consolidation theories agree on the hippocampal-neocortical conversion of episodic information to semantic memory representations but they differ with regard to the storage of the single episodic information.

1.4.1.1 Standard Model and Complementary Learning Systems

One of the most prominent consolidation theories, the standard consolidation theory (Squire & Alvarez, 1995) does not make different predictions with regard to consolidation for episodic and semantic memory (see Frankland & Bontempi, 2005, for a review). According to this theory, new experiences are initially rapidly acquired and bound to distinct memory representations in a hippocampal system and then transferred to a neocortical system, where cortico-cortical links are created and strengthened in order to incorporate the new information into cortical networks. The stored information is assumed to remain sparsely coded in the hippocampal system, which can act as a "pointer" or index that projects back to neocortically distributed areas and triggers the contents to be recalled together in order to retrieve a full memory episode (Teyler & DiScenna, 1986; Teyler & Rudy, 2007). Over time, the connections to the hippocampus become weaker until the new, now cortically represented memories are hippocampus-independent and can be retrieved without hippocampal involvement. Evidence from neuropsychology supports this theory. For instance, patients with hippocampal lesions, such as H. M., can typically access existing cortical memory networks but show severe anterograde amnesia, such that they cannot store any new autobiographic episodes. Interestingly, retrograde amnesia in these patients seems to be temporally graded, that is, memory is especially impaired for recent memories while remote memories are often spared. The standard consolidation theory would assume that remote memories are already well consolidated and can be retrieved independently of the hippocampus (Manns, Hopkins, & Squire, 2003; Squire & Alvarez, 1995).

The Complementary Learning Systems (CLS) theory (McClelland et al., 1995; Norman & O'Reilly, 2003; O'Reilly & Rudy, 2001) builds on the standard theory but additionally provides a computational framework, suggesting that the hippocampal and neocortical system are highly interwoven but differ with regard to their computational mechanisms. It is assumed that the hippocampal system rapidly acquires new information, binds them to distinct memory traces and keeps even overlapping traces separate by means of pattern separation. The neocortical system operates with a generalization process in a sharpening manner. In order to protect from interference in the generalization process, the hippocampal pattern separation process is essential. With regard to the temporal dynamics, rapid learning is only possible in the hippocampal system, whereas the neocortical system learns only slowly.

1.4.1.2 Multiple-Trace Theory of Consolidation

The multiple-trace theory (MTT; Nadel & Moscovitch, 1997; Nadel, Samsonovich, Ryan, & Moscovitch, 2000) also assumes that, based on statistical regularities across many experiences, the neocortical system extracts what is common across episodic experiences and creates gist-like representations that can be retrieved independently of the hippocampus. In contrast to the standard model, the MTT makes different predictions for episodic and semantic representations (e.g., Nadel & Moscovitch, 1997). It is assumed that single episodic memory traces still can be hippocampally retrieved for as long as they exist (Nadel, Ryan, Hayes, Gilboa, & Moscovitch, 2003; Winocur, Moscovitch, & Bontempi, 2010). Consequently, episodic and semantic memories can co-exist. In other words, it is possible to remember the last encounter with a duck while at the same time, this episode also contributes to a person's general knowledge on ducks. This is supported by findings showing that the retrieval of very remote memories still engages the hippocampus (Nadel et al., 2000; Patai et al., 2019). Thus, memory representations do not solely become independent of the hippocampus and the hippocampus not only acts as an index but itself contains contextual episodic information (Nadel et al., 2003). It is further assumed that each time a memory is retrieved, it is automatically re-encoded in a different context, thereby creating new, slightly different representations of the memory (i.e., ”multiple traces”). Over time and retrieval frequency, there are many traces by which a memory can be retrieved, making this memory more robust. The MTT uses this assumption as an explanation for the temporal grade of amnesia. It is assumed that intact postmorbid retrieval of very remote memories is not possible because those memories have become independent over time (as suggested by the standard theory) but because these memories have been re-experienced more often and are thus more robust (Nadel et al., 2003). This is only possible as long as the lesions do not comprise the complete hippocampus.

1.4.2 Traditional Approaches to Memory Consolidation – Outdated?

Contrary to what would be expected by the consolidation theories outlined above, there are studies showing that patients with severe global amnesia are able to postmorbidly acquire new declarative knowledge despite the unability to store new autobiographic episodes (Verfaellie, Koseff, & Alexander, 2000; see Baddeley, Vargha-Khadem, & Mishkin, 2001; Vargha-Khadem, 1997, for this pattern in developmental amnesia). Even patient H. M., who had undergone a resection of the hippocampus and adjacent structures of the MTL (Augustinack et al., 2014; Corkin et al., 1997), showed residual learning (Skotko et al., 2004). This would fit with the idea by Tulving and Markowitsch (1998) that, in contrast to the approaches outlined above, episodic memory initially depends on semantic memory, which can remain intact despite severely impaired episodic memory. According to Tulving's (1995) serial–parallel–independent (SPI) model, encoding is serial such that new information is first processed by a perceptual, then by a semantic, and finally by an episodic memory system. Storage occurs separately and in parallel in each system and retrieval is independent, that is, the episodic and semantic system can be accessed independently, depending on the nature of the test. As this approach assumes that new episodic memories depend on semantic memory but not vice versa, it might be able explain why some patients with amnesia can acquire new semantic memories despite severely impaired episodic memory due to hippocampal lesions. However, Hamann and Squire (1995) could not replicate Tulving, Hayman, and Macdonald's (1991) findings in different amnesic patients using the same tasks. They state that the MTL lesions of the patient reported by Tulving et al. (1991) might not completely impair episodic memory. Furthermore, Tulving's (1995) model is not able to explain how individuals with semantic dementia can develop episodic memories despite impaired semantic memory. Therefore, even the SPI cannot fully account for all findings in lesion studies without any additional assumptions. An extension of the SPI model suggests that there are additional direct pathways from the perceptual to the episodic system (Graham, Simons, Pratt, Patterson, & Hodges, 2000). However, it has been questioned if the new semantic memories acquired by patients with severe lesions to the hippocampus are of the same quality as those in healthy adults since the learning rate is typically much slower. Skotko et al. (2004) state that the knowledge acquired by H. M. in their experiment was “qualitatively different from the general conceptualization of semantic learning. It was not permanent, and it was relatively inflexible” (Skotko et al., 2004, p. 765). Tulving (2002) posits that this might be due to additional impairments caused by lesions outside the hippocampus or due to the fact that amnesic patients cannot additionally benefit from their episodic memory as healthy controls would. Other approaches explain the finding of intact semantic memory in amnesic patients as a result of repetitive learning which might be possible due to some residual episodic memory (Squire & Zola, 1998). This could be an explanation for findings reported by O'Kane, Kensinger, and Corkin (2004) that when H. M. was presented with the first name of personalities who became famous after his surgergy (e.g., ”Ronald”) and to whom he was often exposed in the media, he could successfully recall about one third of their last names (e.g., ”Reagan”). Interestingly, he recalled twice as many last names if the cue was anchored to semantic information on the personalities, such as their profession (see also Skotko et al., 2004). Thus, H. M. seems to have acquired semantic knowledge postmorbidly that goes beyond non-declarative skill learning. Furthermore, he could remember new information if it could be linked to premorbidly acquired knowledge (Skotko et al., 2004). Hence, not all declarative memories might necessarily be initially hippocampus-dependent. There might possibly be other structures within or outside the MTL that could enable hippocampus-independent learning.

Apart from amnesia studies, there is further evidence that direct neocortical learning can be achieved under certain conditions. First, the availability of prior knowledge into which the new information can be embedded may enable rapid cortical integration, potentially bypassing or even suppressing hippocampal processing (see Section 1.4.2.1; Tse et al., 2007; Tse et al., 2011; Van Kesteren, Ruiter, Fernández, & Henson, 2012). Second, the importance of cortical structures to learning of arbitrary associations has been observed if the associations had been encoded as a single unit, that is, if two arbitrarily matched items had been merged to a single item in the sense of an intra-item (instead of inter-item) association (see Section 1.4.2.2; Haskins et al., 2008; Quamme et al., 2007). Third, the learning paradigm *fast mapping* (FM) has proven to enable rapid cortical integration of novel associations, potentially bypassing the slow hippocampal consolidation route (see Chapter 2; Atir-Sharon, Gilboa, Hazan, Koilis, & Manevitz, 2015; Coutanche & Thompson-Schill, 2014; Coutanche & Koch, 2017; Himmer, Müller, Gais, & Schönauer, 2017; Korenic et al., 2016; Merhav et al., 2014, 2015; but see Cooper, Greve, & Henson, 2019; Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016).

1.4.2.1 Building on Prior Knowledge

Tse et al. (2007) created flavor-place associations in rats by means of traditional hippocampal learning. These associations should serve as abstracted neocortical schemas, into which new information can be quickly incorporated. Indeed, novel associations were rapidly integrated if they were congruent with these schemas, even after only a single exposure (which will be referred to as *schema-congruency effect*; see also Tse et al., 2011). These findings challenged traditional consolidation theories such as the CLS theory (McClelland et al., 1995). McClelland (2013) conducted further simulations of the previous CLS model but this time with prior knowledge taken into account. The simulations showed that the congruency of new information with prior knowledge modulates the pace of learning in the neocortical system. He thus suggested that the terminology of a slow neocortical system might be misleading, as the pace of learning

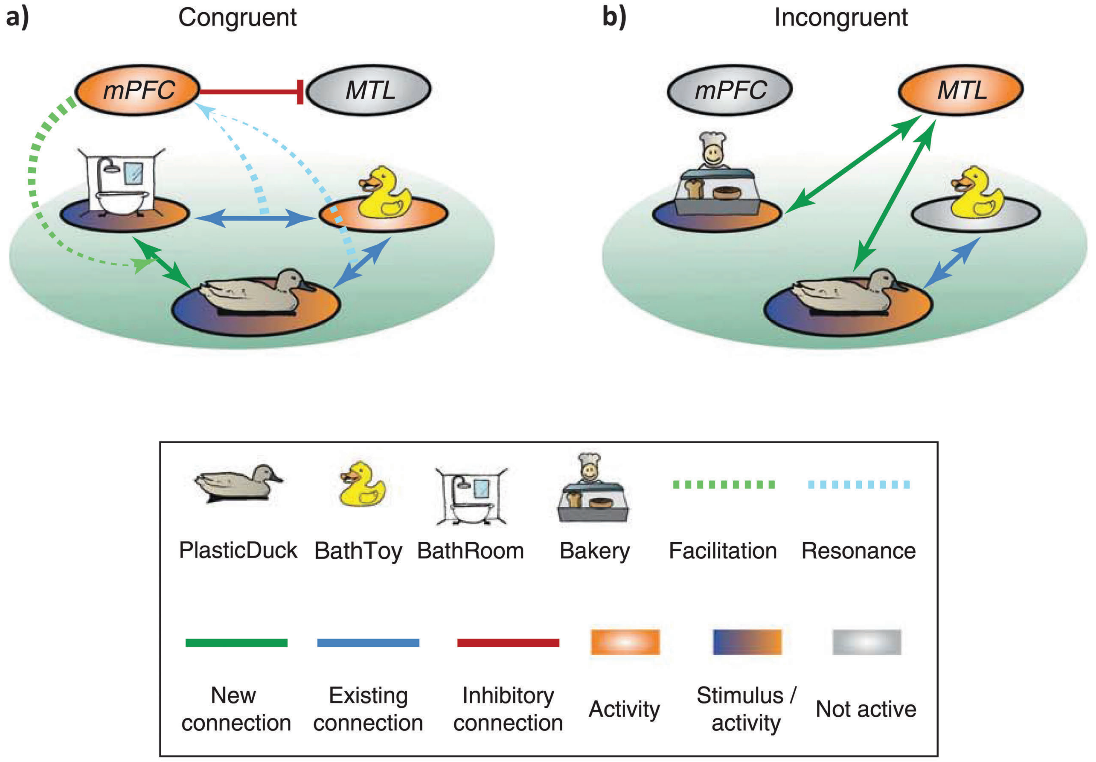

Figure 1.7 Schematically depicted predictions made by the schema-linked-interactions-between-medial-prefrontal-and-medial-temporal-regions (SLIMM) model by Van Kesteren, Ruiter, Fernández, and Henson (2012) for the encoding of a new item (plastic duck) that is congruent versus incongruent with a provided environment or schema (bathroom vs. bakery, respectively). **a)** Schema-congruency means that the new item (e.g., plastic duck) and the schema (e.g., bakery) are synchronously co-activated by information to which they are both related (e.g., a rubber duck as a bath toy). This co-activation or "resonance" elicits mPFC recruitment, which results in an mPFC-mediated creation of a direct connection between the schema and the new item. The SLIMM model suggests that at the same time, the MTL is inhibited by the mPFC. **b)** If the schema (e.g., bakery) is not connected to the bath toy and thus, there is no resonance that could trigger mPFC involvement, no beneficial effects of schema-congruency occur. In addition, the MTL is not inhibited, which allows for hippocampal-neocortical consolidation processes. Adapted from Van Kesteren, Ruiter, Fernández, and Henson (2012, p. 215), with permission from Elsevier.

in the neocortical model of the CLS theory is strongly dependent on the availability of prior knowledge, with faster learning rates for information congruent with prior knowledge structures and slower learning rates for incongruent information. Gilboa and Marlatte (2017) recently defined such prior knowledge structures as schemas, that is, "higher-level knowledge structures that organize lower-level representations from long-term memory" and "serve as general-form reference templates against which new information can be compared, binding multiple features that consistently co-occur" (Gilboa & Marlatte, 2017, p. 618).

Beneficial effects of prior knowledge and rapid learning of schema-congruent information were also confirmed in humans and the mPFC has been identified as strongly involved in schema learning (Van Kesteren, Fernandez, Norris, & Hermans, 2010; Van Kesteren, Rijpkema, Ruiter, & Fernandez, 2010; Van Kesteren et al., 2013). If the new information is not related to common knowledge structures, slow hippocampal-neocortical consolidation is required. Within their schema-linked-interactions-between-medial-prefrontal-and-medial-temporal-regions (SLIMM) framework, Van Kesteren et al. (2012) suggested that the mPFC shows synchronous co-activation ("resonance") if a schema (e.g., bathroom) and a new item (e.g., plastic duck) are both semantically related to another item (e.g., rubber duck as a bath toy; see Figure 1.7). If this is the case, the mPFC creates a direct connection between the new item and the schema. At the same time, mPFC activation inhibits MTL processing (see also Van Kesteren, Fernandez, et al., 2010; Van Kesteren et al., 2013). However, the role of the hippocampus in schema learning is under debate. Other models emphasize that instead of a counteracting relationship between the hippocampus and the mPFC and particularly the ventromedial prefrontal cortex (vmPFC), the hippocampus is actively involved in relating the new information to the schema. Bidirectional relations between the hippocampus and the mPFC might foster the integration of new information into a schema (McKenzie et al., 2014; Preston & Eichenbaum, 2013). Sommer (2016) found stronger coupling of the vmPFC with the hippocampus during encoding of schema-congruent compared to unrelated information, which led to accelerated systems consolidation. Although tested in rodents, Tse et al. (2007) reported no new learning after hippocampus resection, despite schema congruency. Preston and Eichenbaum (2013) suggested that the vmPFC might have a control rather than inhibition function in schema-congruent memory, in the sense of conflict resolution at the encoding of highly overlapping associations, and Gilboa and Marlatte (2017) posit that the vmPFC might possibly not be a structure predestined for schema learning but rather serves as metacognitive structure supporting gist extraction of specific events or the general organization of concepts.

1.4.2.2 Unitization

Even though consolidation theories such as the standard model or the CLS theory do not refer specifically to the associative nature of the memory representations, they imply that the hippocampus is especially involved in encoding and retrieval of arbitrary associations between items, compared to associations between non-arbitrary, previously related items. The schema-congruency effect refers to non-arbitrary associations, that is, new information must by definition be conceptually related to the schema in order to benefit from schema-based learning. One way to reduce the demands on hippocampal binding is to unitize the arbitrarily matched information, that is, to integrate different units to a coherent whole or, in other words, to transform the inter-item to an intra-item association (i.e., to a single unit). These units can then be bound in cortical MTL regions such as the PrC prior to hippocampal processing. This can be done using encoding paradigms in which participants are explicitly instructed to actively imagine two items as a unit (e.g., Staresina & Davachi, 2006) or by providing a definition for a compound word (e.g., *milk taxi* defined as *delivery service directly dispatched from a farm*) that is created from two previously unrelated words (e.g., *milk* and *taxi*; Bader, Opitz, Reith, & Mecklinger, 2014). Please note that I will differentiate between unitization paradigms and unitization as a process. Unitization as a process can occur in different situations and with an increasing degree to which arbitrary inter-item or item-context associations are unitized, they can be more or less closely processed as a unit on an item level (e.g., Montaldi & Mayes, 2010). For example, Memel and Ryan (2017) found beneficial effects of unitization simply by depicting an item within its context instead of presenting them next to each other (but note that they suggest that these units were still processed similarly to item-context associations), whereas in other experiments using actual unitization paradigms, unitization was explicitly instructed by asking participants to merge items to compounds. It has been shown that the processing of unitized associations resembles the processing of single units rather than that of associations (Bader, Mecklinger, Hoppstädter, & Meyer, 2010; Bader et al., 2014; Haskins et al., 2008; Jäger & Mecklinger, 2009; Liang, Elfaki, & Barense, 2019; Tibon, Gronau, Scheuplein, Mecklinger, & Levy, 2014; but see Memel & Ryan, 2017). There is electrophysiological evidence for familiarity-based recognition of previously unitized words whereas non-unitized associations evoke an electrophysiological correlate for recollection-based recognition (Bader et al., 2010; see also Diana, Yonelinas, & Ranganath, 2008; Jäger, Mecklinger, & Kipp, 2006; Kamp, Bader, & Mecklinger, 2016; Li, Han, Guo, & Tibon, 2019), which is typically associated with hippocampal processing (e.g., Yonelinas, 2002). Interestingly, there is also evidence for PrC contribution to learning of associations but only if they have been unitized (Haskins et al., 2008; Staresina & Davachi, 2006). Moreover, it has been shown that amnesic patients with lesions circumscribing the hippopcampus benefit from unitization, in contrast to patients with extended lesions to the MTL cortex, which has been attributed to lesions to the PrC (Quamme et al., 2007; see e.g., Bastin et al., 2013, for similar effects in healthy elderly with degraded hippocampal volume). A more recent study revealed that patients with mild cognitive impairment do not benefit from unitization (Delhaye, Mechanic-Hamilton, et al., 2019). Interestingly, their memory performance for unitized associations correlated with structural PrC integrity (see also Delhaye, Bahri, Salmon, & Bastin, 2019, for a similar correlation of unitization success with PrC atrophy in Alzheimer's dementia). This is also in line with the finding that unitization is not restricted to uni-modal binding (Li et al., 2019) as cross-modal intra-item binding is typically ascribed to the PrC (see Section1.1).

Summary: The Formation of New Memories

System-level memory consolidation is typically described by means of two distinct but highly interwoven systems, that is, a hippocampal and a neocortical system. Whereas the acquisition of new information through the hippocampus is fast, the consolidation process that transfers hippocampal representations to the neocortical system and integrates information into cortical networks is a slow and gradual process. There is also evidence that rapid learning is possible if the new information can be integrated into already existing, related knowledge structures (i.e., schemas). The rapid incorporation of arbitrary inter-item or item-context associations into the neocortical system, which is typically ascribed to the hippocampus, is possible by means of unitization, that is, if arbitrarily matched, independent information is integrated to a single unit. The role of the hippocampus in these ways of rapid learning has not yet been completely understood. Its involvement in schema-based learning has been extensively discussed but there is converging evidence that hippocampus-mediated processes play, if at all, a minor role in unitization.

Significance for This Thesis

In this thesis, it shall be investigated if it is possible to rapidly integrate novel, arbitrary associations into semantic memory networks even without providing instructions to unitize the items and already after only one single exposure. The FM encoding paradigm might provide a learning mechanism by which hippocampal processing can be completely bypassed, thereby enabling direct cortical integration. After the introduction of previous FM literature and general information on FM in the following chapter, the underlying mechanisms and neural underpinnings of learning by means of FM will be experimentally examined in this work.

Chapter 2

Fast Mapping

Contrary to what traditional consolidation theories would assume, there is evidence that arbitrary picture-label associations can be rapidly incorporated into the neocortical system if these associations are acquired through *fast mapping* (FM). Learning by means of FM has not only proven to be *rapid* but the transfer from the experience to neocortical networks also seems to be *direct*, that is, hippocampal processing might even be bypassed. In general, the FM learning procedure requires that multiple objects are presented (two pictures in most FM paradigms), of which one is previously unknown and the others are already known. Typically, a perceptual question is asked, which refers to an unfamiliar name. By exclusion of the known items, one can infer that the name must belong to the unknown item. In contrast to schema-based learning, the picture and the name both are previously unknown and arbitrarily matched, that is, there are no common related memory representations by which they can be coactivated. In contrast to unitization, no explicit intstructions are made to bind the two items to a unit and thus, the to-be-associated items are not explicitly transformed to intra-item associations. The FM paradigm typically used in experimental settings has been adopted from developmental psychology. Although young children typically do not learn new vocabulary through explicit instructions, they show an enormous vocabulary learning rate in the first years of life (e.g., Ganger & Brent, 2004). This is remarkable especially against the background that the hippocampus has not reached maturity at that early age, myelination in hippocampal subfields is not completed before adolescence (Arnold & Trojanowski, 1996), and especially the posterior hippocampus gains mass until the age of 25 (Ghetti & Bunge, 2012). According to Gilmore et al. (2011), hippocampal volume has the slowest growing rate in the MTL within the first two years. In adults, information flow in the hippocampus reaches from the ErC to the hippocampus mainly via a long route through the trisynaptic circuit including the dentate gyrus and CA3, which typically supports pattern separation, or via a short pathway through a monosynaptic circuit with ErC–CA1 connections. According to Lavenex and Banta Lavenex (2013), maturation of CA3 and dentate gyrus is slow whereas CA1 shows an early maturation. The long route might thus not be available in young children at about the age of 18-24 months (Ábrahám et al., 2010; see also Lavenex & Banta Lavenex, 2013). Critically, this is roughly the age of children in studies in which evidence for successful FM learning was found (e.g., Jaswal & Markman, 2001; Spiegel & Halberda, 2011; but see, e.g., Horst & Samuelson, 2008).

It has been extensively discussed how rapid learning is possible in very young children, who have difficulties in explicit learning. Typically, children acquire new knowledge incidentally. Sometimes learning is supported by repetitions but it has been shown that single-exposure learning of object-label associations is possible even in very young children. The children in the study by Carey and Bartlett (1978) learned associations between differently colored trays and the respective color name. For example, they were presented with two trays of different colors, one of which was red and the other one olive. They then were instructed to bring the experimenter ”the chromium one. Not the red one, the chromium one” (Carey & Bartlett, 1978, p. 2). In order to solve this task and choose the tray of a color called chromium, children needed to recognize that the other tray's color is red and thus infer that the unfamiliar color must be ”chromium”. It is reasonable to assume that incidental learning through the exclusion of a previously known item resembles a typical learning environment of children. Carey and Bartlett (1978) found evidence that the new color-label association still could be remembered after a weak or that at least it was remembered that “chromium” describes a color. However, these results should be interpreted carefully as only a single association was learned and repetitions were sometimes necessary. In general, FM in children has only been vaguely defined in the literature and the experimental procedures vary greatly.

Hence, an experimental comparison between hippocampus-dependent learning and FM learning in subjects with severe lesions to the hippocampus might be a more elegant way in order to draw conclusions on hippocampal contribution to learning by means of FM. In addition, findings on FM learning in children might not necessarily be applicable to adults as the semantic networks into which the new associations can be incorporated is likely more elaborate in adults and thus, FM encoding could have more promising effects on memory. Depending on the study, FM is often defined differently and the paradigm itself differs. In this work, I will refer to FM as specific on-line encoding procedure as defined by Sharon et al. (2011). The actual learning process will be referred to as learning by means of FM. Here, FM itself is *not* defined as the mechanism underlying learning by means of the FM paradigm.

2.1 Fast Mapping in Adults

Sharon et al. (2011) were the first to systematically investigate learning by means of FM as potentially hippocampus-independent encoding paradigm in adults, with the assumption that FM is supposed to trigger a general learning mechanism that goes beyond vocabulary learning in children. They compared healthy adults to patients with severe and selective hippocampal lesions and patients with additional lesions to the MTL cortex in order to draw conclusions on the brain structures involved in FM learning. The FM paradigm was compared to a standard explicit encoding (EE) paradigm, in which participants were explicitly asked to remember a picture together with its name (e.g., *Remember the numbat.*; see Figure 2.1), and by which learning would be assumed to rely on slow hippocampal-neocortical consolidation.

2.1.1 The Typical Fast Mapping Paradigm

The specific paradigm that will be used in this thesis goes back to Sharon et al. (2011). In their FM paradigm, participants read and heard a question referring to an unknown label (e.g., *Is the numbat's tail pointed up?*), which required a *yes* or *no* response. Then they were presented with two pictures, one of which was supposed to be previously known (e.g., a zebra) and the other one unknown (e.g., a numbat; see Figure 2.1). Participants could answer the question by recognizing the previously known item and inferring that the unknown item must be the one to which the question refers. Thereby, they likely linked the picture of the unknown item to the unfamiliar label, creating new picture-label associations out of arbitrarily matched pairs of a picture and a word. Sharon et al. (2011) tested memory for associations by means of an explicit three-alternative forced-choice recognition test, in which participants were asked to indicate which of three previously unknown pictures from the encoding phase had been presented together with a certain label. Recognition was tested twice, once 10 minutes after encoding and again after one week (see Figure 2.1). After completing both tests of the associations learned by means of FM, the same procedure was administered using the EE paradigm for encoding. Sharon et al. (2011) defined three criteria that need to be fulfilled in order to enable rapid cortical integration of novel associations by means of FM: (1) Encoding must be incidental, that is, participants must not know about the subsequent recognition test. (2) The novel associations need to be actively discovered by the participant by means of *disjunctive syllogism*, that is, exclusion of the previously known item in order to link the label to the unknown item. (3) An already existing semantic context must be available, into which the novel associations can be integrated. It has later been added that (4) the new associations must not overlap with previously learned associations in order to prevent catastrohpic interference (Atir-Sharon et al., 2015; Merhav et al., 2014; see also Gilboa, 2019, for a recent commentary).

It was not surprising that the four amnesic patients with severe lesions predominantly to the hippocampus did not recognize the picture-label associations encoded through (putatively hippocampus-dependent) EE in a subsequent recognition test above chance level, neither in an immediate test nor after a week (see Figure 2.1). Strikingly, recognition accuracy of the same patients was as good as that of healthy controls if they had encoded the novel associations by means of FM, both immediately after encoding and after a week (see Figure 2.1). This study can be considered the first evidence for beneficial effects of FM in patients with severe lesions predominantly to the hippocampus, and for rapid and direct learning of arbitrary associations by means of FM.

2.1.2 Previous Findings

Rapid learning through FM has also been observed in other studies investigating FM in patients (Korenic et al., 2016; Merhav et al., 2014), in healthy adults using behavioral measures (Coutanche & Thompson-Schill, 2014; Coutanche & Koch, 2017; Himmer et al., 2017; Merhav et al., 2014) or fMRI (Atir-Sharon et al., 2015; Merhav et al., 2015). For example, Himmer et al. (2017) compared recognition accuracy for associations acquired by means of FM versus EE immediately after encoding and retention after a delay of 12 hours that was either filled with sleep or wakefulness. As traditional theories of memory consolidation would expect, participants who learned associations that had been encoded by means of EE benefitted from sleep, that is, they forgot more of the associations when they stayed awake between the immediate

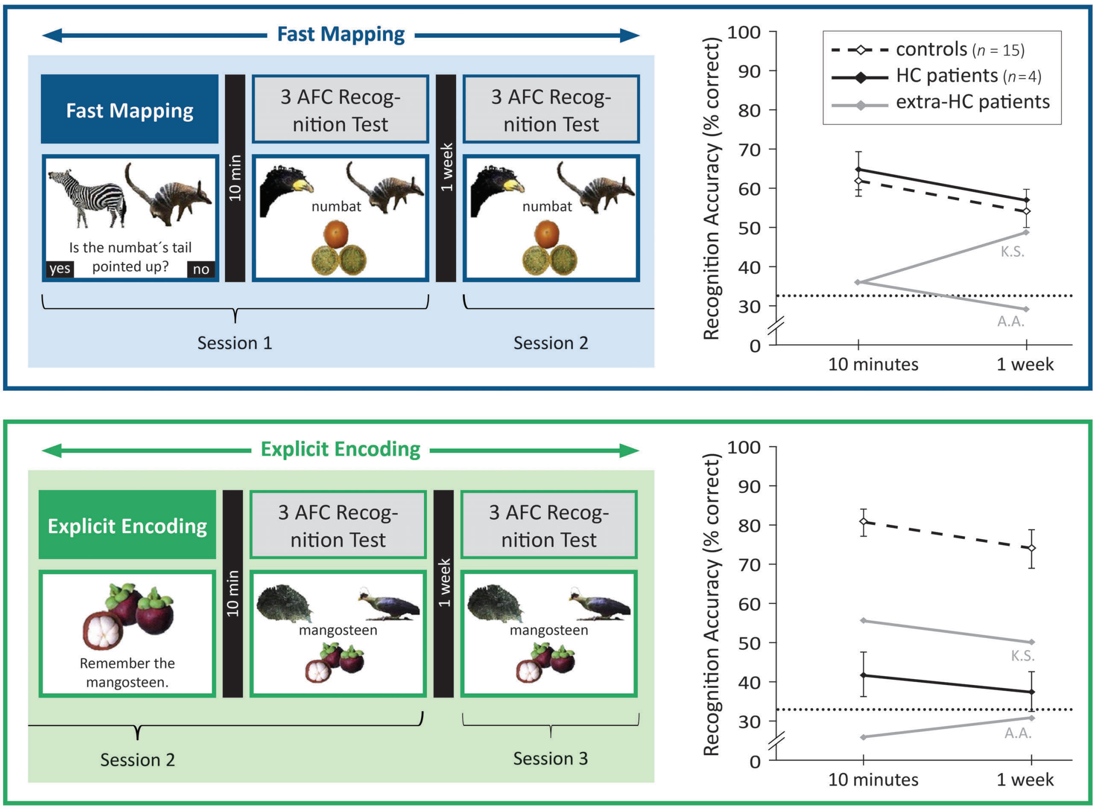

Figure 2.1 Sharon, Moscovitch, and Gilboa (2011). Experimental design and procedure of the fast mapping (FM) and explicit encoding (EE) condition on the left, the condition-specific results of the three-alternative forced-choice (3AFC) recognition test on the right. Blue color = FM, green color = EE. The experiment consisted of three sessions. In the first session, participants encoded the associations through FM, which were tested after a 10-min delay. At the beginning of the second session (i.e., after one week), these associations were tested again. Thereafter, participants encoded new associations by means of EE and were tested for these after 10 minutes and again in the third session after one week. HC patients = amnesic patients with lesions predominantly to the hippocampus, extra-HC patients = patients with extended lesions to extra-hippocampal structures of the medial temporal lobe. Pictures of the items reprinted and results reconstructed from Sharon, Moscovitch, and Gilboa (2011), both with permission from the National Academy of Sciences of the United States of America.

and delayed test than when they were asleep. However, if associations had been encoded by means of FM, participants who went to sleep and those who stayed awake did not differ with regard to retention. This leads to the assumption that novel associations had already been stored immediately after learning. If learning by means of FM allows for rapid incorporation of associations into cortical networks, potentially bypassing the hippocampus, this should also become apparent in the lack of a protection from interference that would usually be provided through hippocampal pattern separation. Merhav et al. (2014) used an interference paradigm in order to investigate susceptibility to catastrophic interference (i.e., both proactive and retroactive interference) for associations encoded by means of FM. If associations acquired by means of FM are prone to catastrophic interference, this would support the idea of a direct neocortical pathway bypassing hippocampal processing (i.e., hippocampal pattern separation). Merhav et al. (2014) induced interference by means of an AB–AC design, that is, the picture of an unknown item A was first encoded together with the label B and was then encoded again together with the label C. If catastrohpic interference occurred, neither of the picture-label pairs should be correctly recognized. In the EE group, there were no interference effects compared to a non-interfered group. However, catastrophic interference was indeed observed in an FM condition if interference (i.e., the AC pairing) had been induced 22 hours after the first encoding phase (the AB pairing; see Chapter 8 for a discussion of the time scale of interference induction). This suggests that a direct neocortical pathway can be triggered through FM, bypassing hippocampal pattern separation. Merhav et al. (2014) found in a second experiment that three amnesic patients also suffered from interference on both the AB and AC pair whereas their accuracy in the non-interfered FM condition was as good as that of healthy controls, thereby replicating Sharon et al. (2011; but note that two of these patients had additional lesions to MTL cortex). Korenic et al. (2016) found that patients with schizophrenia, who typically exhibit hippocampal abnormalities, showed a smaller memory impairment compared to healthy controls if associations were learned by means of FM compared to EE, similar to the amnesic patients with predominantly hippocampal lesions reported by Sharon et al. (2011; but note that the schizophrenia patients still performed better in the EE paradigm).

Despite this evidence, contradictory findings have been reported (Cooper et al., 2019; Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016). In order to resolve these contradictions, we set out to ask three questions: (1) In which aspects do the studies in which rapid learning through FM was successful differ from those in which no FM learning was observed? (2) The functional integrity of which brain structures might be decisive for success or failure in learning by means of FM? (3) What are the task demands at FM encoding and which underlying neurocognitive mechanisms would be especially qualified to solve the task and store the associations?

2.1.2.1 Deviations From the Original Paradigm

Some studies on FM learning are difficult to compare with the results by Sharon et al. (2011) as not all criteria for successful FM learning were always fulfilled and even if so, the specific paradigms deviated from the original study with regard to other critical aspects. For example, Warren and Duff (2014) did not find an FM benefit for patients with hippocampal lesions or atrophy, neither in an explicit recognition test nor by means of implicit eye-tracking measures (see also Warren et al., 2016, for similar results). However, they had informed their participants about a subsequent memory test prior to the experiment and hence, it must be assumed that learning was intentional (for the effects of a learning intention on FM, see Chapter 7). Moreover, the unfamiliar labels were presented only auditorily but not visually and participants were instructed to click on the respective item at encoding instead of answering a yes/no question referring to the items' perceptual features. In addition, the administration of two free-recall tests between encoding and recognition might have blurred potentially beneficial effects on recognition memory that would have been attributable to FM. In other studies, the delay between encoding and test phase varied greatly with regard to the duration (between no delay and one week) and regarding the filler task. Whereas Sharon et al. (2011), Coutanche and Thompson-Schill (2014), and Coutanche and Koch (2017) administered a vocabulary test, and Coutanche and Koch (2017) added a questionnaire on learning types, Smith et al. (2014) filled the delay with conversation and Greve et al. (2014) with an intelligence test. Also, the encoding phase itself greatly differed between studies. For example, feedback on the yes/no decision was not always provided (Himmer et al., 2017), response deadlines were different (between 2380 ms and self-paced) and the number of trials greatly differed (between 16 and 50 trials). The latter is difficult to circumvent, however, as different cognitive capacities between different groups (healthy young adults, older adults, and patients) need to be taken into account. Importantly, the number of repetitions also differed (between two and four presentations of the same picture-label pair). However, if we want to investigate if rapid and direct learning by means of FM is possible, we would consequently need to expect learning effects already after a single exposure. It is unclear if and in what way the variations outlined above can account for contradictions in the literature as none of these factors can clearly differentiate between studies showing FM learning and those reporting contradictory findings and none of these factors has been manipulated systematically. As FM studies differ with respect to several other factors, the differences in the encoding paradigms reported here cannot be evaluated in isolation.

2.1.2.2 Appropriateness of Measures of Cortical Integration

As Sharon et al. (2011) assessed cortical integration by means of an explicit forced-choice recognition test, subsequent studies followed this procedure and used the same explicit test paradigm. Despite the advantages of keeping as many parameters as possible constant between studies, using the same tests as measure for cortical integration is not equally applicable for all samples. Explicit testing can be considered a valid measure of cortical integration in studies examining FM in patients with severe and selective lesions to the hippocampus: If retrieval cannot be hippocampus-based, any above-chance recognition performance must consequently reflect retrieval from cortical semantic networks. However, in people who can rely on hippocampal processing such as young and healthy adults, explicit recognition tests do not necessarily reflect pure cortical retrieval. Above-chance recognition performance could as well be driven by hippocampus-based retrieval, which would typically be expected in explicit recognition tests in healthy adults (Shimamura, 1986; Squire et al., 1992). At least, by using behavioral recognition accuracy as the only measure of memory, it cannot be disentangled to what extent retrieval is driven by the hippocampal or neocortical system. Therefore, the absence of evidence for FM learning in behavioral experiments in which solely explicit tests were used to assess cortical integration in healthy young adults (e.g., Cooper et al., 2019) should not be over-interpreted as it is unclear what is reflected by recognition accuracy. Even though in healthy old adults (see Cooper et al., 2019; and Greve et al., 2014, for a lack of an FM benefit in healthy elderly), a degradation of hippocampal volume is typically observed, explicit recognition tests should only be interpreted very carefully as, although certainly correlated, it might be oversimplified to draw conclusions from hippocampal volume on the functional integrity in healthy aging. It is still possible that retrieval in healthy elderly is hippocampus-based after FM learning or, at least, it cannot be excluded.

One idea to circumvent the problem of explicit testing in behavioral experiments with healthy adults is to assess memory integration using implicit tests (e.g., a semantic priming task) as implicit measures are supposed to provide direct access to semantic networks and depend less on hippocampal involvement (e.g., Goshen-Gottstein, Moscovitch, & Melo, 2000; Shimamura, 1986; Squire et al., 1992). The rationale behind, for example, semantic priming as a measure of cortical integration is that response times for decisions on target words should be facilitated (and thus, responses should be faster) if they are preceded by a semantically related prime word compared to an unrelated prime word. Such a semantic priming effect can only appear if both the prime word (e.g., *duck*) and the target word (e.g., *goose*) have a semantic connotation and are part of a common semantic network through which they can be mutually activated through spreading activation. If in an FM experiment, the previously unknown items (e.g., the label of an exotic bird called *satellote*) are used as primes and real words (e.g., goose) as targets, such a facilitatory priming effect can only occur if the label of the unknown item has been successfully integrated into cortical networks together with its semantic connotation. If the semantic incorporation of the picture-label associations has not been successful, responses to semantically related targets should remain unaffected. Coutanche and Thompson-Schill (2014; see also Coutanche & Koch, 2017) were the first to use behavioral implicit measures to assess rapid incorporation into semantic networks (as measured by semantic priming effects) and lexical networks (as measured by lexical competition effects). They found no semantic priming effect directly after encoding, neither in an FM condition nor in an EE condition. After a 24-hours delay between encoding and the recognition test, a semantic priming effect was observed in the FM condition only. Consequently, the authors concluded that *rapid* semantic integration was not possible through FM. However, the priming effects might have been masked by a confound in the experimental design: As stimulus material consisted of animals only, the related targets in the priming task necessarily needed to be animals as well, whereas the unrelated targets were always artifacts. It cannot be excluded that the artifacts had generally been processed faster on a baseline level, irrespective of relatedness, which would mask a potential priming effect that is calculated by subtracting response times of related (i.e., animals) from response times to unrelated targets (i.e., artifacts). As the pattern reported by Coutanche and Thompson-Schill (2014) seems consistent with their assumptions but simply downshifted, these data might actually be more promising than they assumed. Coutanche and Thompson-Schill (2014) also assessed the incorporation of the new labels into lexical networks by means of a lexical competition task. This is based on the idea that responses to real words (e.g., *satellite*) should be slowed if a new label that lexically neighbors that word (e.g., *satellote*) has been successfully integrated, with the rationale that it takes more time to uniquely identify the real word. Coutanche and Thompson-Schill (2014) found evidence for rapid lexical integration of the labels on an item level in the FM but not EE condition. This is no evidence for the integration of the complete picture-label association but at least a prerequisite for that.

Warren and Duff (2014) and Warren et al. (2016) used implicit eye-tracking measures in order to investigate the fixation times on targets versus foils at the recognition test. They compared eye movements between healthy participants and patients with complete resections of the left temporal lobe (Warren et al., 2016) or individuals with different grades of amnesia (mildly amnesic vs. severely amnesic — half of the latter group with extra-hippocampal lesions to ATL and MTL cortex; Warren & Duff, 2014). They found that healthy participants (and mildly amnesic patients in Warren & Duff, 2014) looked at the target longer than at the foils, even if they incorrectly chose a foil. Severely amnesic patients (Warren & Duff, 2014) and patients with temporal lobe lesions (Warren et al., 2016) did not show this pattern. They only showed a selection effect, that is, they always looked longer at the chosen item, irrespective if it was the target or not. The authors interpreted the tendency to look at the target longer even though it has not been selected as an implicit indicator for memory. However, this pattern was also observed for the EE condition. Due to the deviations from the original paradigm named above, however, this lack of a benefit from FM is difficult to interpret.

Another method to assess cortical integration is functional magnetic resonance imaging (fMRI) as it allows to determine if recognition recruited the hippocampus or was indeed based on cortical retrieval. To my knowledge, there is so far only one FM study in which the recognition test phase was scanned. In Merhav et al. (2015), two groups of healthy young adults (one FM group, one EE group) learned half of the stimuli 24.5 hours before testing (*remote* condition) and the other half of the items 30 minutes before testing (*recent* condition). By contrasting the fMRI activation pattern at test of the recently learned associations with activation of items of the remote condition, overnight changes would become visible. As expected, they observed overnight changes in a widespread neocortical network for EE learning, indicating that system-level consolidation has occured (see Figure 2.2). No critical overnight changes were observed for associations acquired through FM while participants clearly showed above-chance recognition performance in both conditions. This strongly indicates that in the FM group, associations were rapidly integrated into neocortical networks (see also Himmer et al., 2017, for supporting behavioral findings).

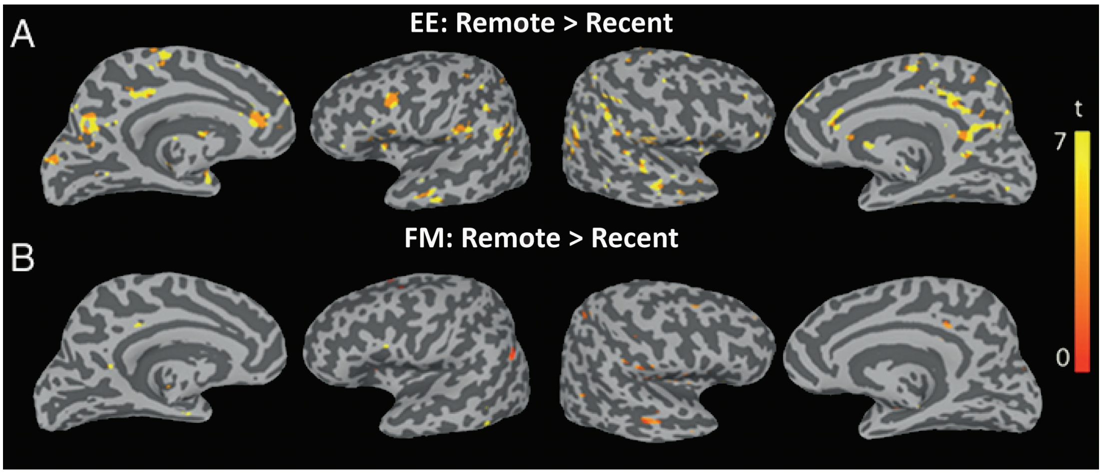

Figure 2.2 Results reported by Merhav, Karni, and Gilboa (2015). Comparisons of brain activations between recent and remote memories, separately for the fast mapping (FM) and explicit encoding (EE) condition. **A** In the EE condition, remote memories (i.e., associations that had been learned 24.5 hours ago) clearly activated a more widespread neocortical network compared to recently acquired associations (30 min before testing). This might indicate overnight consolidation. **B** In the FM condition, no difference in brain activation is observed for associations that had been learned the day before and those that had been acquired only recently. This might indicate that associations acquired through FM might have been rapidly consolidated. Adapted from Merhav, Karni, and Gilboa (2015) with permission from Elsevier.

2.1.3 Fast Mapping and Its Neural Underpinnings

If the hippocampus can be bypassed in learning by means of FM, the question arises which other structures possibly contribute to FM learning. Much of the previous literature points to the ATL and specifically the temporal poles as potential candidate structures. Sharon et al. (2011) reported two other patients, A. A. and K. S., with extended lesions to extra-hippocampal structures of the MTL (i.e., PrC and ErC) and ATL (especially the temporal poles). Interestingly, these patients did not show any benefits from FM encoding. Patient K. S. did not perform above chance level in the recognition test following the FM condition, although he reached above-chance accuracy after encoding through EE, which might be due to his morphologically intact hippocampi. Patient A. A. did not perform above chance level, irrespective of encoding condition and delay (see Figure 2.1). This might be first evidence that regions of the PrC, ErC, or ATL are involved in rapid cortical integration of novel associations through FM. Interestingly, the patients reported by Warren et al. (2016), who did not benefit from FM learning, not only exhibited lesions to the hippocampus but they had undergone resections of the complete left temporal lobe. It is thus well conceivable that in these patients, structures were damaged that are necessary for successful FM learning (but see also Warren & Duff, 2014, showing no differences in FM learning between patients with selective hippocampal lesions and patients with extended lesions to medial and anterior temporal structures). The contribution of the ATL to FM learning in young and healthy adults was also confirmed by fMRI evidence. Atir-Sharon et al. (2015) found that whereas subsequent recognition accuracy following EE was best predicted by hippocampal activity at encoding, recognition accuracy following FM encoding was better predicted by activity in the ATL (albeit they also observed hippocampal involvement in FM learning; see Chapter 8 for discussion of the role of the hippocampus). This is in accordance with the description of the ATL as an amodal semantic hub that is especially qualified to integrate multimodal information to a conceptual, semantically meaningful unit (see Section 1.3; Lambon Ralph et al., 2017; Patterson et al., 2007). In line with that, Merhav et al. (2015) reported that the ATL and ATL-related networks are involved in recognition of the picture-label associations shortly after they had been acquired through FM but not EE. ATL involvement in FM learning is further indirectly supported by behavioral results reported by Coutanche and Koch (2017), who found better lexical integration of the labels (i.e., larger lexical competition effects) if the previously known item in the FM encoding display was very atypical for its category than if it was highly typical. Although only behavioral data, it is important to note that especially atypical items are processed by the ATL (Rogers et al., 2015).

Against the background of the involvement of the ATL in FM learning, a lack of an FM benefit in patients with extended lesions to the ATL does not allow for conclusions on the existence of rapid semantic integration through FM. However, even a near-replication of Sharon et al. (2011) still did not find any benefits from FM encoding (Smith et al., 2014; but see Merhav et al., 2014, for a replication of the findings by Sharon et al., 2011), even though the items were exactly the same as in Sharon et al. (2011) and the lesion pattern spared at least the ATL in all patients (but note that one patient exhibited extended lesions to the MTL cortex). Although ATL volume in the study by Sharon et al. (2011) separates best between the four patients who showed an FM benefit and the two who did not, the latter two also exhibited severely reduced PrC volumes. A potential PrC involvement in FM learning is further supported by the notion that in the patients with lesions predominantly to the hippocampus reported by Sharon et al. (2011), recognition accuracy tends to correlate with PrC volume. A similar pattern can also be observed in unpublished data of the FM experiment to which Cooper et al. (2018) referred, that is, the recognition accuracies they mention for each participant seems to correlate with the parahippocampal volume (most likely including the PrC; as reported in Henson et al., 2016).

Furthermore, considering the FM task demands, the functional characteristics of the PrC seem to be crucial for solving the FM encoding task. The two pictures of items that have to be discriminated in the FM encoding task essentially are highly complex feature conjunctions. As outlined in Chapter 1, the PrC is especially qualified to discriminate between highly similar feature conjunctions as it is able to create distinct feature combinations even if the single features are the same. Thus, the PrC might likely be involved in the picture discrimination process in FM, and this involvement might be stronger the more features the previously unknown and the previously known item have in common. Interestingly, in the study in which an FM benefit was found for patients with lesions predominantly to the hippocampus but not extended extra-hippocampal lesions including the PrC (Sharon et al., 2011), feature overlap was high (Sharon, 2010). Although not mentioned explicitly, at least from subjective visual inspection of the example in their article, Smith et al. (2014) did not present the items in pairs in which the unknown and the known item share many features. This also seems to have been the case in several other studies in which no rapid learning through FM was found (Cooper et al., 2019; Warren & Duff, 2014; Warren et al., 2016). Apart from picture discrimination, learning by means of FM also involves a binding process, which fosters the creation of links between the unknown item and the label. There is a large body of evidence that the PrC is involved in the binding of inter-item associations to intra-item associations or units (see Chapter 1; see also Section 1.4.2.2 for PrC involvement in explicitly instructed unitization). Against this background, it is reasonable to assume that the PrC might essentially contribute to learning by means of FM, especially in the discrimination between the unknown and the known item and, in a next step, in the binding of the unknown item and its label. It is further conceivable that increasing the demands on perirhinal processing in the FM task, which has most likely been the case in Sharon et al. (2011) due to the high feature overlap, might possibly boost PrC involvement at encoding and thus be supportive for successful FM learning. One possibility to increase demands on the PrC in the FM task would be to increase feature overlap between the unknown and the known item. The role of feature overlap and PrC involvement in FM learning is yet unclear as feature overlap has so far not been manipulated systematically and neither of the two previous fMRI studies used explicitly high-overlap item pairs.

Summary: Fast Mapping

Contrary to traditional theories of memory consolidation, there is evidence that rapid and direct cortical integration is possible by means of FM. However, contradictory findings have been reported and it has been extensively discussed if rapid learning through FM should be considered a generalizable memory phenomenon at all (see Cooper et al., 2018, and the respective commentaries). The contradictory findings can partly be explained by the operationalization of FM encoding as in some studies not all criteria were fulfilled that had been suggested by Sharon et al. (2011). Moreover, the lesions of the patients in whom FM learning was investigated greatly differed between studies, sometimes including the complete temporal lobe – and thus, possibly including structures that might contribute to learning through FM. In studies in which FM was investigated in healthy young adults, behavioral explicit recognition tests were used as only measure of cortical integration, which makes the results difficult to interpret as cortical and hippocampal retrieval might be conflated. However, even if all FM criteria were fulfilled, Smith et al. (2014) still did not find rapid learning through FM (but note that one patient in their study exhibited extended lesions to the MTL cortex).

Significance for This Thesis

The missing piece in the debate on FM learning might be reflected in the specific characteristics of the FM task and their underlying neurocognitive mechanisms. The PrC seems to be especially qualified in order to solve the FM encoding task as it is involved in the discrimination of highly complex objects and also in the binding of cross-modal information to a coherent unit. Therefore, this thesis aims to investigate the underlying neurocognitive mechanisms of FM learning, suggesting that increasing demands on perirhinal processing as operationalized by a high feature overlap might foster rapid cortical integration through FM and also perirhinal contribution to FM learning.

Chapter 3

Research Objectives

3.1 The Role of Feature Overlap in Learning by Means of Fast Mapping

As the typically compared FM and EE conditions differ in several aspects, the influence of the criteria suggested for successful FM learning is conflated and their role has not been tested in isolation. Chapter 5 and Chapter 7 aim to identify factors moderating learning by means of FM in healthy young adults. The role of feature overlap as one such factor will be investigated in Chapter 5, by direct comparison between two FM conditions that are identical apart from the similarity between items. In Experiment 1, we investigated rapid lexical integration of the novel labels, similarly to Coutanche and Thompson-Schill (2014), as this can be considered a prerequisite of the incorporation of the complete picture-label associations into semantic networks. The latter is investigated in Experiment 2, in which we examined the effects of feature overlap on semantic integration. We expected to find a beneficial effect for an FM condition in which feature overlap between the unknown and the known item was high (fast mapping, high overlap; FMHO) but not when it was low (fast mapping, low overlap; FMLO). In Experiment 1, better lexical integration in the FMHO condition should become evident in greater competition of the newly learned labels with already existing words that are closely related in the lexical network. In Experiment 2, we expected a facilitatory effect for targets preceded by a semantically related studied item (versus a semantically unrelated item). Such a semantic priming effect was expected for an FMHO group but not for an FMLO or an EE group. In order to examine long-term effects of FM learning, we tested participants twice, once immediately after encoding and again after 24 hours.

3.2 The Neural Underpinnings of Learning by Means of Fast Mapping

A potential moderating role of feature overlap in FM learning does not allow for conclusions on the neural underpinnings. In Experiment 3 (Chapter 6) it will be examined if the PrC is indeed involved in FM learning and if its contribution to learning varies depending on feature overlap. By means of subsequent memory effects, we investigated if PrC involvement at encoding is greater for subsequently remembered compared to forgotten items, and if this difference is greater for an FMHO group compared to an FMLO group. The aim of this study was not to investigate a potential independence of the hippocampus but rather the neurofunctional underpinnings of the rapid cortical integration of novel associations.

3.3 Further Critical Determinants for Learning by Means of Fast Mapping

In Chapter 7, we further aimed to identify critical determinants for learning by means of FM, such as the presence of the known item and incidental learning. In line with the argumentation that the PrC might be highly involved in FM learning and that a high feature overlap might trigger perirhinal discrimination and binding processes, rapid semantic integration (as measured by means of semantic priming effects) should only occur in an FMHO condition but not in any condition in which only one picture was presented. Moreover, it has not yet been tested if incidental learning is actually a prerequisite in FM learning in healthy young adults. After all, one could argue that hippocampal processing is not necessary in learning through FM but it might as well not disturb the learning process, which was examined in Experiment 4. We investigated the effect of object discrimination again in Experiment 5 but only for incidental learning. In addition, we took recently published findings by Coutanche and Koch (2017) into account, who reported effects of the typicality of the known item on rapid lexical integration, and added a typicality rating to the experiment.

Chapter 4

Rating Study

4.1 Introduction

Prior to the experiments, pictures of mammals, birds, fish, insects, reptiles, fruit, vegetables, and plants were drawn from the internet. One half of these pictures was supposed to be known and the other half was supposed to be unknown to the participants. For each putatively unknown item, a highly similar putatively known item was included in the item pool. Within a rating study, these items were rated with regard to familiarity, previous knowledge, category, and feature overlap, in order to ensure that the experimental manipulation of feature overlap and our assumption previous knowledge was valid and the materials were appropriate to be used in subsequent experiments.

4.2 Methods

4.2.1 Participants

Stimulus material was rated by 46 students from Saarland University ($M_{\text{age}} = 23.1$ years, age range: 18-34 years; 30 female). All participants were native German speakers and had normal or corrected-to-normal vision. Participants gave written informed consent prior to the experiment and were compensated for their participation with 8€ per hour. The study was approved by the local ethics committee of Saarland University in accordance with the Declaration of Helsinki.

4.2.2 Materials

Stimulus material consisted of 360 experimental items of two higher-level categories (i.e., animals and plants), subdividable into eight lower-level categories (*animals*: mammals, birds, fish, insects, reptiles; *plants*: fruits, vegetables, other plants). One half of the items was supposed to be previously unknown, the other half was supposed to be previously known. In order to manipulate feature overlap between the putatively known and the putatively unknown items, we created high-overlap and low-overlap item pairs, consisting of one putatively known and one putatively unknown item each (see Figure 4.1). Feature overlap was defined as visual similarity between the items. The degree of feature overlap at stimulus creation was subjectively determined but high-overlap item pairs were always from the same taxonomic higher- and lower-level category (e.g., both were birds), whereas low-overlap pairs were always from different lower-level categories but could either be from the same higher-level category (e.g., a bird and a mammal) or from different higher-level categories (e.g.,a bird and a fruit).

In order to allow for counterbalancing between overlap conditions in subsequent experiments, each putatively unknown item was part of a picture triplet (e.g., Triplet 1a in Figure 4.1), consisting of two item pairs: One putatively unknown item was paired with one highly similar known item (for the high-overlap condition) and with one less similar known item (for the low-overlap condition). In a different triplet (e.g. Triplet 1b in Figure 4.1), these two putatively known items were paired with another unknown item in the respective other overlap condition. Such two interrelated triplets, comprising two unknown and two known items in sum, will be referred to as *triplet pair*. This arrangement made it possible that each unknown item and each known item could be encoded in each overlap condition. In addition, items that would receive weak ratings in the rating study could be excluded together with the complete triplet pair, allowing for fully counterbalanced stimulus sets in the experiments.

Additional 144 items were added in order to serve as filler trials in subsequent experiments. In the encoding phase of all experiments, filler trials were inserted in which the question referred to the previously known item. This should prevent participants from developing strategies such as always responding with regard to the unknown item without paying attention to the label in the question. In the rating study, these items were arranged in 48 triplets of one putatively unknown item and two putatively known items each (one for each overlap condition). For reasons of practicability, the putatively known items could only appear within either a high-overlap pair or a low-overlap pair. Thus, of the 144 items, 48 were putatively unknown items and 96 were putatively known items.

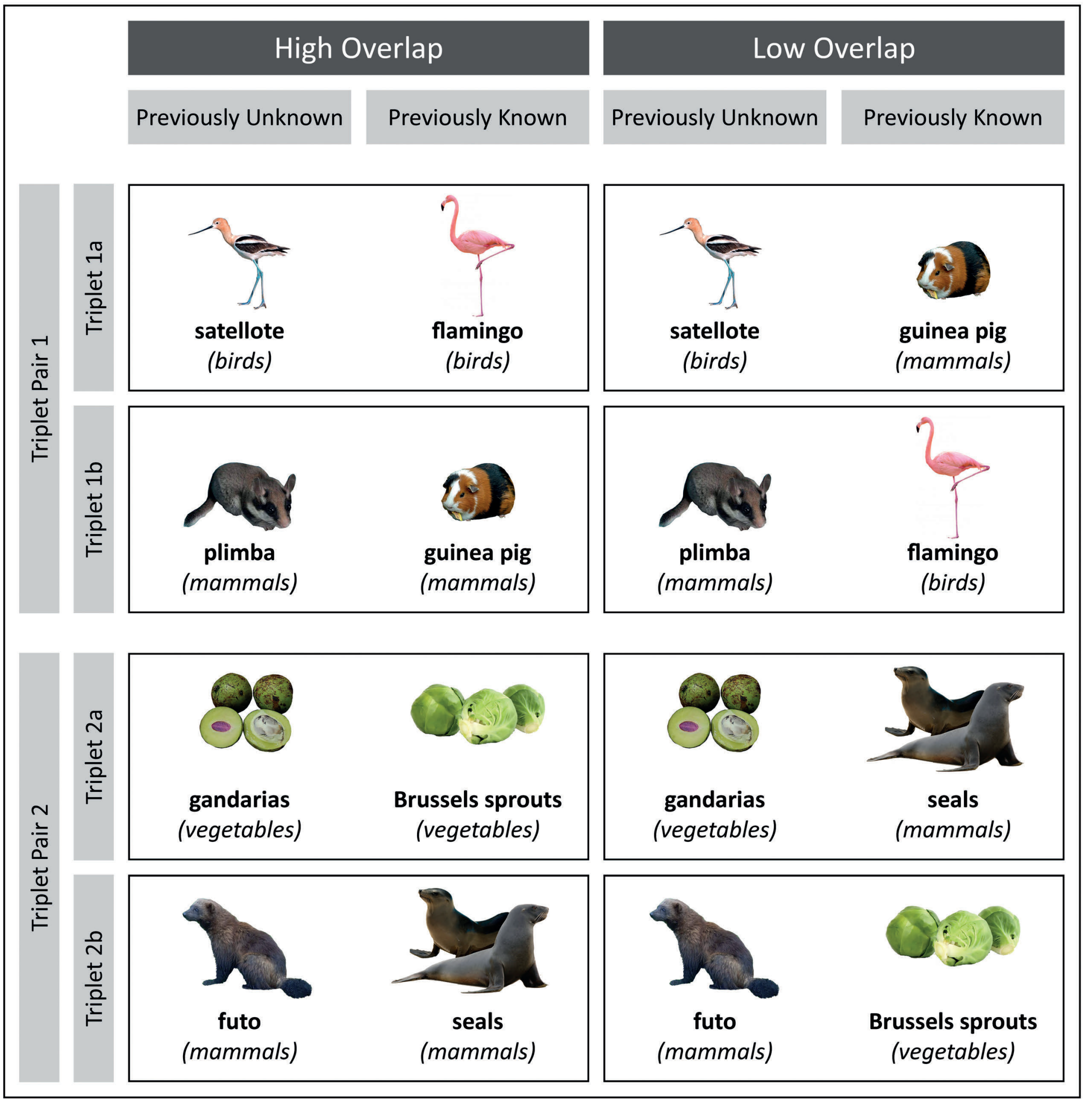

Figure 4.1 Example stimulus material. Each line depicts a picture triplet, consisting of one previously unknown item and two previously known items. Triplets were arranged in triplet pairs (e.g., Triplet Pair 1: Triplet 1a and 1b), within which overlap of the unknown and known items was counterbalanced. One of a triplet's previously known items was for the high-overlap encoding condition (e.g., Triplet 1a: flamingo) and one for the low-overlap encoding condition (e.g., Triplet 1a: guinea pig). Overlap condition of the previously known item was interchanged in the other triplet of a triplet pair (e.g., flamingo as low-overlap known item and guinea pig as high-overlap known item in Triplet 1b). High-overlap item pairs were always from the same lower-level category (e.g., Triplet 1a: both birds). Low-overlap item pairs could consist of items from the same higher-level category but different lower-level categories (Triplets 1a and 1b: both animals, with birds and mammals as lower-level categories) or from different higher-level categories (Triplets 2a and 2b: plants and animals, with vegetables and mammals as lower-level categories).

4.2.3 Design and Procedure

The rating study was programmed using the experimental software PsychoPy (Peirce, 2008; http://www.psychopy.org/). Participants were instructed to rate pictures of animals and plants for familiarity, previous knowledge, item category, and feature overlap between items. Ratings were conducted block-wise, that is, all items had been rated with regard to one variable of interest before the next rating task began, in which a different variable was rated for all items. All tasks throughout the study were self-paced and trials were always separated by a fixation cross that was presented in the center of the screen for 500 ms. All participants were presented with all single experimental items plus the 48 putatively unknown filler items and those 48 (out of 96) putatively known filler items that would be rated in the overlap rating at the end of the rating study (i.e., the known items of 24 high-overlap pairs and the known items of 24 low-overlap pairs, counterbalanced between subjects). Thus, each participant categorized and rated 456 single items (including 180 unknown and 180 known experimental items plus 48 unknown and 48 known filler items) for familiarity and prior knowledge, and rated the respective 228 item pairs for feature overlap, of which 114 were supposed to be high-overlap pairs and 114 were supposed to be low-overlap pairs.

Familiarity. First, participants were asked to rate all 456 items for familiarity on a 5-point Likert scale (1 = *not at all familiar*, 5 = *very familiar*). The picture of an item was presented above the rating scale, which was located slightly below the center of the screen. Ratings could be made by moving a slider to the respective point of the rating scale and confirming the response by clicking on a button on the screen. Item presentation was in random order, with putatively known and unknown items intermixed.

Prior knowledge and naming. After completion of the familiarity rating, all items were presented again in random order. The participants' task was to indicate their prior knowledge of an item by pressing one of two keys on the computer keyboard (*known* vs. *unknown*; key assignment counterbalanced between subjects). If they stated to know an item, a visual prompt to type in the item's name appeared on the screen, with the picture remaining visible. Participants were explicitly instructed to name the item at the lowest category level possible (e.g., *greyhound* instead of *dog*). The naming was included in order to reduce the participants' potential bias to always indicate that they know an item. Moreover, this allowed for the detection of falsely identified items, such that most participants might believe that they know an item but they confuse it with a different item – which would become evident if they have to name the items. After having confirmed their answer by mouse click, they moved on to the next trial. Naming was skipped if they indicated that they do not know an item.

Categorization. At categorization, participants were again presented with all 456 items in random order. They were asked to indicate to which of eight taxonomic categories (mammals, birds, fish, insects, reptiles, fruits, vegetables, plants) they thought an item fits best. The picture of the item was presented slightly above the center of the screen. Categorization was possible by clicking on one of eight gray buttons bearing the category names, which were horizontally aligned below the picture.

Feature overlap. In the last phase of the study, feature overlap of the previously matched item pairs was rated. Each participant was either presented with the high-overlap or the low-overlap pair of a triplet (counterbalanced between subjects). Two item pairs belonging to the same triplet pair were presented as either both high-overlap or both low-overlap pairs in order to prevent that a putatively known item was presented twice (see Figure 4.1). Feature overlap was rated on a 5-point Likert scale (1 = *not at all similar*, 5 = *very similar*) and was defined as the visual similarity of the items and the number of features they have in common, such as the presence and nature of fur, a tail, a fin, legs, the smoothness of a fruit's skin, color, and so forth.

4.2.4 Analyses

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org). For the calculation of reliability measures, the "psych" package in R was used (Revelle, 2018; https://cran.r-project.org/package=psych).

4.3 Results

Familiarity. The assessment of item familiarity was highly reliable, with Cronbach's $\alpha = .99$. For the experimental trials, mean familiarity for the putatively unknown items ($M = 2.12$, $SD = 0.59$) was significantly lower than for the putatively known items ($M = 4.29$, $SD = 0.50$), $t(358) = 37.52$, $p < .001$. The same accounted for the filler items, with mean familiarity ratings for the putatively unknown items (M

= 2.27, *SD* = 0.73) significantly lower than for the putatively known items (*M* = 3.88, *SD* = 0.72), *t*(142) = 12.62, *p* < .001.

Prior knowledge and naming. With Cronbach's α = .99, the rating of prior knowledge proved highly reliable. Of the experimental trials, the putatively unknown items were rated as *unknown* by *M* = 84.13 % (*SD* = 16.90 %) of all participants and the putatively known items were rated as *known* by *M* = 86.78 % (*SD* = 16.23 %) of all participants. The putatively unknown items of the filler trials were rated as *unknown* by *M* = 80.07 % (*SD* = 21.43 %) of all participants and the putatively known items of the filler trials were rated as *known* by *M* = 72.78 % (*SD* = 24.73 %) of all participants. The number of participants rating the putatively unknown items as *known* differed significantly from the number of participants rating the putatively known items as *known*, for both the experimental trials, *t*(358) = -40.60, *p* < .001, and the filler trials, *t*(142) = -12.62, *p* < .001. The naming data revealed that there were no items that were identified as known by most participants but confused with a different item. There were cases in which participants named the object on a basic instead of subordinate level (e.g., *onion* instead of *shallot*), which we still judged as correctly identified.

Categorization. On average, items were assigned to the same category by *M* = 89.57 % (*SD* = 15.33 %) of all participants, with *M* = 85.69 % (*SD* = 18.46 %) participants agreeing on the category of the putatively unknown experimental items and *M* = 91.88 % (*SD* = 12.55 %) agreeing on the category of the putatively known items. For the filler trials, *M* = 87.32 % (*SD* = 16.75 %) of participants agreed on the category of the putatively unknown item and *M* = 93.66 % (*SD* = 10.46 %) agreed on the category of the putatively known items. Of the experimental items, 113 were categorized as mammals by most participants, 68 as fruit, 58 as birds, 46 as plants, 40 as vegetables, 14 as insects, 13 as fish, and 8 as reptiles. Of the filler items, 23 were categorized as mammals by most participants, 19 as fruit, 19 as birds, 40 as plants, 18 as vegetables, 3 as insects, 19 as fish, and 3 as reptiles (see Table 4.1).

Feature overlap. The feature overlap rating was again highly reliable with Cronbach's α = .99. Of the experimental trials, mean feature overlap between the items of high-overlap pairs was *M* = 3.54 (*SD* = 0.55) and *M* = 1.37 (*SD* = 0.31) between the items of the low-overlap pairs. The difference between feature overlap of the high- and low-overlap item pairs of a triplet was highly significant, *t*(179) = 46.76, *p* < .001, with a mean difference between the high-overlap pair of an unknown item and its respective low-overlap pair of *M* = 2.17 (*SD* = 0.62). Of the filler trials, mean feature overlap between the items of high-overlap pairs was $M = 3.63$ ($SD = 0.69$) and $M = 1.27$ ($SD = 0.30$) between the items of the low-overlap pairs. The difference between feature overlap of the high- and low-overlap item pairs of a triplet was highly significant, $t(47) = 21.64$, $p < .001$, with a mean difference of $M = 2.36$ ($SD = 0.76$).

4.4 Discussion

In line with our intention at stimulus creation, familiarity for the putatively known items was higher than for the putatively unknown items, more participants indicated prior knowledge for the putatively known than for the unknown items, and similarity ratings between item pairs were higher for the high-overlap compared to the low-overlap pairs. For the experiments reported in this thesis, such item pairs were chosen for which the putatively unknown item had obtained the lowest familiarity ratings in the rating study and the putatively known item had obtained the highest familiarity ratings. Furthermore, those item pairs were selected, for which participants showed the highest agreement that the putatively unknown item is actually unknown and the putatively known item is known. In experiments in which overlap was manipulated, triplets were chosen for which the high-overlap pair had obtained the highest similarity rating and the low-overlap pair had obtained the lowest similarity rating.

Table 4.1 Number of items per category in the stimulus material as classified by participants, separately for experimental and filler trials, and putatively unknown and known items

	Experimental items		Filler items		
	Unknown	Known	Unknown	Known	Total
Animals					
Mammals	56	57	8	15	136
Birds	29	29	9	10	77
Fish	8	5	7	12	32
Insects	7	7	0	3	17
Reptiles	3	5	0	3	11
Plants					
Fruit	38	30	7	12	87
Vegetables	17	23	5	13	58
Plants	22	24	12	28	86
Total	180	180	48	96	504

Note. Animals and plants are defined as *higher-level categories* within which five and three *lower-level categories*, respectively, were nested. Experimental item pairs were originally created in a way that allows for equal numbers of putatively unknown and known items per category. Deviations from equal numbers result from participants' responses (e.g., when most participants classified a fruit as a vegetable). For the filler items, the unequal relation mainly resulted from an (intended) imbalance already at stimulus creation.

Chapter 5

Feature overlap modulates rapid semantic but not lexical integration of novel associations by means of fast mapping.

5.1 Introduction

According to traditional theories of declarative memory, consolidation of novel associations is a gradual, time-consuming process. The complementary learning systems theory (McClelland et al., 1995; Norman & O'Reilly, 2003) proposes that storage of new associations into long-term memory underlies two strongly interleaved processes, that is, the initial, fast acquisition of new information by means of hippocampal processing and the gradual incorporation of this information into lexico-semantic networks, represented in cortical structures. Consolidation of novel associations is assumed to be achieved by means of continuous reactivation through hippocampal-neocortical interplay (see Frankland & Bontempi, 2005, for review). However, recent findings revealed that rapid, direct integration of novel associations – potentially bypassing the hippocampus – can be successful if a learning procedure called *fast mapping* (FM) is used for knowledge acquisition (e.g., Himmer et al., 2017; Merhav et al., 2014, 2015; Sharon et al., 2011; see also Coutanche & Koch, 2017; and Coutanche & Thompson-Schill, 2014, for evidence for rapid lexical integration of the labels on an item-level and delayed semantic integration of the associations). In the typical FM paradigm, participants are presented with two pictures of objects, one of which is supposed to be previously known (e.g., a flamingo), whereas the other one is supposed to be previously unknown (e.g., an exotic, blue-footed bird). Their task is to answer a question referring to a previously unknown label (e.g., *Does the satellote have blue feet?*). In order to do so, participants need to recognize the previously known item, infer that the unknown label refers to the previously unknown item – thereby presumably incidentally creating a picture-label association –, and respond to the question with regard to the unknown item. Sharon et al. (2011) examined this learning procedure in four amnesic patients suffering from severe lesions to the MTL, predominantly to the hippocampus. These patients did not recognize the picture-label associations above chance level if the associations were intentionally learned within a standard EE task, in which they were explicitly asked to remember an unknown item together with its label. This might be attributed to their reduction in hippocampal volume as this is a task in which the hippocampus typically would be recruited. Interestingly, when the same patients encoded novel associations within the FM paradigm, their recognition performance was as good as that of healthy controls, implying that hippocampal processing can be bypassed through learning by means of FM. [1]

Despite this evidence that FM might enable successful direct integration of associations, other studies revealed contradictory findings (c.f. Cooper et al., 2019; Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016; see also Cooper et al., 2018). In order to resolve these contradictions, factors mediating learning success in the FM paradigm yet need to be identified. Sharon et al. (2011) suggested three key determinants to be crucial for successful learning by means of FM: (1) Learning needs to be incidental. (2) The picture-label associations need to be actively discovered by the participants themselves through a process called disjunctive syllogism, that is, excluding the previously known item in order to create a link between the label and the unknown item. (3) The new associations need to be learned in the context of previously known information, activating already existing semantic structures into which the new information can be integrated. However, there are studies in which these criteria were entirely fulfilled but still, no learning benefits of FM were observed (e.g., Greve et al., 2014; Smith et al., 2014). Hence, these three determinants might be essential but not necessarily sufficient for successful learning by means of FM and yet undiscovered parameters possibly moderating learning success in the FM paradigm need to be detected. A promising approach could be to ask which known functional

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[1] This does not necessarily mean that learning by means of FM is always hippocampus-independent. It has been shown that the hippocampus contributes to FM learning in healthy young adults (Atir-Sharon et al., 2015) or at least it cannot finally be excluded that it is not involved (Merhav et al., 2015). We propose that in patients with severe and selective hippocampal lesions it is valid to conclude that hippocampal activity cannot have contributed to FM learning or retrieval. This does not apply if the hippocampus is functionally intact.

characteristics of candidate brain structures could appropriately support this learning mechanism. Most of the previous literature points to the ATL, specifically the temporal poles, as a structure critical for FM (e.g., Atir-Sharon et al., 2015; Greve et al., 2014; Merhav et al., 2015; Sharon et al., 2011). This fits nicely with the notion that the ATL serves as an amodal semantic hub, integrating information from modality-specific cortices (see Lambon Ralph et al., 2017; and Patterson et al., 2007, for reviews). It is therefore plausible that these anterior temporal structures may serve as a system supporting rapid semantic integration through FM. Sharon et al. (2011) also reported two patients with additional damage to the ATL who were not able to benefit from FM, which further supports this idea. However, these patients also exhibited extensively reduced volumes of the left PrC. The PrC, a structure located in the anterior part of the MTL, was found to be involved in conceptual and perceptual processing of complex, higher-order object representations (e.g., Bussey et al., 2005; Cowell et al., 2010; Tyler et al., 2004), specifically in the discrimination of objects sharing many features (e.g., Barense et al., 2005; Bussey, Saksida, & Murray, 2002; Tyler et al., 2013). In addition, the PrC is involved in semantic processing (e.g., Meyer et al., 2013; Meyer et al., 2010; Meyer et al., 2005; Wang et al., 2010; Wang et al., 2014), familiarity-based item recognition (e.g., Bowles et al., 2007; Bowles et al., 2010; Wang et al., 2014; see Brown & Aggleton, 2001, for a review), and also in associative memory but only if item pairs are processed as a single unit (e.g., Haskins et al., 2008; Quamme et al., 2007). It is therefore well conceivable that the computational mechanisms of the PrC during the processing of highly complex picture-label associations might be especially qualified to support the encoding and integration of these associations into semantic memory within the FM paradigm. If this is the case, higher demands on perirhinal functions (e.g., object discrimination) during FM encoding might foster integration into neocortical networks through deeper encoding. It is important to note that although higher demands in general can be very resource-consuming and could therefore lead to worse memory, we refer to higher demands selectively on processes involved in FM learning, that is, amongst others, the discrimination of highly complex objects.

Although a key characteristic of the FM paradigm is that the unknown item must be encoded in the context of a previously known item (see Coutanche & Thompson-Schill, 2014, Experiment 2), inter-item similarity has not yet been explicitly manipulated. However, it is noticeable how similar the unknown and the known items were in studies conducted by Sharon et al. (2011; see also Sharon, 2010, for further examples).

Following the rationale outlined above, we predict that higher feature overlap between the known and the unknown item in the FM task promotes faster and better neocortical integration. Explicit recognition tests do not necessarily measure neocortical integration in healthy young adults but could as well reflect hippocampal reactivation. This could also explain why no evidence for successful semantic integration through FM learning was found in studies in which healthy participants were tested using explicit recognition tests and why it has been concluded that the previously known item is irrelevant (Cooper et al., 2019; but see Coutanche & Thompson-Schill, 2014; and Coutanche & Koch, 2017, who found rapid lexical integration of the label only if the known item was presented, using implicit measures in healthy adults). We therefore tested this prediction using implicit tests. Although conclusions on underlying neurocognitive mechanisms cannot be drawn by means of behavioral measures only, these implicit measures of memory can serve as indicators for (cortical) integration instead of hippocampus-based retrieval as they provide direct access to semantic networks represented in cortical structures and it has been shown that they less likely involve hippocampal processing (Goshen-Gottstein et al., 2000). In order to implicitly measure integration into lexico-semantic networks, we assessed the effects of the newly learned associations on the processing of already known lexically or semantically related items following a procedure used by Coutanche and Thompson-Schill (2014; see also Coutanche & Koch, 2017). They argued that successful integration of new associations into neocortical structures should result in lexical competition on one hand, and in semantic priming on the other hand. Generally, lexical competition leads to inhibition due to interference caused by co-activation of lexically neighboring items at retrieval. Therefore, it takes more time until a target word is uniquely identified if it has more lexical neighbors (e.g., slowed response times to mouse as it has many lexical neighbors such as house, horse, etc.). In contrast, in semantic priming, access to semantically related items is facilitated (e.g., faster response times to mouse if it was preceded by hamster). Thus, if new information, such as newly learned labels, lexically competes with or semantically primes old information, it can be assumed that it is integrated into neocortical lexico-semantic networks. Coutanche and Thompson-Schill (2014) found lexical competition, that is, slowed responses to English words which lexically neighbored labels of the learning phase, 10 minutes after encoding trough FM and again after 24 hours. For the EE group, no lexical competition was observed, neither immediately nor on the following day, indicating that successful rapid and persistent lexical integration is possible after encoding through FM but not through EE. In order to measure semantic integration, Coutanche and Thompson-Schill (2014) conducted a semantic priming task, in which newly learned labels of previously unknown animals were expected to prime semantically related but not unrelated targets. Contrary to their expectations, no priming effects were found for neither encoding condition after 10 minutes. After 24 hours, they found a significant priming effect for the FM group only. Unfortunately, potential confounds could have influenced the data pattern. As related targets in the priming phase were always animals and unrelated targets were always artifacts, semantic categories of the targets were not counterbalanced. Since response latencies between related and unrelated targets might have differed already on a baseline level, it cannot be excluded that faster processing of the artifacts could have masked a potential priming effect. In addition, semantic integration was measured using a lexical decision task, which might not have required sufficient semantic processing in order to observe semantic priming effects (De Houwer, Hermans, Rothermund, & Wentura, 2002).

In order to investigate the role of feature overlap in FM learning, we followed Coutanche and Thompson-Schill's (2014) experimental design, but with a few important adaptations. In Experiment 1, we examined lexical integration by means of FM separately for a condition in which the previously unknown and the known item share many features (*fast mapping, high overlap*; FMHO) compared to a condition in which they share few features (*fast mapping, low overlap*; FMLO), assuming that rapid integration into lexico-semantic networks can be fostered by a high feature overlap between the previously unknown and the known item at encoding. In Experiment 2, we investigated if immediate semantic integration by means of FM is possible and if it can be strengthened in an FMHO condition but not in an FMLO and an EE condition. We assessed semantic integration both immediately after encoding and again after 24 hours in order to examine stability over time.

5.2 Experiment 1

Analogously to Coutanche and Thompson-Schill (2014), we used a lexical competition task in order to measure lexical integration. For this purpose, labels in the encoding task needed to be artificially created lexical neighbors of already existing English hermit words (i.e., words which are not transformable into other words by changing one letter).

If such hermit words that naturally do not have any lexical neighbors (e.g., *tomato*) obtain a new lexical neighbor at encoding (e.g., if the label *torato* is successfully learned), the relative increase of the number of neighbors of the hermits is large. Therefore, competition effects are expected for responses to hermits that obtained a new neighbor at encoding but only if this new neighbor has been successfully integrated. We expected to observe a general lexical competition effect for associations acquired by means of FM. This competition effect was assumed to be larger when the known and the unknown item share many features (FMHO) than when they share few features (FMLO). As stable lexical competition effects for FM and no effects for EE have previously been reported (Coutanche & Thompson-Schill, 2014), we decided to only set focus on the effects of feature overlap within the FM paradigm in Experiment 1. In addition to this implicit measure of integration, we conducted a forced-choice recognition test in order to examine if participants also showed explicit learning above chance level. As it cannot be disentangled if recognition accuracy in healthy young participants is driven by hippocampus-dependent retrieval or by retrieval of associations already incorporated into lexico-semantic networks, we did not make assumptions about differences in recognition accuracy between the overlap conditions. However, assessing recognition accuracy was necessary in order to tell if a potential lack of a lexical competition effect would have been an issue of encoding difficulties (e.g., too short presentation times, too difficult questions, etc.) or if selectively rapid neocortical integration did not work but there still was explicit (perhaps hippocampal) learning.

5.2.1 Methods

5.2.1.1 Participants

Thirty-six students from Saarland University took part in the experiment (M_{age} = 23.4 years, age range: 20-30 years; 31 female). All participants were native German speakers and had normal or corrected-to-normal vision. Participants gave written informed consent prior to the experiment and completed the experiment within approximately 50-60 minutes. They were compensated for their participation with 8€ per hour. The experiment was approved by the local ethics committee of Saarland University in accordance with the declaration of Helsinki.

5.2.1.2 Materials

All pictures were obtained from the internet and were drawn from an item pool of a previously conducted rating study, in which a different sample of 46 participants ($M_{\text{age}} = 23.1$ years, age range: 18-34 years; 30 female) had rated pictures of items of eight categories (mammals, birds, insects, fish, reptiles, fruit, vegetables, plants) for familiarity (5-point Likert scale; 1 = *not at all familiar*, 5 = *very familiar*) and previous knowledge (*known* vs. *unknown*). At stimulus creation for the rating study, each of 180 putatively unknown items was assigned two putatively known items, thereby creating two picture pairs per unknown item (see Figure 4.1). One of the putatively known items was supposed to be highly similar to the unknown item (for usage in the FMHO condition) and the other one less similar to the unknown item (for usage in the FMLO condition). The putatively known items were also used with two different unknown items, such that a putatively known item (e.g., a flamingo) was once part of a high-overlap item pair together with an unknown, similar-looking item (e.g., a wading bird) and once part of a low-overlap item pair together with another, dissimilar unknown item (e.g., a mouse-like mammal). Putatively known items of such a pair of item pairs were interchanged for the respective other unknown item (e.g., guinea pig as low-overlap known item for the wading bird and as high-overlap known item for the mouse-like mammal). Each participant was presented with either the high-overlap or the low-overlap item pair (counterbalanced between subjects). Feature overlap between the two pictures of an item pair, which was defined as the number of features the two pictures have in common, was rated on a 5-point Likert scale (1 = *not at all similar*, 5 = *very similar*). Examples in the instructions of the rating study made clear that feature overlap refers to features such as the presence and nature of fur, a tail, a fin, legs, the smoothness of a fruit's skin, color, and so forth.

The encoding phase in Experiment 1 contained 92 pairs of previously known and unknown items, arranged in two lists, which were assigned to one half of the sample each. In each list, 46 item pairs were presented in the FMHO encoding condition and 46 pairs in the FMLO condition (counterbalanced between lists). Lists did not differ with regard to feature overlap ratings between participants, neither for FMHO trials nor for FMLO trials (both ts < 1). Between overlap conditions, semantic categories of the items were distributed equally and items did not differ with regard to familiarity ratings or ratings of previous knowledge, neither of the previously known nor the unknown items (all *p*s $< .219$). Within each overlap condition, 50 % of the questions at encoding required a positive response, 50 % a negative response, and the question referring to a previously unknown item was identical for both overlap conditions. Only those item pairs were included for which the previously unknown item had been classified as unknown by most participants in the rating study (on average, by 87 %; $SD = 12$ %) and had been rated with the lowest familiarity ($M = 2.09$, $SD = 0.45$), and for which the previously known item had been rated as known by most participants in the rating study (on average, by 91 %, $SD = 12$ %) and with the highest familiarity ($M = 4.41$, $SD = 0.39$). Moreover, only pairs of item pairs with the highest difference between the overlap ratings of the high-overlap item pair (e.g., satellote – flamingo; see Figure 4.1) and the low-overlap item pair (e.g. satellote – guinea pig) were included ($M_{\text{FMHO}} = 3.57$, $SD_{\text{FMHO}} = 0.49$; $M_{\text{FMLO}} = 1.41$, $SD_{\text{FMLO}} = 0.32$; $M_{\text{diff}} = 2.16$, $SD_{\text{diff}} = 0.56$). In the final item set, familiarity for the previously unknown items was significantly lower than for the previously known items, significantly more participants of the rating study had rated the previously known item as known than the previously unknown items, and overlap of the high feature overlap pairs was higher than overlap of the low feature overlap pairs (all *p*s $< .001$). In addition, the high overlap item pair with the lowest overlap still had a higher overlap rating than the low overlap item pair with the highest overlap.

Additional 20 item pairs (10 FMHO, 10 FMLO) were added as filler trials, in which the question referred to the previously known item in order to prevent participants from always responding with regard to the unknown item without paying attention to the label. In order to prevent primacy and recency effects, further two filler trials were inserted as buffer trials each at the beginning and at the end of the encoding phase. Filler trials were excluded from all analyses. The size of all pictures in the experiment varied depending on their relative size in reality, but was 300 x 300 pixels at maximum, leading to a maximum visual angle of approximately 8.2°. In order to measure lexical competition, we created 48 new lexical neighbors to existing concrete German nouns (see Appendix). We will refer to the latter as hermits, albeit eleven of them already had one lexical neighbor (but with a mean normalized lemma frequency of the neighbor of < 0.01 per million words, $SD < 0.01$; Dudenredaktion, 2009; Heister et al., 2011). Word length of the hermits was between 4 and 8 letters ($M = 6.50$, $SD = 0.98$) and normalized lemma frequencies between 0.52 and 133.94 per million words ($M = 19.58$, $SD = 34.25$; Heister et al., 2011). The artificially created new labels should deviate from the hermit words in one grapheme at maximum, either by adding, deleting, or substituting a grapheme, and this deviation should preferably occur late in the word, in order to shift the point of uniqueness backwards and thus provoke maximum lexical competition with the hermits (Davis & Gaskell, 2009; Gaskell & Dumay, 2003). Of the 48 newly created labels, 32 were used as labels in the encoding phase (16 within FMHO trials, 16 within FMLO trials) and their respective hermits were later used as neighbor hermits in the lexical competition task (e.g., *satellite* tested as neighbor hermit if the label *satellote* was encoded). The remaining 16 labels were not encoded as their direct lexical neighbors were used as non-neighbor hermits in the lexical competition task (e.g., satellite as non-neighbor hermit if the label satellote was not encoded). The allocation of labels to neighbor hermit FMHO trials, neighbor hermit FMLO trials, or non-neighbor hermit trials was counterbalanced between subjects, which required that each item was assigned three labels, with each appearing together with this item in one third of the participants. Labels of the remaining 60 items that were not used for the lexical competition task were substituted either with a pseudo-word or with an item's botanical or zoological name (sometimes slightly modified) if these labels might have subjectively triggered expectations about an item's category or features. For example, items were renamed if parts of the name included information about the category, such that *giraffe gazelle* (which was given its alternative name *gerenuk* in our experiments) would indicate that the item is an animal. Word length of all labels, including the newly created neighbors of the hermits, was between 4 and 10 letters (M = 7.21, SD = 1.17). Each test display in the two-alternative forced-choice recognition test consisted of a label used in the encoding phase, its respective associated picture, and one foil picture. Test foils had all been used as previously unknown items in the encoding phase in order to control for item familiarity. Moreover, both pictures of a test screen were from the same higher-level category: They were either both plants or both animals. Thus, it was not sufficient to remember an item's semantic category but participants were required to retrieve the specific picture-label combination. No two test pictures appeared together twice. In order to prevent participants from developing strategies, additional 12 filler trials were included, in which both pictures had already been presented twice.

5.2.1.3 Design and Procedure

Stimulus presentation and timing were controlled using the experimental software PsychoPy (Peirce, 2008; http://www.psychopy.org/). Participants were seated in front of a 17-inch screen, at a viewing distance of approximately 60 cm. All stimuli throughout the experiment were presented against a white background.

Encoding. In order to ensure that encoding was incidental, participants were told that the experiment aimed to investigate visual perception of animals, fruit, vegetables, and plants. All participants encoded the associations by means of FM, and feature overlap was manipulated within subjects. Participants first completed six practice trials (3 FMHO, 3 FMLO), followed by the 116 experimental trials (including 24 filler and buffer trials), which were presented in random order with the constraint that stimulus presentation began and ended with two filler trials each. At the beginning of each trial, a fixation cross was displayed for 700 ms, horizontally centered and slightly below the center of the screen, at the same height as the question would appear. The question was then displayed for 5500 ms, with the plain text presented separately for the first 2000 ms (Arial 27 point font) and together with the pictures for 3500 ms (see Figure 5.1). The label within the question was always presented in the horizontal center of the screen and in bold font. Participants were encouraged to read the question thoroughly, focus on what exactly is asked for and, as soon as the pictures appear, to figure out to which item the question refers and how it is thus to be answered. After the pictures and the question had disappeared, the words yes and no were displayed in orange and blue color on the left and right side of the screen (color and position counterbalanced between subjects), requesting to press the key marked with the respective color on a computer keyboard. As soon as an answer was given, participants received feedback and the next trial started. If no answer was given within 3000 ms, they were encouraged to respond faster and moved on to the next trial.

Lexical competition. After a retention interval of 4 minutes, in which participants solved simple mathematical equations, the lexical competition phase was administered. First, participants were familiarized with the task in a practice phase consisting of four trials using German nouns that did not appear elsewhere in the experiment. In contrast to the experimental trials, feedback was given at the end of each practice trial and participants were encouraged to respond faster if they had not responded within the given time window of 2500 ms. The actual lexical competition task contained 48 trials, which were presented in random order. Each trial began with a fixation cross in the center of the screen for 500 ms, followed by the presentation of the hermit word (see Figure 5.1). Hermits were displayed in Arial 27 point font. Participants were instructed to decide if a hermit is man-made or natural by keypress. The words *man-made* and *natural* were displayed in blue and orange color on the left and right side on the bottom of the screen (color and position counterbalanced between subjects). The next trial started as soon as a response was given but after 2500 ms of stimulus presentation at maximum. Instructions emphasized speed over accuracy and participants were additionally informed that due to the fast pace of the task, they might make mistakes but nevertheless should focus on responding as fast as possible (as recommended by Wentura & Degner, 2010).

Recognition. In the recognition test, participants were presented with two pictures and a label, and were asked to indicate which of the pictures belonged to the label. After the presentation of a fixation cross for 500 ms in the center of the screen, the label was displayed horizontally centered slightly underneath the position of the fixation cross in Arial 27 point font, together with a test target and a test foil picture to the left and to the right (50 % of the target and foil pictures on each side) slightly above the position of the fixation cross (see Figure 5.1). This test display stayed on the screen until a response was made by pressing the respective left or right key on the computer keyboard, but for 3500 ms at maximum. If no key had been pressed within this time, participants were encouraged to respond faster and the next trial started. All 92 picture-label associations were tested, including the 32 associations of which the neighbor hermits were presented in the lexical competition task. Each picture of an unknown item was presented twice, once as target and once as foil. Twenty-four unknown pictures were presented three times in order to create 12 additional filler trials. Repeated presentations of a picture were separated by at least eight trials and no combination of test pictures appeared twice. Both pictures of a test display were encoded within the same encoding condition. Again, this phase was also preceded by a practice phase, in which the items from the encoding practice phase were used as test items. Feedback was given only in the practice phase.

Rating of previous knowledge. At last, previous knowledge of all items was assessed with a rating scale. After debriefing participants about the intention of the study and the renaming of the stimuli, they were instructed to indicate on a 5-point Likert scale how well they had known the item before the experiment, no matter under which name (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, participants were asked to type in the item's name at the lowest category level possible (e.g., hawk instead of bird).

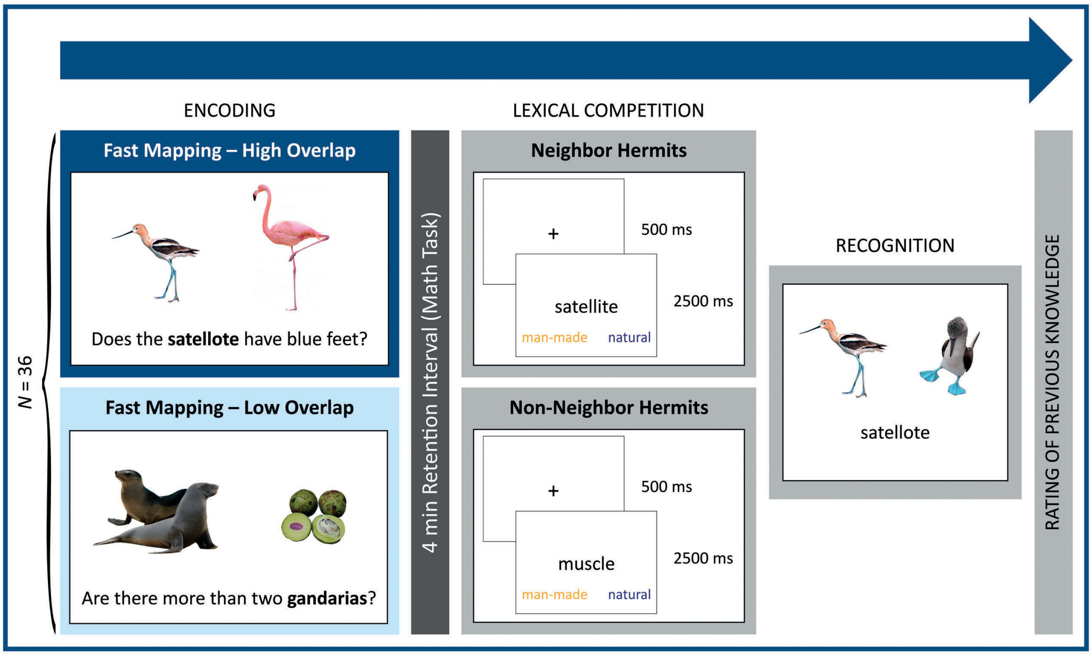

Figure 5.1 Experimental design and procedure of Experiment 1. **Encoding**. Encoding condition was manipulated within subjects. After the question had been presented for 2000 ms, pictures were inserted and presented together with the question for 3500 ms. Response options (*yes*/*no*) were provided after both pictures and question had disappeared. Of 92 unknown items, 32 were renamed in order to serve as new lexical neighbors for the lexical competition task (e.g., *satellote* as a neighbor for the hermit *satellite*). Feedback was given after a response had been made. **Lexical Competition**. In the lexical competition task, responses were given to 32 hermits that had obtained a new neighbor at encoding (neighbor hermits) versus 16 hermits that had not obtained a new neighbor (non-neighbor hermits). Sixteen lexical neighbors of the 32 hermits were encoded in the FMHO (fast mapping, high overlap) condition and 16 in the FMLO (fast mapping, low overlap) condition. **Recognition**. In the two-alternative forced-choice recognition test, targets and foils within one display always belonged to the same higher-level category (i.e., either both items were animals or both items were plants).

5.2.1.4 Analyses

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org). Lexical competition effects were calculated by subtracting response times for correct responses to non-neighbor hermits from response times for correct responses to neighbor hermits. Trials were removed if they contained items for which a participant's individual rating of prior knowledge was inconsistent with the expected knowledge (rating of <= 3 for previously known items and >= 4 for previously unknown items; mean dropout rate: 5.7 % of correct trials). We further excluded outlier trials with regard to response times individually for each participant according to the outlier criterion recommended by Tukey (1977; 1.5 inter-quartile ranges below the first and above the third quartile) and, in line with Coutanche and Thompson-Schill (2014; see also Bowers, Davis, & Hanley, 2005) and Coutanche and Koch (2017), all trials with response latencies below 300 ms and above 1500 ms as too long response times are unlikely to be influenced by implicit processes. This resulted in a final mean dropout rate of 12.6 % of correct trials. There were no outlier participants (Tukey, 1977) regarding the lexical competition effect. Recognition accuracy represents the proportion of correct responses. If not noted differently, t tests to compare lexical competition effects were one-tailed and the significance level was set to $\alpha = .05$. Effect size d for the within-subjects comparison of the lexical competition effect were calculated as difference of the mean lexical competition effects divided by the pooled standard deviation of the difference and corrected for the within-subjects correlation of the effects (see Morris & DeShon, 2002). Effect size d for the between-subjects deviation of the lexical competition effect from zero was calculated as the mean lexical competition effect divided by the standard deviation of the effect. Effect size d for the between-subjects deviation of recognition accuracy from zero was calculated as the mean recognition accuracy divided by the standard deviation of recognition accuracy.

5.2.2 Results

Lexical competition. All participants performed above chance level in the lexical competition task ($p < .05$, binomial test; see Table 5.1 for accuracies). The accuracy difference between neighbor hermits and non-neighbor hermits was only marginally significant, $t(35) = -1.99$, $p = .054$, and neither reached significance for the FMHO condition, $t(35) = 1.78$, $p = .084$, nor for the FMLO condition $t(35) = 1.75$, $p = .090$, all two-tailed. Although we only observed a lexical competition effect for the FMLO condition, $t(35) = 2.02$, $p = .025$, $d = 0.34$, but not for the FMHO condition, $t(35) = 1.10$, $p = .141$, there was a general lexical competition effect, $t(35) = 1.94$, $p = .030$, $d = 0.33$ (mean competition effect: $M = 16.36$ ms, $SD = 50.69$ ms; see Figure 5.2), that is, response times to neighbor hermits were significantly slower compared to non-neighbor hermits (see Table 5.1 for response times). Lexical competition in the FMHO condition (mean competition effect: $M = 11.24$ ms, $SD = 61.56$ ms) was numerically smaller than in the FMLO condition (mean competition effect: $M = 20.25$ ms, $SD = 60.08$ ms), contrary to our hypotheses. However, exploratory post-hoc analyses revealed that the

Table 5.1 Mean Response Times (in ms) and Accuracies (in % Correct) to Neighbor Hermits and to Non-Neighbor Hermits by Encoding Condition in the Lexical Competition Task of Experiment 1

	Neighbor hermits			Non-neighbor hermits
	FM	FMHO	FMLO	
Response times (in ms)	865.35	860.22	869.24	848.99
	(121.74)	(122.17)	(130.85)	(113.69)
Accuracies (in % correct)	92.34	92.96	91.79	89.30
	(5.09)	(6.74)	(7.82)	(9.92)

Note. FM = fast mapping, irrespective of feature overlap; FMHO = fast mapping, high overlap; FMLO = fast mapping, low overlap; neighbor hermits = hermits that had obtained a new neighbor at encoding; non-neighbor hermits = hermits that had not obtained a new neighbor at encoding. Standard deviations in parentheses.

lexical competition effect was not significantly different between FMHO and FMLO trials, $t(35) = 0.81$, $p = .423$, two-tailed.

Although the pattern of the accuracy data (see Table 5.1) might indicate a tendency towards a speed-accuracy trade-off, differences in accuracies, which could reflect such a trade-off, did not reach significance. In order to further investigate if a lexical competition effect is also apparent in a sample with an accuracy pattern contrary to what would indicate a speed-accuracy trade-off, we examined lexical competition in a subgroup of participants who showed numerically higher accuracies for non-neighbor hermits than for neighbor hermits. In this group ($N = 16$), a lexical competition effect was also found, $t(15) = -1.85$, $p = .042$, $d = 0.46$, one-tailed, indicating that even if a speed-accuracy trade-off could definitely be excluded, there still was rapid lexical integration.

Recognition. In order to investigate whether participants also showed above-chance explicit associative memory, we checked accuracy in the recognition test. Participants performed above chance level in the FMHO condition, $t(35) = 4.25$, $p < .001$, $d = 0.71$ ($M_{\text{FMHO}} = .56$, $SD_{\text{FMHO}} = .09$) and in the FMLO condition, $t(35) = 4.76$, $p < .001$, $d = 0.79$ ($M_{\text{FMLO}} = .58$, $SD_{\text{FMLO}} = .09$). Exploratory post-hoc analyses showed that recognition accuracy did not differ between encoding conditions, $t(35) = 0.54$, $p = .590$, two-tailed.

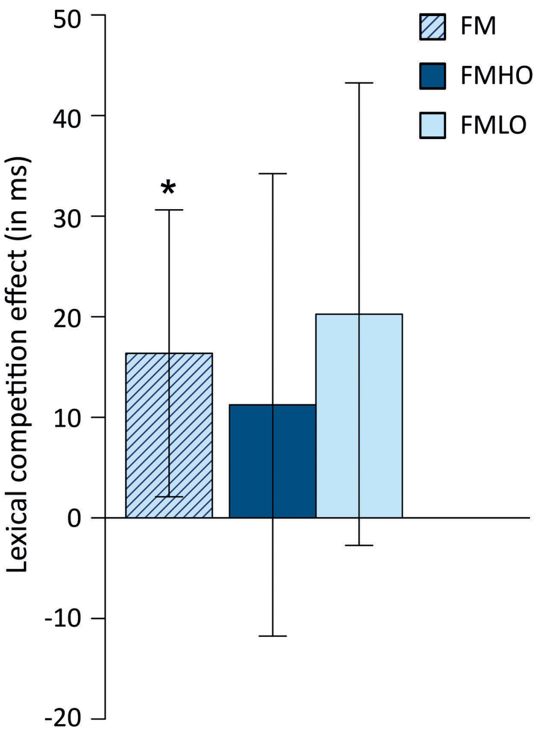

Figure 5.2 Results of the lexical competition task of Experiment 1. The lexical competition effect was calculated by subtracting response times for responses to words that had not obtained a new neighbor at encoding (non-neighbor hermits) from response times for responses to words that had obtained a new neighbor (neighbor hermits). FM = fast mapping, irrespective of feature overlap; FMHO = fast mapping, high overlap; FMLO = fast mapping, low overlap. Error bars for the FM condition represent the one-tailed confidence interval for the lexical competition effect. Error bars for the FMHO and FMLO conditions represent the two-tailed within-subject confidence interval for the differences between the lexical competition effect in the FMHO condition and in the FMLO condition. $^{*}p < .05$

5.2.3 Discussion

If a newly learned label is well integrated in neocortical networks, it is expected to compete with its lexical neighbors. Consequently, more time is required until these neighbors can be uniquely identified. In order to test lexical competition, we assessed response latencies to hermit words, expecting slowed responses to hermits which had artificially been assigned a new neighbor at encoding (neighbor hermit trials), compared to hermits which had not obtained a new lexical neighbor (non-neighbor hermit trials). Since Coutanche and Thompson-Schill (2014) had already shown that rapid lexical integration by means of FM but not EE is possible, we wanted to extend this research question and investigate if feature overlap might modulate rapid lexico-semantic integration of the picture-label associations within the FM encoding condition, using lexical competition as measure of integration. We observed a lexical competition effect already shortly after the labels had been encoded by means of FM. Consistent with

Coutanche and Thompson-Schill's (2014) results, our findings show that the labels of the novel associations were integrated immediately after FM encoding.

In contrast to our expectations, the lexical competition effect for FMHO trials was not different from that for FMLO trials, and numerically even smaller. We would like to offer an explanation for the lack of the expected moderating effect of feature overlap on lexical competition after learning by means of FM. Although we argued that the integration of the picture-label associations should provoke lexical competition, integration of the complete associations (i.e., the specific combination of the picture together with the label) likely is a sufficient but not a necessary condition to observe a lexical competition effect for the label. Contrary to what we proposed prior to the experiment, we now think that it might be more precise to say the lexical competition effect reflects lexical integration of the labels on an item level but not necessarily semantic integration of the labels with their associated pictures. Thus, lexical competition can be observed even though the complete associations are not integrated. The reason why we predicted a larger effect for FMHO trials was that stronger PrC recruitment in this encoding condition should have fostered especially semantic integration of the complete picture-label associations, due to increased PrC involvement in the discrimination of pictures sharing many features. Given that integration of the specific picture-label combination is not necessary to induce lexical competition, the absence of a feature overlap effect on lexical competition does not allow for conclusions about semantic integration of the complete associations. Furthermore, if our assumption holds true that manipulation of feature overlap reflects differential PrC involvement, it might not have been advantageous to manipulate feature overlap within subjects with trials of different overlap conditions presented in random order. It is likely that this could have severely decreased the signal-to-noise ratio, such that residual PrC activity of the previous trials might have blurred PrC activity of the current trial.

The semantic priming task which we used as a measure of semantic integration in Experiment 2 should bring more clarity to the role of feature overlap in the integration of the complete associations. We manipulated feature overlap between subjects and extended the design with an EE condition.

5.3 Experiment 2

In Experiment 2, we administered a semantic priming task on two consecutive days. Since the semantic priming results reported by Coutanche and Thompson-Schill (2014) are difficult to interpret due to potential confounds, we considered it necessary to obtain comparable data not only for the different overlap conditions within FM encoding (as in Experiment 1) but also for an EE condition. As we used items of different semantic categories at encoding, it was possible to counterbalance for categories of the priming targets. In order to provoke stimulus processing on a more elaborate semantic level, we used a task requiring a semantic instead of a lexical decision. We predicted rapid semantic integration (i.e., a priming effect shortly after encoding) in the FMHO condition, and this effect should be larger than in the FMLO condition. We expected no priming effect in the EE condition on the same day but an increased priming effect after 24 hours as there should have been enough time for gradual consolidation into neocortical structures. For the FMLO condition, we did not predict a priming effect immediately after encoding as no use could be made of the catalyzing effect of feature overlap (as in the FMHO condition). It cannot be excluded that there might also be hippocampal engagement at encoding in the FM conditions in young and healthy participants, which potentially could foster semantic priming after 24 hours of consolidation. However, hippocampal involvement at FM encoding is presumably much less than in the EE condition. As no direct integration should have taken place in the FMLO condition and hippocampal contribution to learning should be negligible, we did not expect a semantic priming effect after FMLO encoding on Day 2.

In addition to these implicit measures of integration, we conducted a three-alternative forced-choice recognition test in order to examine if participants also showed explicit learning above chance level and if the EE group showed better recognition performance than the FM groups. This would be expected as healthy participants should benefit from intentional learning in the EE condition if tested with explicit recognition tests. Again, we did not make predictions on differences in recognition accuracy between the two FM conditions (FMHO, FMLO) since it cannot be disentangled to what extent retrieval is based on hippocampal or cortical processing.

5.3.1 Methods

5.3.1.1 Participants

As encoding condition was manipulated between subjects, 120 participants were randomly allocated to one of three encoding conditions (FMHO, FMLO, EE). Four participants had to be excluded from all analyses as they had already taken part in another experiment in which the same stimulus material was used, leading to an overall sample size of $N = 116$ participants ($n_{\text{FMHO}} = 39$, $n_{\text{FMLO}} = 39$, $n_{\text{EE}} = 38$; 96 female; $M_{\text{age}} = 23.1$ years, age range: 18-35 years). There was no age difference between groups, $F < 1$. All participants were students from Saarland University, native German speakers, and had normal or corrected-to-normal vision. The experiment was split into two sessions of approximately 20-25 minutes each, separated by 24 hours (range: 23.4-24.4 hours). Participants gave written informed consent prior to the experiment on Day 1 and were compensated for their participation with 8€ per hour after completion of the experiment on Day 2. The experiment was approved by the local ethics committee of Saarland University in accordance with the declaration of Helsinki.

5.3.1.2 Materials

Forty-eight pairs of picture pairs were drawn from the stimulus material of the previously conducted rating study (see Experiment 1). Only those item pairs were included for which the previously unknown item had been classified as unknown by most participants in the rating study (on average, by 88 %, $SD = 12$ %) and had been rated with the lowest familiarity ($M = 2.01$, $SD = 0.42$; 1 = *not at all familiar*, 5 = *very familiar*), and for which the previously known item had been rated as known by most participants (on average, by 90 %, $SD = 13$ %) and with the highest familiarity ($M = 4.44$, $SD = 0.41$). Moreover, only pairs of item pairs with the highest difference between the overlap rating of the high-overlap and the low-overlap item pair were included ($M_{\text{FMHO}} = 3.62$, $SD_{\text{FMHO}} = 0.53$; $M_{\text{FMLO}} = 1.42$, $SD_{\text{FMLO}} = 0.39$; 1 = *not at all similar*, 5 = *very similar*; $M_{\text{diff}} = 2.20$, $SD_{\text{diff}} = 0.68$). In the final item set, familiarity for the previously unknown items was significantly lower than for the previously known items, significantly more participants of the rating study had rated the previously known item as known than the previously unknown items, and overlap of the high feature overlap pairs was higher than overlap of the low feature overlap pairs (all *p*s $<$ .001). In addition, the high overlap item pair with the lowest overlap still had a higher overlap rating than the low overlap item pair with the highest overlap. Further 16 trials were added as filler trials, of which two trials were presented as buffer trials each at the beginning and at the end of the encoding phase. Filler trials matched the participants' encoding condition and were excluded from all analyses. The size of the pictures varied depending on the items' relative size in reality, but was 300 x 300 pixels at maximum, leading to a maximum visual angle of approximately 8.2°.

Labels remained the same as in Experiment 1. Those items which had been assigned three hermit neighbor labels for usage in the lexical competition task in Experiment 1 were given one of these three names. The labels used for Experiment 2 consisted of 4-9 letters with a mean length of $M = 6.13$ letters ($SD = 1.18$). In the two semantic priming phases, the labels of the previously unknown items were presented as primes, followed by a familiar German noun as target. Target words were either animals or plants. Each prime was assigned to four targets: two semantically related targets (same category as the prime) and two unrelated targets (different category). Unrelated prime-target pairs were created by reallocating targets to unrelated primes. All primes were presented twice, once on each day, whereas targets were only presented once. Within each participant, 25 % of the primes were presented together with a related target only on Day 1, 25 % only on Day 2, 25 % on both days, and 25 % on neither day. Assignment of trials to relatedness condition was counterbalanced across participants. Targets were of low frequency (lemma frequencies between 0.01 and 12.57 per million words; $M = 1.82$, $SD = 2.48$; Heister et al., 2011) and preferably long (4–13 letters; $M = 7.33$, $SD = 1.89$) since it has been shown that priming effects can be strengthened if processing of the target word takes more time (Hines, Czerwinski, Sawyer, & Dwyer, 1986). None of the targets had been presented previously in the experiment, neither as words nor as pictures of previously known items in the encoding phase. All prime and target words were displayed in the center of the screen in Arial 27 point font.

For the three-alternative forced-choice recognition test the target picture was paired with two foil pictures from the same higher-level category (either all plants or all animals). All pictures appeared three times (once as target, twice as foil), separated by at least four trials. Test foils had all been used as previously unknown items in the encoding phase in order to control for item familiarity. All other constraints were as in Experiment 1.

5.3.1.3 Design and Procedure

Encoding. The experimental settings for all three groups (FMHO, FMLO, EE), the cover story, and the encoding procedure for the two FM groups were equal to Experiment 1. In contrast to the FM groups, learning was intentional in the EE group as this group was informed about the later associative recognition memory test. In the EE encoding phase, participants were only presented with the picture of the previously unknown item (see Figure 5.3). Contrary to previous studies (cf. Atir-Sharon et al., 2015; Coutanche & Thompson-Schill, 2014; Greve et al., 2014; Himmer et al., 2017; Korenic et al., 2016; Merhav et al., 2014, 2015; Sharon et al., 2011; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016), the EE group was presented with the same questions as the FM groups, in order to prevent any confounds due to inconsistencies in task demands apart from the critical FM determinants. Before the actual experiment started, all three groups conducted a practice phase of six encoding trials. In addition to the 48 experimental encoding trials, 16 filler trials were inserted. In the filler trials, the question referred to the previously known item, of which two trials were inserted as buffer trials each at the beginning and at the end of the encoding phase. Stimulus presentation was as in Experiment 1.

Semantic Priming. All following phases were identical for the three groups. After a 4-minute retention interval, in which participants solved simple mathematical equations, the first of two priming phases started. Both priming phases were preceded by a practice phase of six trials, in which primes were pseudo-words that had not appeared in the encoding phase. In order to accustom participants to the task demands, two buffer trials of the same nature as the practice trials were inserted at the beginning of each priming phase. Each trial began with the presentation of a fixation cross in the center of the screen for 700 ms, followed by a prime for 300 ms, which was the label of a previously unknown item of the encoding phase (see Figure 5.3). Next, the prime was replaced by the target, which was either semantically related or unrelated to the prime. The participants' task was to indicate by keypress if the target was an animal or a plant, and as in Experiment 1, instructions emphasized speed over accuracy. Participants were informed that due to the fast pace of the task, they might make mistakes but nevertheless should focus on responding as fast as possible (as recommended by Wentura & Degner, 2010). The words animal and plant were displayed in blue and orange color on the left and right side on the bottom of the screen (color and position counterbalanced between subjects). Targets remained on the screen until participants responded by pressing the respective orange or blue key on the computer keyboard but for 800 ms at maximum. If no key had been pressed within 800 ms of target presentation, a blank screen was inserted for additional 200 ms in which the target was not visible but responses were still recorded. All stimuli of the priming phase were presented in random order in the center of the screen and displayed in Arial 27 point font. After a delay of 24 hours, a second priming phase was administered, in which the same primes were presented as on Day 1 but together with different targets. Apart from that, the procedure was kept identical with the Day 1 priming phase.

Recognition. After the completion of the second priming phase on Day 2, a three-alternative forced-choice recognition test was administered. A fixation cross was displayed in the center of the screen for 500 ms, before it was replaced by the recognition test label in Arial 27 point font (see Figure 5.3). The test target picture and the two test 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 clicking on the respective picture. In order to ensure that all participants had enough time to thoroughly look at all three pictures, responses could not be given before 3000 ms of stimulus presentation, after which a verbal prompt to respond appeared at the bottom of the screen. As soon as a decision was made, the next trial started and the mouse cursor was automatically set back to the center of the screen. If no key had been pressed within 6000 ms of stimulus presentation, participants were encouraged to respond faster and the next trial started.

Rating of previous knowledge. At last, participants rated how well they had known the items prior to the experiment. Rating instructions and procedure were identical to Experiment 1, except that a 6-point Likert scale was used (1 = *had not known the item at all before the experiment*; 6 = *had known the item very well before the experiment*). If a rating of >= 4 was given, participants were asked to type in the item's name at the lowest category level possible.

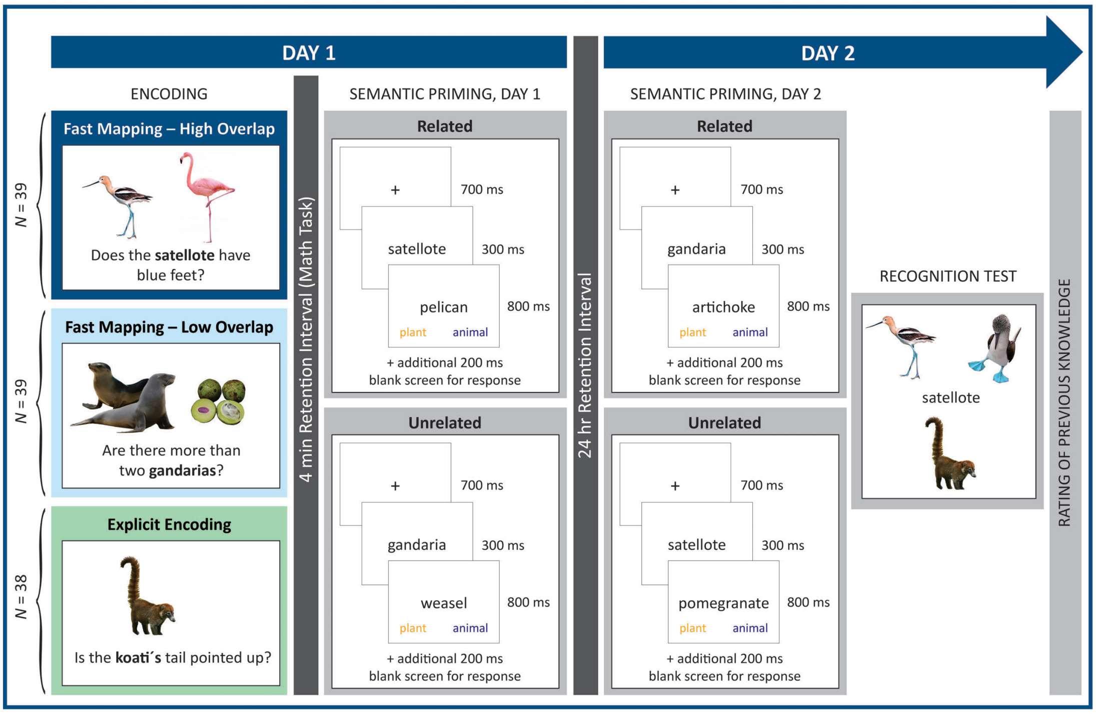

Figure 5.3 Experimental design and procedure of Experiment 2. **Encoding**. Encoding condition was manipulated between subjects. Participants in the explicit encoding condition were explicitly instructed to remember the item. After the question had been presented for 2000 ms, pictures were inserted and presented together with the question for 3500 ms. Response options (*yes/no*) were provided after both pictures and question had disappeared. Feedback was given after a response had been made. **Semantic Priming**. For the semantic priming phases on Day 1 and Day 2, relatedness was fully counterbalanced across participants and study-test delays. **Recognition**. In the three-alternative forced-choice recognition test, the screen was presented as depicted in the figure for 3000 ms and then a prompt to respond appeared at the bottom of the screen. Targets and foils within one display always belonged to the same higher-level category (i.e., either both items were animals or both items were plants).

5.3.1.4 Analyses

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org). The semantic priming effect was calculated by subtracting response times for correct responses to related targets from response times for correct responses to unrelated targets, individually for each participant. Analyses included all correct trials for which the individual ratings of both the known and the unknown item (EE: only the unknown item) were congruent with the expected knowledge, that is, items classified as unknown in the rating study with an individual knowledge rating of <= 3, and items previously classified as known with a rating of >= 4 (mean dropout rate was 7.7 % for both days). Further trials were excluded if response latencies were 1.5 interquartile ranges below the first quartile or above the third quartile of individual response times (Tukey, 1977).

For Day 1 analyses, nine participants had to be excluded because they had not performed above chance level in the semantic priming task (2 participants of the FMHO group, 3 FMLO, 1 EE; $p > .05$, binomial test) or were outliers with regard to the semantic priming effect according to Tukey (1977; 1 FMLO, 2 EE), resulting in an overall sample size of $N_{\text{Day1}} = 107$ ($n_{\text{FMHO}} = 37$, $n_{\text{FMLO}} = 35$, $n_{\text{EE}} = 35$). Participants who were classified as outliers with regard to the priming effect were again included in Day 2 analyses whereas chance performers were excluded from all further analyses as we took low performance in such an easy task as an indicator of a lack of motivation and subsequent performance would likely be based on less overall attendance to the stimuli.

In addition to the chance performers of Day 1, two more participants were excluded for the same reason on Day 2 (1 FMLO, 1 EE). Four participants were outliers regarding the priming effect on Day 2 (4 FMHO), resulting in an overall sample size of $N_{\text{Day2}} = 104$ ($n_{\text{FMHO}} = 33$, $n_{\text{FMLO}} = 35$, $n_{\text{EE}} = 36$). For the recognition test, only participants who performed at chance in at least one priming phase were excluded ($N_{\text{rec}} = 108$; $n_{\text{FMHO}} = 37$, $n_{\text{FMLO}} = 35$, $n_{\text{EE}} = 36$). Recognition accuracy represents proportion of correct responses.

If not noted differently, t tests to compare semantic priming effects were one-tailed and the significance level was set to $\alpha = .05$. Effect size d for the between-subjects comparisons of the semantic priming effect was calculated as difference of the mean semantic priming effects, divided by the pooled standard deviation of the effects. All other analyses remained the same as in Experiment 1.

5.3.2 Results

Semantic Priming, Day 1. Accuracies in the semantic priming task were above chance in all encoding conditions (all ps $< .001$; see Table 5.3 for accuracies). A one-way ANOVA with the between-subjects factor encoding condition (FMHO, FMLO, EE) did not show a significant effect of encoding condition on the semantic priming effect, $F(2,104) = 2.14$, $p = .123$. As we were especially interested in the comparison of the FM groups, we investigated the differences between FMHO and FMLO. In line with our hypotheses, planned comparisons showed that the semantic priming effect was significantly larger for the FMHO group than for the FMLO group, $t(70) = 1.96$, $p = .027$, $d = 0.46$, although the difference between the FMHO and the EE group

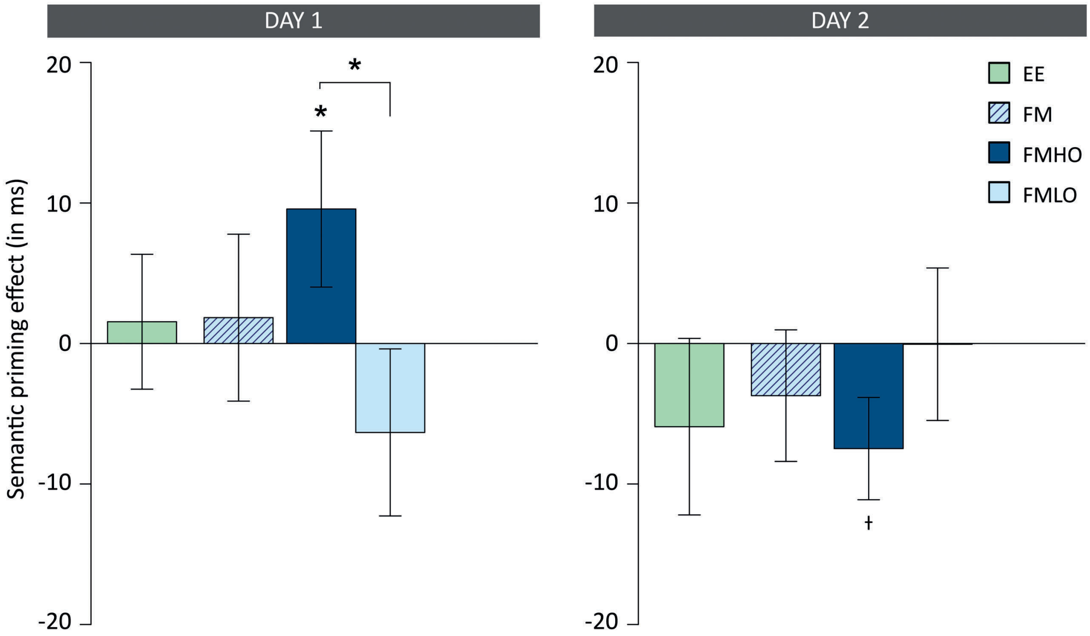

Figure 5.4 Results of the semantic priming task of Experiment 2 for Day 1 and Day 2. The semantic priming effect was calculated by subtracting response times to related targets from response times to unrelated targets. Error bars represent the standard error of the means. EE = explicit encoding; FM = fast mapping, irrespective of feature overlap; FMHO = fast mapping, high overlap; FMLO = fast mapping, low overlap. †$p < .10$, *$p < .05$

was not significant, $t(70) = 1.09$, $p = .140$ (see Figure 5.4; see Table 5.3 for response times). There was a significant semantic priming effect in the FMHO condition, $t(36) = 1.72$, $p = .047$, $d = 0.28$ ($M = 9.57$ ms, $SD = 33.79$ ms), but neither in the FMLO condition, $t(34) = -1.07$, $p = .294$, two-tailed ($M = -6.33$ ms, $SD = 35.17$), nor in the EE condition, $t(34) = 0.32$, $p = .749$, two-tailed ($M = 1.55$ ms, $SD = 28.40$). If the semantic priming effect after FM encoding was calculated across overlap conditions, no priming effect was found, $t < 1$.

Semantic Priming, Day 2. Accuracies in the semantic priming task were above chance in all encoding conditions (all ps $< .001$; see Table 5.3 for accuracies). For the Day 2 semantic priming task, the one-way between-subjects ANOVA again did not reveal a significant effect of encoding condition on the semantic priming effect, $F < 1$ (see Figure 5.4; see Table 5.3 for response times). Contrary to our hypotheses, post-hoc t tests revealed a numeric tendency towards a negative semantic priming effect for the FMHO group and the EE group. As there is literature on the phenomenon of negative priming effects which might be interesting in the context of learning by means of FM, we wanted to further investigate if this negative tendency deviated significantly from zero, clearly stressing that these analyses were calculated post hoc and are to be considered as exploratory only. These two-tailed post-hoc t tests revealed a marginally significant negative semantic priming effect, $t(33) = -1.97$, $p = .057$, two-tailed, $d = 0.39$ ($M = -7.48$ ms, $SD = 22.15$), for the FMHO group and again no significant priming effect for neither the FMLO group ($M = -0.05$ ms, $SD = 32.10$) nor the EE group ($M = -5.92$ ms, $SD = 37.16$), both ts < 1, two-tailed. If the semantic priming effect after FM encoding was calculated across overlap conditions, no priming effect was found, $t(68) = -1.11$, $p = .270$.

Recognition. In the three-alternative forced-choice recognition test, which was conducted after the semantic priming phase on Day 2, all groups performed above chance level (all ps $< .001$). A one-way between-subjects ANOVA of encoding condition on recognition accuracy did not reach significance, $F(2,105) = 2.23$, $p = .113$. As expected, accuracy of the EE group was superior to accuracy of the FM groups, $t(106) = 1.67$, $p = .049$, $d = 0.40$ ($M_{\text{EE}} = .52$, $SD_{\text{EE}} = .13$; $M_{\text{FM}} = .48$, $SD_{\text{FM}} = .08$; $M_{\text{FMHO}} = .50$, $SD_{\text{FMHO}} = .08$; $M_{\text{FMLO}} = .47$, $SD_{\text{FMLO}} = .08$).

5.3.3 Discussion

When the semantic priming effects of Experiment 2 are calculated across both FM groups, we did not observe semantic priming for the FM condition, neither on Day 1 nor on Day 2. Strikingly, when the FMHO and FMLO groups were analyzed separately, we found a semantic priming effect for the FMHO group on Day 1, but neither for the FMLO group nor for the EE group. Moreover, the priming effects in the FMHO group and in the FMLO group were significantly different. This indicates that rapid semantic integration of novel associations by means of FM is possible, but only if feature overlap between the previously known and the previously unknown item is high, leading to better integration of the picture-label association. Although the semantic priming effect for the FMHO group did not significantly differ from the priming effect for the EE group, a semantic priming effect for associations encoded through EE immediately after encoding was not observed, indicating that there was no rapid semantic integration after encoding by means of EE.

Whereas the lack of a priming effect in the FMLO group on Day 2 had been predicted, the expected semantic priming effect for the EE group on Day 2 was not found. It is conceivable that consolidation processes might possibly have been overshadowed by a weakening of the associations overnight. Despite better integration of the asso-

Table 5.3 Mean Response Times (in ms) and Accuracies (in % Correct) by Relatedness and Encoding Condition in the Semantic Priming Task of Experiment 2, Separately for Day 1 and Day 2

	Day 1				Day 2			
Relatedness	EE	FM	FMHO	FMLO	EE	FM	FMHO	FMLO
Response times (in ms)								
Related	644.25	647.16	640.63	654.06	651.97	629.87	632.42	627.41
	(70.14)	(69.33)	(75.92)	(61.97)	(73.65)	(55.70)	(53.84)	(58.12)
Unrelated	645.80	649.00	650.20	647.73	646.05	626.16	624.94	627.35
	(68.01)	(62.45)	(66.16)	(53.64)	(71.03)	(50.91)	(48.71)	(59.20)
Accuracies (in % correct)								
Related	86.07	83.17	83.97	82.37	86.84	86.97	88.14	85.79
	(8.52)	(12.53)	(12.19)	(12.98)	(9.42)	(8.92)	(8.47)	(9.30)
Unrelated	82.23	83.17	83.97	82.37	86.84	86.97	88.14	85.79
	(13.24)	(10.43)	(10.84)	(10.10)	(11.56)	(9.73)	(9.51)	(9.90)

Note. EE = explicit encoding; FM = fast mapping, irrespective of feature overlap; FMHO = fast mapping, high overlap; FMLO = fast mapping, low overlap. Standard deviations in parentheses.

ciations after 24 hours, explicit retrieval might still have become too effortful after a longer delay, especially considering that, contrary to other studies (e.g., Coutanche & Thompson-Schill, 2014; Greve et al., 2014; Merhav et al., 2014, 2015; Sharon et al., 2011; Warren & Duff, 2014; Warren et al., 2016), participants encoded the associations only once. This is additionally evident in rather weak recognition accuracy levels (which were also assessed on Day 2), compared to recognition performance typically found in EE learning, which might also be due to more effortful encoding task requirements. Whereas participants are typically only instructed to remember the depicted item in the EE condition, we additionally asked them to answer the same question as in the FM condition.

Contrary to our expectations, exploratory post-hoc analyses revealed a marginally significant negative semantic priming effect for the FMHO group on Day 2. Although this marginally significant negativity should only be interpreted very carefully as it was not expected, we would like to provide an explanation for such a tendency as negative priming effects are a not an uncommon phenomenon and we do not want to leave this unexpected pattern uncommented. In previous literature on semantic priming, negative priming effects are explained by a center-surround approach (Walley & Weiden, 1973; see also Carr & Dagenbach, 1990). According to this approach, strongly related targets are inhibited if access to the primes is weak, thereby leading to prolonged response latencies for related targets. In line with this, it is conceivable that primes in the FMHO condition were more difficult to access after 24 hours. We want to clearly point out that this is only a post-hoc explanation trying to address the numerically strong negativity but should not be over-interpreted.

5.4 General Discussion

It has been proposed that FM might be a learning paradigm that allows for rapid, direct integration of novel associations (e.g., Atir-Sharon et al., 2015; Coutanche & Koch, 2017; Coutanche & Thompson-Schill, 2014; Himmer et al., 2017; Merhav et al., 2014, 2015; Sharon et al., 2011). Yet, contradictory findings have been reported (e.g., Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016) and it remains to be clarified which factors could possibly moderate the learning benefit of FM.

In Experiment 1, we observed a general lexical competition effect across feature overlap conditions, indicating that lexical integration by means of FM is generally possible. This is also consistent with the findings by Coutanche and Thompson-Schill (2014), who additionally showed that lexical integration was only found for an FM condition but neither for an EE condition nor for incidental learning per se. Here, we set out to further examine the essential criteria for learning success within the FM condition. Unexpectedly, the lexical competition effect we found was not larger in the FMHO condition than in the FMLO condition. This might have been due to the nature of the task as the paradigm we used only captures lexical integration of the label, which might be independent of semantic integration of the complete picture-label combinations. Thus, we might only have captured lexical integration of the labels on an item level but not lexico-semantic integration of the complete associations. We think that it is conceivable that the FM paradigm as defined by Sharon et al. (2011) is not only appropriate to evoke immediate semantic integration of the associations but also lexical integration of the labels only, irrespective of feature overlap, although it has been shown that at least the presence of two pictures is a necessary determinant for rapid lexical integration (Coutanche & Thompson-Schill, 2014). In a more recent study, Coutanche and Koch (2017) further investigated the role of the previously known item at encoding. Using a similar design as Coutanche and Thompson-Schill (2014), they observed lexical competition after FM encoding but only if the previously known items were atypical for their category. In our experiments, the previously known items were counterbalanced across conditions and thus typicality was kept constant. Hence, the lack of an effect of feature overlap on lexical competition in our Experiment 1 does not contradict their effect of typicality. Whereas typicality of the previously known items might affect lexical integration, visual discrimination and in particular the degree of feature overlap does not, as shown in our Experiment 1. Further research is needed in order to identify potentially differential effects of feature overlap and typicality of the previously known item.

In Experiment 2, we found a semantic priming effect immediately after learning for the FMHO group but neither for the FMLO group nor the EE group, indicating that rapid semantic integration of the complete picture-label associations is possible in an FM paradigm, but only if the unknown and the known item share many features. This might be due to higher PrC involvement in the FMHO condition, although these behavioral data do not allow for interpretations on a neurofunctional level.

5.4.1 Potential underlying neurocognitive mechanisms

Although we do not draw conclusions from our behavioral findings on underlying neurocognitive mechanisms, we originally approached the identification of factors potentially moderating rapid learning by means of FM from a neurocognitive perspective. The functional and representational characteristics of the PrC, that is, its involvement in recognition memory and perceptual and conceptual processing of higher-order object representations, suggest that it is especially qualified to support learning by means of FM. We manipulated feature overlap between the previously known and the previously unknown item in the FM encoding phase, based on the idea that PrC recruitment is associated with the discrimination of items sharing many features. Whereas most previous studies point to the ATL as candidate structure to be mainly involved in learning by means of FM, we do not assume that the implementation of neocortical integration in the FM paradigm is restricted to either the ATL or the PrC but rather suggest that both structures might be highly involved. Ranganath and Ritchey (2012) even consider the PrC a core component of an anterior temporal system that also includes the ATL. Whereas the ATL is ascribed the integration of features of various modalities from their respective cortical sensory areas to a coherent whole (see Lambon Ralph et al., 2017, for a review), the PrC is considered especially responsible for the distinct identification of unique cross-modal feature combinations and their discrimination from similar objects (e.g., Kivisaari, Monsch, & Taylor, 2013; Kivisaari, Tyler, Monsch, & Taylor, 2012; Taylor et al., 2006; Tyler et al., 2004). With regard to learning by means of FM, it is conceivable that ATL engagement might increase when the previously known item is atypical for its category (see Coutanche & Koch, 2017) and that PrC engagement might increase when the known and the unknown item share many features. However, this remains to be further investigated in brain imaging studies.

5.4.2 Visual or semantic overlap?

We primarily defined feature overlap as visual similarity between two items, that is, the number of (visual) features they have in common. However, in doing so, we might inevitably have manipulated semantic similarity as well, as highly similar looking objects usually also belong to the same semantic category. There would be no need to disentangle visual and semantic overlap if both addressed the same underlying process. However, it is conceivable that whereas the manipulation of visual overlap in the FM paradigm most likely affected the initial visual discrimination between pictures, the simultaneous manipulation of semantic overlap might, in a next step, have influenced semantic integration. In order to disentangle the effects of visual and semantic overlap in our data pattern, we conducted further post-hoc analyses, although it needs to be said that these do not allow for final conclusions on the exact contributions of each process. The discrimination between highly overlapping items in our experiments always required a decision within the same lower-level category (e.g., both were birds), whereas low-overlap item pairs were always from different lower-level categories but sometimes from the same higher-level category (e.g., both animals: a bird and a mammal) and sometimes from different higher-level categories (e.g., an animal and a plant; see Figure 4.1). In order to further examine if semantic overlap is the crucial factor on which the difference between the FMHO and FMLO priming effects is based, we calculated the semantic priming effect post-hoc for the FMLO condition of Day 1 separately for FMLO pairs from the same higher-level category and for FMLO pairs from different higher-level categories. These analyses revealed that the semantic priming effect was not different between FMLO pairs of the same higher-level category and those of different higher-level categories, $t < 1$. Moreover, if the difference between the semantic priming effects of the FMHO and FMLO group was simply based on semantic overlap, this difference should disappear if only FMLO item pairs of the same higher-level category were considered for the analyses. Although the comparison between the semantic priming effect of the FMHO group and the FMLO group showed only a trend towards significance after the exclusion of FMLO trials using pairs of different higher-level categories, $t(71) = 1.28$, $p = .102$, one-tailed, the pattern remained the same, as the priming effect for FMLO trials of the same higher-level category (M = -4.04 ms, SD = 52.05 ms) still was on a similar level as the priming effect for all trials of the FMLO group (M = -6.33 ms, SD = 35.17). We therefore suggest that visual feature overlap between the unknown and the known item decisively drives the difference between the priming effect in the FMHO and the FMLO condition although we would assume that both visual and semantic overlap are essential for successful learning by means of FM. However, valid conclusions on the contribution of visual versus semantic overlap would require an a-priori manipulation of both processes separately.

5.4.3 Stability of memory representations acquired by means of FM

Previous notions in the literature often emphasize that memories acquired by means of FM are maintained over time, based on the finding that recognition test performance remains above chance even after longer delays (e.g., Coutanche & Thompson-Schill, 2014; Greve et al., 2014; Korenic et al., 2016; Merhav et al., 2015; Sharon et al., 2011; but see Smith et al., 2014). However, it is difficult to draw general conclusions on the robustness of memory representations in FM learning from the present literature. There is a great variety of study-test delays, regarding the duration of the delay (from no delay to a one-week delay), the nature of the filler task and its level of interference (e.g., a vocabulary test: Sharon et al., 2011, and Coutanche & Thompson-Schill, 2014; conversation: Smith et al., 2014; an intelligence test: Greve et al., 2014; math tasks in our experiments), and potential carry-over effects through other (memory) tests that were conducted between the encoding and recognition phase (e.g., free recall of the associations prior to the recognition test; Warren & Duff, 2014; Warren et al., 2016).

In addition, accuracy in explicit forced-choice recognition tests might not be an appropriate measure to investigate robustness in a longitudinal design. Repeated explicit testing within participants inevitably adds noise to measures of neocortical integration and hence, test accuracy no longer represents pure incidental FM learning. We consider repetition of implicit measures, such as the semantic priming task in Experiment 2, to be less critical, since the newly learned associations have never been explicitly retrieved before the recognition test, which was administered only once and after all semantic priming tasks had been completed. At a first glance, our finding that the semantic priming effect on Day 1 for the FMHO group in Experiment 2 disappeared and even (numerically) turned into a negative direction on Day 2 seems to contradict the assumption of stability of memories acquired by means of FM. However, a potential explanation could be that access to the newly acquired labels (which were presented as primes in the semantic priming task) might have been weakened overnight, leading to lateral inhibition of semantically related items in order to suppress interference while accessing the weaker memories. Therefore, a stable association between prime and target after one day could be reflected in prolonged response times to the targets if the primes are only weakly accessible (see e.g., Carr & Dagenbach, 1990)).

5.4.4 Limitations

In our experiments, the number of trials was higher than in most FM experiments, with 92 trials in Experiment 1 and 48 trials in Experiment 2, instead of 16-24 trials per encoding condition (see e.g., Coutanche & Thompson-Schill, 2014; Greve et al., 2014; Sharon et al., 2011; but see also Merhav et al., 2015, who used 50 trials per encoding condition). This could have led to more interference already during encoding, thereby impeding the integration of the associations. Moreover, using more trials makes it difficult to provide a stimulus list consisting of heterogeneous materials. Homogeneity of the stimulus material could have increased this interference, especially for unfamiliar items (see Brandt, Zaiser, & Schnuerch, 2018). Apart from that, questions were only presented visually instead of bimodally as in other FM studies (e.g., Greve et al., 2014; Merhav et al., 2014; Sharon et al., 2011; Smith et al., 2014) and, in contrast to other studies (see above), each association was encoded only once. We nevertheless think such a single-exposure encoding procedure is suited best to investigate differential effects between encoding conditions as in that way, they can clearly be attributed to differences in pure encoding processes and cannot be influenced by retrieval processes during repeated presentations at encoding. These deviations of the encoding phase could have led to smaller effects of integration than we might have observed if associations were encoded on a deeper level. It is noticeable, however, that the results of both experiments clearly revealed immediate integration of novel associations through FM encoding, despite relatively high numbers of trials and, most importantly, even after only a single exposure to the associations.

5.4.5 Conclusions

Our findings provide further evidence for rapid integration of novel, arbitrary picture-label associations by means of FM. Integration of the newly learned labels led to both lexical competition and semantic priming immediately after encoding. Whereas lexical competition was unaffected by feature overlap in the FM encoding phase, an immediate semantic priming effect was only found if the items shared many features, implying that a high feature overlap is essential for semantic integration of novel picture-label associations. Evidence for rapid semantic integration has not yet been observed and with our findings we can provide explanations of results previously reported in the literature. However, the underlying mechanisms of these findings yet need to be identified. As we cannot draw conclusions on the role of PrC involvement in learning by means of FM with our behavioral results, this remains to be further investigated on a neurofunctional level.

Acknowledgments

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Chapter 6

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

6.1 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 interaction (Frankland & Bontempi, 2005; McClelland et al., 1995; Nadel et al., 2003; Winocur et al., 2010). However, there is evidence that rapid and direct cortical integration of picture-label associations is possible by means of an encoding procedure called *fast mapping* (FM; Himmer et al., 2017; Merhav et al., 2014, 2015; Sharon et al., 2011; see also Chapter 5; see also Coutanche & Koch, 2017; Coutanche & Thompson-Schill, 2014, for delayed semantic integration of picture-label associations and rapid item-level lexical integration of the labels). Sharon et al. (2011) reported a clear benefit from FM learning in patients with severe lesions predominantly to the hippocampus. Whereas these patients did not recognize novel picture-label associations above chance level after encoding through a standard EE condition that is typically expected to rely on hippocampal processing, 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 and thus, participants are not informed about later memory tests. They are presented with a picture of a previously unknown item (e.g., an exotic blue-footed bird; see Figure 4.1) 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?*; see Figure 6.1). 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 enables the binding of the picture and the label to a new association that can be rapidly integrated into semantic networks (Sharon et al., 2011). Despite evidence that FM can enable direct integration of arbitrary associations, other studies revealed contradictory findings (cf. Cooper et al., 2019; Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016). However, the experimental designs and procedures of some of these studies deviated from the original paradigm, such that learning was intentional (e.g., Warren & Duff, 2014) or the associations had been repeatedly recalled before the recognition memory test was administered (e.g., Warren & Duff, 2014; Warren et al., 2016). Moreover, FM learning was not always investigated in patients with lesions confined to the hippocampus but also across patients with extended lesions to extra-hippocampal structures or with complete left-temporal lobectomies (Warren et al., 2016). In addition, it is difficult to draw conclusions on rapid cortical integration by studies in which behavioral recognition tests have been used as the only measure to assess cortical integration in healthy young adults (e.g., Cooper et al., 2019) as these explicit tests do not allow for the dissociation between hippocampus-dependent and cortical retrieval in such samples. A recent debate has underpinned the necessity to clarify more systematically if and under which conditions rapid semantic integration of novel associations by means of FM is possible (see Cooper et al., 2018, and the respective commentaries) by identifying factors potentially moderating FM learning success (Zaiser et al., 2019). Here, we approached this issue from a neurocognitive perspective, asking which underlying mechanisms and corresponding brain structures are likely to contribute to successful FM learning.

Apart from the FM learning benefit for patients with lesions predominantly to the hippocampus, Sharon et al. (2011) showed that two other patients who exhibited extended lesions to the ATL did not benefit from FM learning. Most of the literature suggests the ATL as a structure involved in FM learning (Atir-Sharon et al., 2015; Merhav et al., 2015; Sharon et al., 2011). 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), potentially affording a direct route to semantic incorporation of the associations. This is in line with the view of the ATL as an amodal semantic hub, in which separate information from modality-specific cortices is integrated to a coherent, semantically meaningful whole (see Lambon Ralph et al., 2017; and Patterson et al., 2007, for reviews). 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. On a functional level, the anterior temporal system represents semantic information and is involved in object perception, familiarity-based memory, and the generalization of different exemplars to conceptual classes of entities.

There is a large body of evidence that a key component of the anterior temporal system, the PrC, is involved in the processing and discrimination of complex objects (i.e., of the previously unknown and the known item; see e.g., Bussey et al., 2005; Cowell et al., 2010; Tyler et al., 2004), which is one of the most central operations required in the FM encoding task. The PrC is located in the anterior part of the MTL and is especially involved in the processing of objects sharing many features (e.g., Bussey et al., 2005; Mundy et al., 2012; Tyler et al., 2013). For example, Barense et al.(2007; see also Barense et al., 2005) 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 of less similar objects. Apart from its perceptual role, the PrC is involved in familiarity-based recognition memory (e.g., Bowles et al., 2007; Bowles et al., 2010; Ranganath et al., 2003; Wang et al., 2014; see Brown & Aggleton, 2001, for a review), in semantic processing (e.g., Meyer et al., 2013; Meyer et al., 2010; Meyer et al., 2005; Wang et al., 2010; Wang et al., 2014), and in the memorization of associations between single items if they can be bound to a novel conceptual unit (Haskins et al., 2008; Quamme et al., 2007). A representational-hierarchical view of the medial temporal lobe integrates these findings of both perceptual and mnemonic relevance of the PrC, suggesting that, in contrast to the processing of single features in caudal regions of the ventral visual stream, complex feature conjunctions are processed in more rostral regions, such as the PrC, irrespective of the domain (Cowell et al., 2019; Cowell, Bussey, & Saksida, 2006; O'Neil et al., 2013). Correspondingly, the perceptual-mnemonic feature-conjunction model (Murray & Bussey, 1999; see also Bussey et al., 2005) suggests that the PrC is ascribed the discrimination of object representations with maximum complexity and feature ambiguity, in both mnemonic and perceptual tasks (see also Bussey & Saksida, 2002, 2005; Bussey et al., 2002, 2005). Chen et al. (2019) recently reported the activation of the PrC when two highly similar items needed to be differentiated, compare to the discrimination between items from different categories. This increased recruitment at encoding of the similar-item encoding condition was predictive for later item recognition memory (see also Zhou, Chen, & Yang, 2018, for supporting eye-tracking subsequent memory effects indicating an item memory benefit for items encoded in similar-item pairs).

Interestingly, in the study by Sharon et al. (2011), the patients with extended lesions to the ATL who did not show an FM benefit also exhibited lesions to the PrC, and, most importantly, the two pictures in the FM encoding screen were highly similar (see also Sharon, 2010). With reference to the rationale outlined above, 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 perirhinal lesions might have benefitted. Although feature overlap might well constitute a moderating factor, its effects on FM learning have not been investigated until recently. In a previous behavioral FM experiment (Chapter 5, Experiment 2), we systematically manipulated feature overlap and found that in healthy young adults, rapid semantic integration as measured in a semantic priming task is possible through FM but only if the previously known and unknown item share many features (e.g., a bird called *satellote* presented together with a flamingo) and not if they share few features (e.g., the satellote and a guinea pig; see Figure 4.1). However, despite this evidence for feature overlap as a moderating factor in FM learning, it is still unclear if it is PrC-mediated discrimination of highly similar objects that drives these effects in learning by means of FM. Hence, here we explicitly manipulated feature overlap between the previously known and the unknown item (as in Chapter 5) in an fMRI experiment, contrasting an FM encoding condition in which the previously unknown and the known item shared many features (*fast mapping, high feature overlap*; FMHO) to an FM encoding condition in which they shared few features (*fast mapping, low feature overlap*; FMLO). We expected that PrC involvement at encoding should be greater if the demands on perirhinal processing (i.e., the discrimination of complex objects) are higher (as in the FMHO condition) than if they are lower (as in the FMLO condition). We assume that this should also be reflected in differential PrC contribution to learning, that is, especially in the FMHO condition 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. If PrC engagement drives learning by means of FM and this can be enhanced by increasing feature overlap, this could pave the way to hippocampus-independent learning and might explain why hippocampal consolidation could be bypassed in an FM study using high feature overlap pairs (Sharon et al., 2011).

6.2 Methods

6.2.1 Participants

Data were collected until 48 complete datasets of healthy participants showing above-chance recognition performance were obtained. Participants were pseudo-randomly assigned to an FMHO and an FMLO group until both groups contained 24 participants (FMHO: $M_{\text{age}} = 24.1$ years, age range: 19-30; FMLO: $M_{\text{age}} = 22.1$ years, age range: 18-26) and gender distribution was the same in both groups (14 female each). All participants were right-handed in accordance with the Edinburgh Handedness Inventory (Oldfield, 1971) and native German speakers. 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 as not enough trials (< 10) remained after exclusion of trials based on a post-experimental rating of prior knowledge (see Section 6.2.3). Of the remaining 79 participants, further 31 participants were excluded from the analyses as they did not show above-chance performance ($p > .05$, binomial test; $n_{\text{FMHO}} = 23$; $n_{\text{FMLO}} = 8$). 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 local ethics committee of Saarland University in accordance with the declaration of Helsinki.

6.2.2 Materials

All pictures were drawn from the internet and were selected from an item pool of a previously conducted rating study, in which a different sample of 46 participants had rated 360 pictures of items (180 putatively unknown, 180 putatively known), arranged in pairs of one putatively known and one putatively unknown item each. For reasons of counterbalancing between encoding conditions, each unknown item of the rating study 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 Figure 4.1). Analogously, each known item could appear together with one highly similar and one less similar unknown item. Items in the rating study belonged to eight categories (mammals, birds, insects, fish, reptiles, fruit, vegetables, plants) and were rated for familiarity (5-point Likert scale; 1 = *not at all familiar*, 5 = *very familiar*) and previous knowledge (*known* vs. *unknown*). Item pairs, consisting of one putatively unknown and one putatively known item, were 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*).

Forty-eight item triplets, consisting of one unknown item, its highly similar known item, and its less similar known item, 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 and known item appeared within a high-overlap pair in the FMHO group and within a low-overlap pair in the FMLO group. 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 = 0.43), and 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 = 0.40). 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} = 0.51; M_{FMLO} = 1.42, SD_{FMLO} = 0.37; M_{diff} = 2.17, SD_{diff} = 0.62). In the final item set, significantly more participants of the rating study had rated the previously known item as known than the previously unknown items, familiarity for the previously unknown items was 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 (e.g., the question *Does the satellote have blue feet?* was asked no matter if the satellote was paired with the highly similar flamingo or the less similar guinea pig). 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 named *gerenuk*). Word length of all labels was between 4 and 10 letters ($M = 6.88$, $SD = 1.84$).

6.2.3 Design and Procedure

Stimulus presentation and timing were controlled using the experimental software PsychoPy (Peirce, 2008, 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. 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 (left and right thumb and index finger).

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 asking for the previously known item), 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 prevent 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 ms in equally distributed steps of 500 ms. After the fixation cross had disappeared, the question was displayed separately for the first 2000 ms in Arial 27 point font and

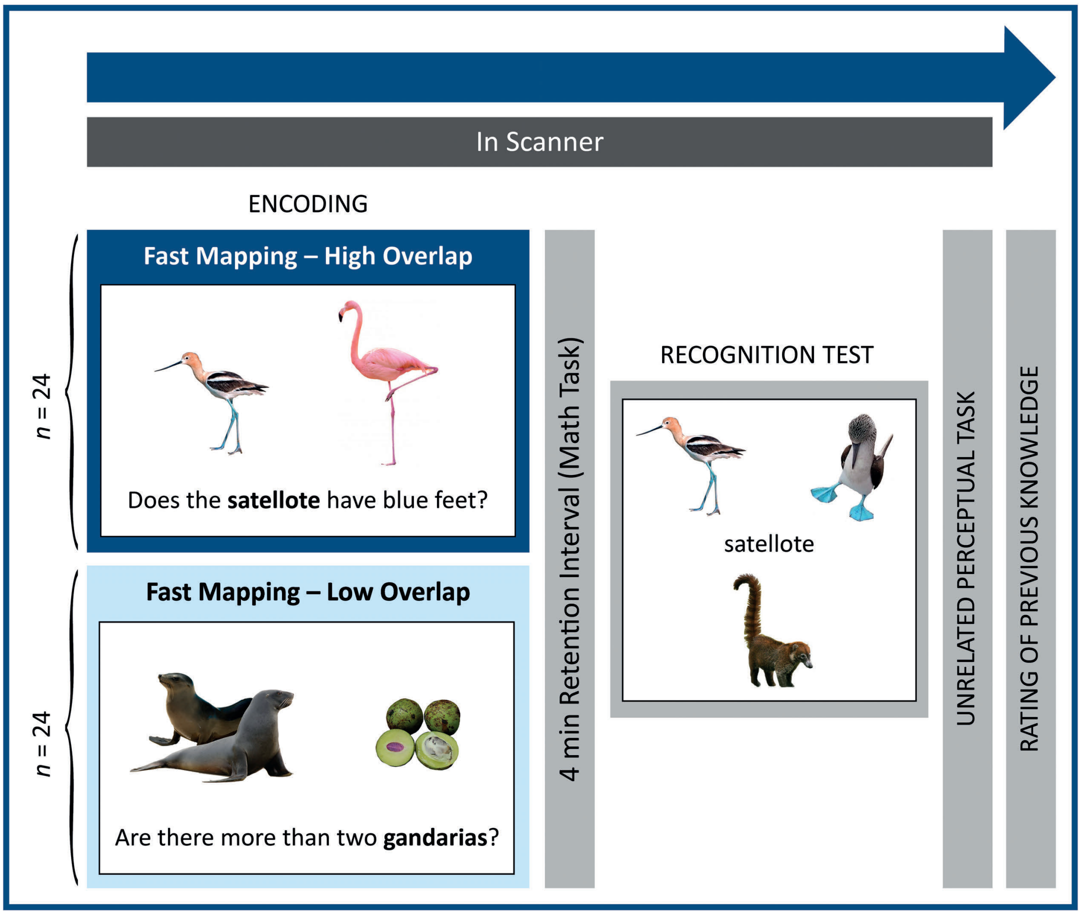

Figure 6.1 Experimental design and procedure of Experiment 3. **Encoding**. Encoding condition was manipulated between subjects. After the question had been presented for 2000 ms, pictures were inserted and presented together with the question for 3500 ms. Response options (*yes*/*no*) were provided after both pictures and question had disappeared. **Recognition**. In the three-alternative forced-choice recognition test, targets and foils within one display always belonged to the same higher-level category (i.e., either all were animals or all were plants).

together with the pictures for further 3500 ms (see Figure 6.1). The label within the question was always presented in the horizontal center of the screen and in bold font. Participants were instructed to read the question thoroughly and, as soon as the pictures 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). Responses could be made by pressing the keys at the respective left or right index finger on the response grips. After 3000 ms, participants received written verbal feedback and moved on to the next trial. If no answer had been given within this time, they were encouraged to respond faster.

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. 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. A fixation cross was displayed in the center of the screen for a jittered interval between 1000 and 8000 ms in equally distributed steps of 500 ms (with 1000 ms, 4500 ms, and 8000 ms appearing four times), before it was replaced by the recognition test label (see Figure 6.1). 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 higher-level category (i.e., both animals or both plants) in order to control for item familiarity. Responses could not be given before 3000 ms 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 ms of overall stimulus presentation. No feedback was provided. After completion of the recognition task, an unrelated perceptual task was administered.

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. They were also informed that the stimuli were renamed and were asked to indicate prior knowledge irrespective of an item's label in the experiment. They then were sequentially presented with all pictures in random order and were instructed to rate on a 5-point Likert scale how well they had known each item prior to the experiment (1 = *had not known the item at all before the experiment*; 5 = *had known the item very well before the experiment*). After ratings of $>= 4$, participants were asked to type in the item's name at the lowest category level possible (e.g., *hawk* instead of *bird*).

6.2.4 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 ms; TE = 2.13 ms; sagittal orientation; flip angle = 9°; voxel size = 0.9 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 ms; TE = 30 ms; flip angle = 90°; voxel size = 3 mm isotropic; distance factor = 25%; matrix = 64 x 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), oriented in parallel with the anterior-posterior commissure plane and then tilted by -30° (anterior upward) in order to reduce susceptibility artifacts in anterior and medial temporal lobe structures. Before scanning, it was made sure that the FoV covers 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 fist slice of each volume as a reference image. They were motion-corrected by realignment of all images of a run to its first image and then coregistered to each participant's anatomical 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.

6.2.5 Analyses

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 ($n = 3$) and replaced by new participants.

6.2.5.1 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 $\alpha = .05$.

6.2.5.2 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. 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 effects. In order to investigate differential subsequent memory effects between the FMHO and FMLO group, a second-level difference of FMHO subsequent memory effects and FMLO subsequent memory effects will be referred to as interaction contrast in the following. The interaction contrast at recognition is the group difference between the contrasts between correct and incorrect trials. For each run, six motion parameters were added as regressors of no interest and a high-pass filter with a 128-seconds 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. An explicit mask was applied covering the whole brain (constructed from the WFU Pickatlas toolbox 3.0.5; Maldjian, Laurienti, Kraft, & Burdette, 2003). Generally, the *p*-value threshold was set to $p = .001$, uncorrected, and a minimum cluster size of 10 contiguous voxels was used for the analyses. The *p*-value threshold for analyses within the PrC, the hippocampus, and anterior temporal structures was set to $p = .005$, uncorrected, at a minimum cluster size of five contiguous voxels, due to the lower signal-to-noise ratio as a consequence of susceptibility artefacts in the MTL and ATL and adjacent structures (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 and the ATL as BA 20, 21, and 38, with BAs according to the WFU Pickatlas 3.0.5 (Maldjian et al., 2003).

6.3 Results

6.3.1 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.

6.3.2 Imaging Results

Encoding. In order to check the manipulation of differential PrC activation during perception of highly similar versus dissimilar pictures, we investigated if the PrC was generally more involved at encoding in the FMHO condition than in the FMLO condition, irrespective of subsequent memory success. This was the case in the left PrC, t = 3.81 (peak: x = -22, y = -10, z = -28; cluster size = 32 voxels), and 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). As expected, greater subsequent memory effects in the FMHO condition than in the

Table 6.1 Local Maxima of Clusters Showing Differential Subsequent Memory Effects Between Encoding Conditions, at $p < .001$, Uncorrected

Lobe	Region	Hem.	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
	Medial 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								
Other	Cerebral white matter	left		-42	-16	-18	10	3.29*

Note. *$p < .005$, uncorrected, 5 contiguous voxels. t values of clusters depicted in Figure 6.2 are printed in bold fond. Please note that within these three clusters, suprathreshold clusters also remain at $p < .001$, uncorrected, 10 contiguous voxels. Hem. = Hemisphere, BA = Brodmann area

FMLO condition were found in the right PrC, t = 4.51 (peak: x = 28, y = -12, z = -26; see Table 6.1 and Figure 6.2). 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 = 0.55, and a negative subsequent memory effect for the FMLO condition, $t(23)$ = -2.49, p = .021, d = -0.51, two-tailed. This differential memory contribution within this PrC region was driven by subsequently remembered items, that is, engagement of the PrC in the FMHO condition was greater than in the FMLO condition at encoding for remembered items, $t(46)$ = 2.83, p = .003, d = 0.82, whereas no differences in PrC involvement between encoding conditions were observed for subsequently forgotten items, $t < 1$ (see Figure 6.2). In addition to the perirhinal contribution to learning, the analyses revealed, amongst others, further clusters showing the interaction effect in the ATL and anterior (but not posterior) hippocampus bilaterally, the mPFC, and the left orbitofrontal cortex (see Table 6.1). 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 Figure 6.2).

Recognition. Further analyses comparing involvement for correct vs. 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 found in the left ErC, t = 2.98 (peak: x = -18, y = -2, z = -34), cluster size = 8.

6.4 Discussion

There has been an extensive debate on the phenomenon of FM learning, questioning if FM enables rapid, direct cortical integration of novel associations, potentially bypassing slow hippocampus-dependent consolidation processes that would typically be expected in memory for associations (e.g., Frankland & Bontempi, 2005; McClel-

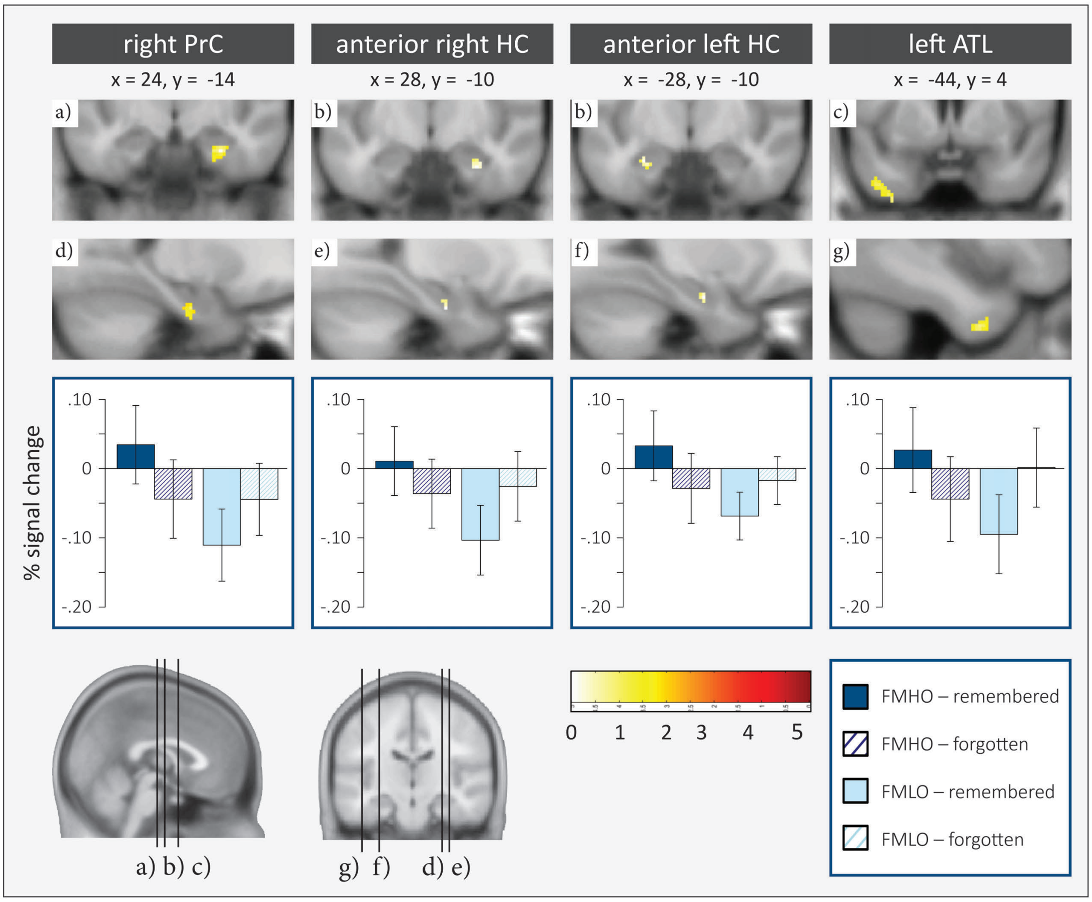

Figure 6.2 Selected clusters in which subsequent memory effects were observed to be greater for the FMHO condition compared to the FMLO condition. Error bars represent the two-tailed within-subjects confidence intervals of the difference between percent signal change at encoding of subsequently remembered compared to subsequently forgotten trials. Perirhinal cortex, hippocampus, and anterior temporal lobe clusters we determined using masks created with the WFU Pickatlas toolbox 3.0.5 (Maldjian, Laurienti, Kraft, & Burdette, 2003, dilated by two voxels in three dimensions). PrC = perirhinal cortex, HC = hippocampus, ATL = anterior temporal lobe; FMHO = fast mapping, high overlap, FMLO = fast mapping, low overlap

land et al., 1995). We used a neurocognitive approach in order to identify factors that could potentially moderate FM learning and its underlying neurofunctional processes. There is behavioral evidence that rapid semantic integration of associations through FM is only possible if the unknown and the known item share many features, or, in other words, if highly similar objects need to be discriminated at encoding (FMHO) but not if they share few features (FMLO; Chapter 5, Experiment 2). The discrimination of similar objects is typically ascribed to the PrC as it is especially qualified for binding features to unique feature conjunctions, thereby creating distinct object representations even though the objects' single features are not unique (e.g., Barense et al., 2005; Barense et al., 2007; Bussey et al., 2002; Mundy et al., 2012; Tyler et al., 2013). In terms of memory, there is evidence for perirhinal involvement in especially familiarity-based memory for single items (Wang et al., 2014; see Brown & Aggleton, 2001, for a review). Familiarity-based retrieval of associations has also been reported but only if the to-be-associated items are merged to one novel conceptual unit at encoding, for instance, if two arbitrary words are combined to a new, semantically enriched compound (e.g., Bader et al., 2010; Wiegand, Bader, & Mecklinger, 2010). Such familiarity-based memory for associations encoded as single units was found to be associated with enhanced PrC contribution to learning (Haskins et al., 2008). Here, we set out to ask if the PrC could similarly support memory processes in learning of associations through FM, such that stronger PrC involvement would support the discrimination between items, by binding new information (i.e., visual features of the unknown item and the unfamiliar label) to feature conjunctions, thereby leading to their rapid incorporation into cortical networks. 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, which should recruit the PrC more strongly. This should lead to a stronger contribution of the PrC to learning in the FMHO condition compared to the FMLO condition. This was confirmed in the present experiment, revealing subsequent memory effects within the right PrC in the FMHO condition but not in the FMLO condition and greater subsequent memory effects for the FMHO condition than for the FMLO condition. Most previous FM studies point to the ATL as key candidate for rapid semantic integration through FM (Atir-Sharon et al., 2015; Sharon et al., 2011; Merhav et al., 2015). This is reasonable insofar that the ATL has repeatedly been identified as a semantic hub, receiving input information from multiple sensory areas which are then integrated into a coherent concept (see e.g., Lambon Ralph et al., 2017; Patterson et al., 2007). 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 showed no learning benefit. In addition, there is complementary fMRI evidence for ATL contribution to FM learning (Atir-Sharon et al., 2015) and the involvement of ATL-related networks in retrieval after FM learning (Merhav et al., 2015). However, we do not assume that contribution to rapid neocortical integration in the FM paradigm is restricted to either the ATL or the PrC but rather suggest that both structures might be relevant for FM learning. FM encoding comprises the discrimination of pictures of complex objects, binding the visual features of an unknown item with an unfamiliar label to a feature conjunction, the integration of this conjunction to a new semantic concept, and finally its incorporation into cortical memory networks. Considering the functional characteristics of the PrC and the behavioral findings of successful FM learning when high feature overlap item pairs were used (Sharon et al., 2011, Chapter 5, Experiment 2), our approach here was to increase the demands on the discrimination between the unknown and the known item. Object discrimination is associated with stronger PrC recruitment, which might then also trigger PrC-mediated binding mechanisms, by which the picture and the label can be bound to a unit. Beside PrC involvement, we also found the ATL to contribute to successful FM learning, potentially tackling the integration of the feature conjunctions to semantically meaningful conceptual units which can be incorporated into semantic networks. We have previously discussed behavioral findings (i.e., semantic priming effects immediately after FMHO but not FMLO encoding) with respect to differential contribution of a discrimination and an integration process on a behavioral level (Chapter 5, Experiment 2). We proposed that both the discrimination between highly similar objects and the integration of their features to concepts might be equally relevant for successful FM learning. It is conceivable that this is reflected on a neurofunctional level. In particular, greater demands on a likely ATL-mediated integration process could support rapid semantic integration in FM comparably to increased PrC recruitment with increased demands on object discrimination.

Coutanche and Koch (2017) reported that lexical integration of the unfamiliar label on an item level varies as a function of the typicality of the previously known item. They observed that lexical integration of the labels as measured by behavioral lexical competition effects (i.e., prolonged response latencies for lexical neighbors of the newly learned labels) immediately after FM encoding was stronger if the previously unknown item had been encoded together with a known item that is atypical for its category. Keeping with the examples of the present experiment, this would mean better lexical integration of the label satellote (referring to a bird) if the satellote had been encoded together with a flamingo than if it had been encoded together with a more typical bird, such as a sparrow. Against the background outlined above, decreasing the typicality of the known item might potentially increase the demands on the integration of the unknown item into existing semantic concepts. Although only a post-hoc assumption, it is conceivable that the typicality manipulation might influence the semantic integration process, potentially driven by differential ATL engagement, just as feature overlap influences the discrimination and binding process, potentially driven by differential

PrC engagement. However, although feature overlap was manipulated orthogonally to the typicality of the known item in the present experiment and thus, differential ATL subsequent memory effects as a function of feature overlap in our study cannot be attributed to typicality effects, we found greater subsequent memory effects in the ATL for the FMHO condition than for the FMLO condition. Given that ATL involvement is an indicator of the demands on the semantic integration of the picture-label associations, one could reasonably argue that it is not the typicality of the known item as such that fosters semantic integration through FM. It might rather be the relation between the unknown item and the known item. If they are both semantically related and the known item is atypical for the same semantic category, this might indeed be supportive for rapid integration. However, if also the unknown item is atypical for the category and they are both very dissimilar, this might even lead to a reverse effect, such that the known item cannot serve as a semantic referent anymore. Vice versa, if the known item is highly typical but the unknown item is not, this could also result in a more demanding integration process, supporting rapid cortical integration. Therefore, the differential ATL subsequent memory effects we observed here might rather reflect the demands on the integration process that is not completely covered by the typicality of the known item. However, further research is needed in order to investigate typicality effects since the findings of Coutanche and Koch (2017) only refer to lexical item-level integration of the newly learned label and not to semantic integration of the complete picture-label associations which is essential in learning by means of FM. One could also argue that providing a highly similar semantic referent in the FMHO condition might have activated a broader conceptual environment or schema into which the unknown item could be embedded more easily than in the FMLO condition. There is evidence for better and faster consolidation of new information if this information is congruent with a certain schema (e.g., Tse et al., 2007; Van Kesteren et al., 2013; see Van Kesteren et al., 2012, for a review). Schemas can be understood as higher-level structures of prior knowledge to which new information can be related. 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; Van Kesteren et al., 2013). In the present study, we observed greater mPFC subsequent memory effects in the FMHO condition compared to the FMLO condition. Although the mPFC has also been associated with many cognitive functions other than schema learning, the stronger memory contribution in the FMHO condition may reasonably be attributed to the stronger pre-activation of the relevant schema by the known item. For example, at encoding of the bird satellote, a 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 FM learning or if it is rather a by-product that does not add to the contribution of other components such as the PrC and ATL, which might already be sufficient. In addition, schema-based learning might foster especially the item-level integration of the pictures of the unknown items, which are schema-congruent with the known item in the FMHO condition, but it is unclear how schema-based learning alone could account for the binding of the picture of the unknown item and the arbitrarily matched label. Such a binding process would rather be attributed to PrC engagement, which, vice versa, would not be required if the effects reported here would be based on schema-based learning alone (see Van Kesteren et al., 2012, for review). In sum, we suggest that enhanced demands on PrC involvement, operationalized by increasing feature overlap, supports learning by means of FM. ATL involvement may comparably foster learning in the FMHO condition, which we attribute to stronger integration processes. Furthermore, the potentially greater schema-congruency in the FMHO condition might have additionally contributed to the FM learning process, which is supported by a greater memory contribution of the mPFC in the FMHO condition compared to the FMLO condition.

The phenomenon of FM has previously been largely discussed in terms of the role of the hippocampus in memory for associations. It was questioned if hippocampal-neocortical consolidation was necessary to acquire and consolidate novel associations. The findings reported by Sharon et al. (2011) speak to this by suggesting that hippocampal processing can be bypassed in learning of associations through FM. 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 et al., 2014) and hippocampal contribution to FM learning in healthy young adults has been reported by Atir-Sharon et al. (2015). As already proposed previously (e.g., Atir-Sharon et al., 2015; Merhav et al., 2014, 2015; Zaiser et al., 2019), 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 processing 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 temporal poles and object information from the PrC (e.g., Brunec et al., 2018; Brunec et al., 2019; Poppenk & Moscovitch, 2011; see Poppenk et al., 2013, for a review). This fits with the model of two cortical systems for memory-guided behavior by Ranganath and Ritchey (2012), suggesting that anterior parts of the hippocampus belong to the same anterior temporal system as the PrC and the ATL and is associated with semantic representations of objects rather than recollection-like retrieval and the tracking of episodic contexts. Notably, in the current findings, exclusively anterior parts of the hippocampus contributed to FM learning whereas posterior parts were never involved, which might indicate that selectively the anterior hippocampus as part of an anterior temporal system plays a role in FM learning. In previous discussions on the hippocampus-dependency of FM learning, the definition of the hippocampus as a functionally homogeneous structure might not have been precise enough in order to draw conclusions on its role in learning by means of FM. 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 of hippocampal contribution to FM learning is that the observed benefit for patients who cannot rely on hippocampal processing does not allow for the reverse conclusion that FM is necessarily always independent of the (posterior) hippocampus. In patients who are unable to rely on hippocampal processing due to severe hippocampal damage, an alternative route triggered by FM encoding might make it possible to bypass hippocampal-neocortical consolidation.The conditions are less clear in healthy aging. Although hippocampal degradation 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), it is unclear to what extent the (partly dysfunctional) hippocampal route is triggered by FM encoding in healthy older individuals. Greve et al. (2014) reported no learning benefit in healthy elderly as measured by explicit recognition. However, the authors only correlated hippocampal and ATL volume with recognition accuracy but did not report differential hippocampal volumes along its longitudinal axis or volumes of the extra-hippocampal MTL cortex. Furthermore, it is conceivable that healthy elderly are impaired in hippocampal learning of associations but the route by which hippocampal processing could be bypassed was also not sufficiently triggered. This might be different in an FM condition in which the unknown and the known item share many features, which was not the case in Greve et al. (2014). We did not find hippocampal activation in a condition in which items shared few features (FMLO) compared to the FMHO condition. However, it needs to be mentioned that a small cluster in the ErC, which connects the hippocampus with the parahippocampal gyrus, was recruited more strongly in the FMLO condition. Although only a post-hoc explanation, such ErC contribution at retrieval might potentially indicate that in a condition in which the perirhinal pathway has not sufficiently been triggered at encoding, hippocampus-related structures might be involved in retrieval. However, behavioral data of previous experiments using explicit tests cannot speak to that. Here, we made use of the advantage of fMRI, which made it possible to actually capture the contribution of different brain structures to memory. We found that after FM learning, retrieval seemed not to rely on posterior hippocampal regions but mainly involves similar structures as at encoding, such as the PrC, the ATL, and anterior parts of the hippocampus. We propose that irrespective of functional integrity of the hippocampus, boosting PrC involvement could smooth the way to successful FM learning, which can in principle be independent of the hippocampus.

6.4.1 Limitations

The manipulation of visual feature overlap in our materials inevitably led to the simultaneous manipulation of semantic overlap. Although our intention originally was to manipulate visual overlap, we are aware that the current study cannot finally disentangle if it is visual or semantic overlap that drives the subsequent memory effects in the FMHO condition, especially as Martin et al. (2018) recently reported that feature conjunctions are processed by PrC not only on a visual and a semantic level but also on an integrative level of visual and semantic features in combination. It is conceivable that an increase in both visual and semantic overlap could lead to greater PrC contribution to learning by means of FM. One might criticize that our 48 participants included in the subsequent memory analyses constitute a very selective sample of above-chance performers. However, in order to investigate differential effects that are predictive for subsequent memory, we needed to ensure that these effects were based on actual memory rather than guessing. In order to prevent the exclusion of 31 chance performers, we could have made the task easier, for example through the reduction of the number of associations to be learned. However, this would also have reduced signal-to-noise ratio. Another option could have been to repeat the associations. However, as we want to capture the effects of one-shot learning, we would not have been able to tell if subsequent memory can be attributed to direct cortical integration or to repetition. Thus, for the benefit of a proper signal-to-noise ratio and subsequent memory effects that were not blurred by repeated learning, we decided to take the risk that many participants would have to be excluded from the analyses.

6.4.2 Conclusions

Consistent with previous findings showing that feature overlap moderates rapid semantic integration after FM encoding on a behavioral level (Chapter 5, Experiment 2), we conclude from the present results that differential PrC recruitment at encoding essentially influences rapid learning of novel associations by means of FM. Increasing the demands on PrC processing, operationalized by the manipulation of the degree of feature overlap, seems to support FM learning. Beside the PrC, other anterior and medial temporal structures seem to contribute to FM learning in a similar manner, such as the ATL and anterior hippocampus. In future work, it would be interesting to investigate if triggering other processes involved in FM learning, for example by strengthening semantic integration or binding processes rather than object discrimination, can lead to a similar outcome.

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Chapter 7

Incidental encoding and object discrimination are prerequisites for rapid semantic integration of novel associations by means of fast mapping.

7.1 Introduction

Traditional theories of memory consolidation suggest that novel, arbitrary associations can initially be acquired quickly, whereas the incorporation of these associations into long-term memory networks is a comparably slow and gradual consolidation process (see e.g., Frankland & Bontempi, 2005, for a review). On a neurofunctional level, the initial acquisition of associations underlies hippocampal processing and the incorporation into cortical networks is characterized by continuous hippocampal-neocortical interplay, by which cortico-cortical links are created and strengthened until the new memory representations finally become hippocampus-independent (e.g., McClelland et al., 1995; Norman & O'Reilly, 2003; see Frankland & Bontempi, 2005, for a review). However, there is evidence that such time-consuming consolidation processes can be bypassed if the associations are encoded by means of a learning paradigm called *fast mapping* (FM; e.g., Atir-Sharon et al., 2015; Himmer et al., 2017; Merhav et al., 2014; Sharon et al., 2011, see also Chapter 5 and Chapter 6; see also Coutanche & Koch, 2017; Coutanche & Thompson-Schill, 2014, for rapid item-level lexical integration). In typical studies on FM learning, an FM encoding condition is compared to an EE paradigm that is assumed to rely on hippocampal processing and slow hippocampal-neocortical consolidation. Sharon et al. (2011) found that whereas patients with severe hippocampal lesions did not show above-chance recognition performance in the EE condition, they performed as well as healthy controls if the associations had been encoded through

FM, and this was the case already immediately after encoding. This strongly indicates that FM provides a rapid, direct route to cortical integration, potentially bypassing hippocampal-neocortical consolidation processes. Despite this evidence, contradictory findings have been repeatedly reported (cf. Cooper et al., 2019; Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; see also Cooper et al., 2018, and the respective commentaries for a recent discussion).

In the typical FM encoding paradigm, participants are presented with two pictures of animals or plants and a perceptual question referring to an unfamiliar label (e.g., *Does the satellote have blue feet?*). One of the pictures depicts an item that is supposed to be known (e.g., a flamingo) and the other item is supposed to be unknown (e.g., an exotic bird; Figure 4.1). In order to answer the question, participants need to recognize the previously known item and infer that the previously unknown item must be the one to which the question refers. Thereby, they are assumed to create an association between the picture of the unknown item and the unfamiliar label. Sharon et al. (2011) suggested that the following criteria must be fulfilled for successful rapid cortical integration through FM: (1) The new association needs to be integrated into an existing semantic context. (2) The link between the unknown item and the label must not be given but needs to be actively discovered by the participant through the exclusion of the known item. (3) Learning must be incidental. Based on findings by Merhav et al. (2014), Atir-Sharon et al. (2015) added that (4) there must not be interfering information in already existing semantic networks. However, for some of these criteria there is so far no empirical evidence that they need to be fulfilled in FM learning. One reason for that is the lack of studies in which the criteria were investigated in isolation. The conditions that are typically compared in most FM studies, that is, FM and EE, differ in several aspects (e.g., learning intention, the presence of a known item, the requirement to answer a question). Hence, the comparison between FM and EE does not allow for conclusions on any effect in isolation. To our knowledge, the requirement of incidental learning has not yet been manipulated systematically. Moreover, the fulfillment of the second and third criterion has only proven necessary for lexical integration of the label (Coutanche & Thompson-Schill, 2014, Experiment2) or were investigated using explicit recognition tests (Cooper et al., 2019) that might not be appropriate in order to capture cortical integration (Goshen-Gottstein et al., 2000; Shimamura, 1986; Squire, 1992) as it cannot be disentangled to which degree explicit recognition is based on hippocampal or cortical retrieval (see also Zaiser et al., 2019).

Here, we set out to test the criteria of the necessity for the presence of a previously known picture and incidental learning.

In a previous experiment, we compared a condition in which the unknown and the known item shared many features (*fast mapping, high overlap*; FMHO) with a condition in which they shared few features (*fast mapping, low overlap*; FMLO). We found that for successful semantic integration through FM, the previously unknown item must be presented together with a highly similar previously known item, as in the FMHO condition (Chapter 5, Experiment 2). No rapid semantic integration was found in the FMLO condition, in which the items were less similar. The discrimination of complex and especially highly similar objects is ascribed to the PrC (e.g., Barense et al., 2005; Barense et al., 2007; Bussey et al., 2005; Cowell et al., 2010; Mundy et al., 2012). Interestingly, the patients with selective hippocampal lesions reported by Sharon et al. (2011) who show a clear benefit from FM encoded the unknown pictures together with highly similar known items (Sharon, 2010), which would typically recruit the PrC. Within the same study, two other patients with lesions to perirhinal and anterior temporal structures did not show such an FM benefit. Furthermore, it seems likely that feature overlap might be one of the main differences between Sharon et al. (2011) and a near-replication in which no learning benefit for patients with hippocampal lesions was observed (Smith et al., 2014, based on their example item pairs). This fits with our previously reported findings that the PrC essentially drives learning through FM and that this is especially the case if the demands on perirhinal processing are high, such as in the discrimination between items sharing many features (Chapter 6). Against this background, we suggest that the criterion of the availability of an existing semantic context (Sharon et al., 2011) is important insofar as it requires the discrimination of (especially highly similar) items, which seems to be decisive for successful FM learning. Although the manipulation of the presence of the previously known item not only manipulates the availability of a semantic context but also the necessity of an inferential conclusion, it is unlikely that the latter drives rapid semantic integration through FM. We previously did not observe rapid semantic integration in the FMLO condition, in which an inferential conclusion was also required (Chapter 5, Experiment 2). In this previous experiment, two pictures were presented in the FMHO and the FMLO condition and the conditions only differed with regard to feature overlap. It is yet unclear if the rapid semantic integration in the FMHO condition is actually based on beneficial effects of the discrimination of highly similar items. It could also be argued that the presence of a dissimilar known item in the FMLO condition not only had no effect but might even have distracted from deeper encoding. This could explain the absence of rapid semantic integration in the FMLO condition. In order to find out if the FMHO condition has an actual beneficial effect, an incidental encoding (IE) condition is required in which no previously known item is available.

With respect to learning intention, the predictions are less clear. However, on a neurocognitive level, the PrC is responsible for the binding of single, elemental features to unique, distinct feature conjunctions, whereas the hippocampus is involved in the relational binding between items to inter-item or item-context associations. Our previous finding that subsequent memory of picture-label associations by means of FM is predicted by activity in the PrC might possibly indicate that FM creates intra-item associations, given that feature overlap between the known and unknown item is high. In the EE condition, participants are explicitly instructed to bind the picture and the label, thereby creating an inter-item association that is assumed to be represented in the hippocampus. In the FM condition, however, no such binding process is instructed explicitly. However, it is yet unclear if explicitly triggering hippocampal binding processes (as in the EE condition) prevents from the creation of intra-item associations and direct cortical integration. The study by Warren and Duff (2014) is so far the only one in which FM learning was likely intentional as they informed their participants about a subsequent memory test prior to the experiment. No rapid learning through FM was found in their study, neither using explicit tests nor implicit eye-tracking measures. However, as learning intention was not manipulated explicitly and this study differed in several other points from typical FM studies apart from the learning intention, it cannot be concluded that there is no rapid cortical integration if associations are encoded within the FM paradigm (as defined by Sharon et al., 2011) if learning is intentional. Here, we set out to investigate the effect of a learning intention in the FM paradigm in healthy young adults. Together with our hypothesis regarding object discrimination as outlined above, we expected that rapid semantic integration of novel associations by means of FM is possible if highly similar objects need to be discriminated and if learning is incidental (as in Chapter 5, Experiment 2). If no object discrimination is required but hippocampal binding is triggered (as in the EE condition), no rapid cortical integration would be expected. We would further suggest that incidental learning alone does not lead to rapid semantic integration if no object discrimination is required (see Coutanche & Thompson-Schill, 2014, Experiment 2). It is yet unclear if rapid semantic integration through FM would be possible if learning is intentional in an FM paradigm in which the discrimination of highly similar objects is required. We would assume that the instruction to remember inter-item associations would trigger hippocampal binding processes. However, it is unclear if this inhibits perirhinal binding or if both processes run in parallel. It is conceivable that the learning intention has a dominant role. However, perirhinal binding processes might still lead to rapid cortical integration at least to some extent.

7.2 Experiment 4

Using a cross-factorial design, we aimed to disentangle the role of a learning intention and object discrimination on the rapid incorporation of novel picture-label associations into semantic memory networks. In order to capture retrieval from cortically integrated associations instead of hippocampus-based retrieval, we assessed semantic integration by means of semantic priming effects, which are typically less dependent on hippocampal involvement than explicit recognition tests (e.g., Shimamura, 1986; Squire, 1992). We used the previously unknown labels of the encoding phase as primes, which were followed by either semantically related or unrelated real-word targets. If the prime has already been incorporated into semantic memory networks, the response times to the related target should be faster as in this condition the prime should facilitate access to semantically related concepts. If the prime has not been semantically integrated, this should not affect response latencies and thus, no semantic priming effect should be found. Within a group of participants who encoded the unknown items incidentally, we compared an FM condition in which feature overlap was high (*fast mapping, high overlap*; FMHO; as in Chapter 5) with an incidental encoding (IE) condition in which no object discrimination was required (as only one picture was presented) but a perceptual question still had to be answered (as in Coutanche & Thompson-Schill, 2014, Experiment 2; see Figure 7.1). Another group of participants conducted the encoding phase in the same encoding conditions, with the only difference that learning was always intentional. In one of the encoding conditions in this group, object discrimination was required (intentional fast mapping, high overlap; intFMHO), whereas in the other condition, no discrimination was required but the perceptual question still needed to be answered (explicit encoding, EE). No semantic priming effect was hypothesized for the EE condition, in which neither of the two criteria is fulfilled, in line with findings we reported previously (Chapter 5, Experiment 2). No semantic priming effect was expected for the IE condition as we assumed that object discrimination is a prerequisite for FM learning. In the intFMHO condition, we expected at least smaller effects than in the FMHO condition as hippocampal binding might potentially play a dominant role. Moreover, we expected the semantic priming effect in the FMHO condition to be larger than in the other three conditions.

7.2.1 Methods

7.2.1.1 Participants

Of 80 students from Saarland University, $n = 40$ participants were randomly assigned to the group for which learning was incidental and $n = 40$ to the group for which learning was intentional. One participant of the incidental learning group had to be excluded as he had already taken part in another experiment in which the same stimulus material was used. Mean age of the remaining 79 participants (59 female, 20 male) was $M = 22.7$ years (age range: 18-30 years) and there was no age difference between groups, $t < 1$. The completion of the experiment took approximately 50 minutes. All participants were native German speakers and had normal or corrected-to-normal vision. They gave written informed consent prior to the experiment and were compensated for their participation with course credit. The experiment was approved by the local ethics committee of Saarland University in accordance with the declaration of Helsinki.

7.2.1.2 Materials

Encoding. Ninety-six pictures from six categories (i.e., mammals, birds, fish, fruit, vegetables, plants) were drawn from an item pool of a previously conducted rating study in which 46 participants ($M_{\text{age}} = 23.1$ years, age range: 18-34 years; 30 female) had rated 360 pictures that had been obtained from the internet (see Chapter 4 for a detailed description). Of the 96 pictures, 48 had been rated as unknown by most participants of the rating study (93 %, $SD = 5$ %) and with the lowest familiarity ($M = 1.82$, $SD = 0.34$; 1 = *not at all familiar*, 5 = *very familiar*), and the other 48 pictures had been rated as known by most participants (94 %, $SD = 7$ %) and with the highest familiarity ($M = 4.50$, $SD = 0.29$). In the final item set, familiarity for the previously unknown items was significantly lower than for the previously known items and significantly more participants of the rating study had rated the previously known item as known than the previously unknown items (all *p*s $< .001$). Pictures in the rating study had been arranged in pairs of one putatively unknown and one putatively known picture each. For the present experiment, only such pairs were chosen which had been rated with the highest feature overlap in the rating study ($M = 3.66$, $SD = 0.30$; 1 = *not at all similar*, 5 = *very similar*). Feature overlap was defined as the similarity of the two items of an item pair with regard to features such as the presence and nature of fur, a tail, a fin, legs, the smoothness of a fruit's skin, color, and so forth. Half of the unknown items used in Experiment 4 had been categorized as animals in the rating study (i.e., mammals, birds, or fish) and half had been categorized as plants (i.e., fruit, vegetables, or plants). The size of the pictures varied depending on the items' relative size in reality, but was 300 x 300 pixels at maximum, leading to a maximum visual angle of approximately 8.2°. The actual names of the previously unknown items were substituted either with a pseudo-word or with an item's (slightly modified) botanical or zoological name if the original names might have evoked information on the item (e.g., *giraffe gazelle* was renamed *gerenuk*). The final labels of the unknown items consisted of 4-10 letters with a mean length of $M = 6.48$ letters ($SD = 1.27$). In order to ensure that participants did not develop strategies such as always paying attention to the unknown item only, additional 16 filler trials were added in the encoding phase in which the question referred to the previously known item. Filler trials matched the respective encoding condition and were excluded from all analyses.

Semantic Priming. In the semantic priming task, the previously unknown items were used as primes. Targets were either animals or plants and could therefore be of the same higher-level category as the primes (i.e., both were either animals or plants) or of the respective other higher-level category (i.e., the prime was an animal and the target a plant, or vice versa). Overall, 96 different targets were presented, which were chosen to be preferably long (3-16 letters; $M = 8.34$, $SD = 2.17$) while at the same time keeping their lemma frequencies as low as possible (between 0.01 and 3.08 per million words; $M = 0.53$, $SD = 0.51$; Heister et al., 2011) as priming effects can be more pronounced if target processing takes more time (Hines et al., 1986). Each target was presented twice, once together with a related prime and once together with an unrelated prime. Each prime appeared four times, twice together with a related target and twice with an unrelated target (order counterbalanced, i.e., either related–unrelated–unrelated–related or vice versa). The targets were not presented elsewhere in the experiment.

Recognition. All pictures of the three-alternative forced-choice display had been presented as unknown items in the encoding phase and were depicted once as target and twice as foil in the recognition test, separated by at least four trials. All pictures within a trial were from the same higher-level category (i.e., either all plants or all animals) or, if possible, also from the same lower-level category (e.g., all birds, all mammals, etc.; see Figure 7.1), in order to capture memory for the exact associations and not for an item's category only. No two test pictures appeared together twice.

7.2.1.3 Design and Procedure

Stimulus presentation and timing were controlled using the experimental software PsychoPy (Peirce, 2008, http://www.psychopy.org/). Participants were seated in front of a 24-inch screen at a viewing distance of approximately 60 cm. All stimuli throughout the experiment were presented against a white background.

Encoding. Half of the participants encoded the items intentionally. They were informed about the memory test right at the beginning of the experiment, and, in particular, that they would later be tested on the exact combination of the picture together with its label. Right before the encoding phase, they were again explicitly instructed to remember the items together with their names. The other half of the participants encoded the items incidentally, that is, they were not informed about the later memory test. Instead, they were told that the experiment aims to investigate visual perception. The procedure of the experiment was exactly the same for both groups. The only difference between groups was the learning intention at encoding. Both groups encoded the 48 items in four blocks of 12 trials each (plus additional four filler trials in each block) of which two blocks consisted of the respective discrimination condition (incidental group: FMHO, intentional group: intFMHO) and two blocks of the no-discrimination condition (incidental group: IE, intentional group: EE). Hence, the intentional learning group completed two intFMHO blocks and two EE blocks (order counterbalanced, i.e., either intFMHO-EE–EE–intFMHO or EE–intFMHO–intFMHO–EE) and the incidental encoding group completed two FMHO blocks and two IE blocks (order counterbalanced, i.e., either FMHO–IE–IE–FMHO or IE–FMHO–FMHO–IE). At the beginning of the encoding phase, a fixation cross was displayed slightly below the center of the screen for 700 ms in all conditions, which was then replaced by the question for 2000 ms in Arial 27 point font (e.g., *Does the satellote have blue feet?*; see Figure 7.1). The label within the question was always depicted in bold font in the horizontal center of the screen. In the discrimination conditions (i.e., FMHO and intFMHO), two pictures then appeared above the question (left and right of the center of the screen), one of which was previously unknown and one was previously known (see Figure 7.1). In the no-discrimination conditions (i.e., IE and EE), only one picture was presented above the question in the center of the screen. In all encoding conditions, the picture(s) and the question automatically disappeared after 3500 ms of picture presentation (and thus, after the question had overall been presented for 5500 ms) and were replaced by a screen containing the words *yes* and *no* in orange and blue colors on the left and right to the center of the screen (color and position counterbalanced between subjects). Participants could respond by pressing the key marked with the respective color on a computer keyboard. As soon as an answer had been given, verbal feedback was displayed on the screen. If no answer had been given within 3000 ms, participants were encouraged to respond faster and the next trial started. All participants were instructed to read the questions thoroughly, focus on what is asked for and, as soon as the picture(s) would appear, figure out what the answer would be. The four encoding blocks were separated by 30-second breaks in which participants were informed that in the next block, they would be presented with either one picture (IE and EE conditions) or two pictures (FMHO and intFMHO conditions). In order to prevent primacy and recency effects, one of the four filler trials per block was inserted as buffer trials each at the beginning and the end of a block. The other two filler trials were randomly inserted between the experimental trials within a block, with the restriction that they would be separated by at least three trials. Participants completed a practice phase before the encoding phase that consisted of two blocks of six trials (each including two filler trials) in which they were presented with only one picture in the first block and with two pictures in the second block or vice versa (order counterbalanced between participants). Analogously to the actual encoding phase, practice blocks were separated by a short break in which they were informed if one or two pictures would be presented in the next block.

Semantic priming. After a 4-minute retention interval in which participants had solved simple mathematical equations, they conducted the semantic priming task. Each trial started with the presentation of a fixation cross in the center of the screen for 700 ms, followed by the prime word for 300 ms (see Figure 7.1). After the prime had disappeared, a blank screen was displayed for 250 ms, which was then replaced by the target word (prime and target presented in Arial 27 point font), leading to a stimulus-onset asynchrony of 550 ms. Participants were instructed to indicate if the target word was an animal or a plant by pressing either a blue or an orange key on the computer keyboard (color and position counterbalanced between subjects). They were asked to remember the key-response combinations during the task but to make sure they did not forget it, tags with the words *animal* and *plant* were placed below the screen on the left and right side in blue and orange color, respectively. Targets were displayed until a response was made but for 800 ms at maximum. Responses could be made within these 800 ms but were recorded for further 200 ms in which the target was not visible anymore. Instructions emphasized speed over accuracy and participants were informed that due to the fast pace of the task, they might make mistakes but nevertheless should respond as fast as possible (as recommended by Wentura & Degner, 2010). The whole priming phase was arranged in four blocks that were separated by a one-minute break in which participants could rest. Thus, the priming phase comprised 192 trials with 48 trials in each block. Within a block, each prime was presented once and trials were presented in random order. Each target appeared twice in the priming phase, either in the first and third block or in the second and fourth block. The experimental trials were preceded by two buffer trials at the beginning of each block in order to accustom participants to the fast pace of the task. The primes of these buffer trials were pseudowords. Prior to the priming phase, participants were familiarized with the priming paradigm in a practice phase consisting of six trials. Primes in the practice phase were the names of the unknown items of the encoding practice phase.

Recognition. After the priming phase, a three-alternative forced-choice recognition test was administered, in which one of three pictures had to be assigned to a label. The label was presented in the center of the screen in Arial 27 point font and pictures were arranged around the label (top-left, top-right, and at the bottom of the screen; see Figure 7.1). Participants were instructed to indicate which picture had been learned together with the label by mouse click. A response was not possible before 3000 ms of stimulus presentation in order to ensure that participants had enough time to look at all three pictures. After 3000 ms, the mouse cursor appeared in the center of the screen and a verbal prompt to respond appeared on the bottom of the screen. If no key had been pressed within 6000 ms of overall stimulus presentation, participants were encouraged to respond faster and the next trial started.

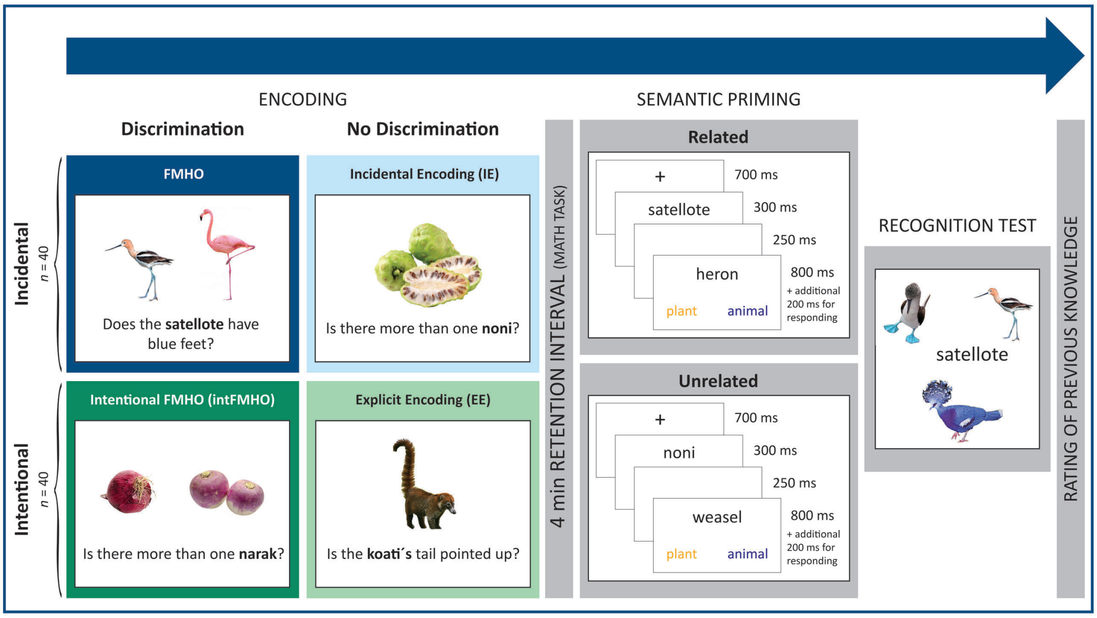

Figure 7.1 Experimental design and procedure of Experiment 4. **Encoding**. Object discrimination was manipulated within participants, learning intention was manipulated between participants (blue = incidental learning group, green = intentional learning group). Within participants, the encoding phase was split into four blocks of each discrimination condition in counterbalanced order. After the question had been presented for 2000 ms, either one or two pictures were inserted and presented together with the question for 3500 ms. Response options (*yes*/*no*) were provided after picture(s) and question had disappeared. Feedback was given after a response had been made. **Semantic Priming**. Each prime appeared four times, twice related to the target, twice unrelated (order counterbalanced). Each target appeared twice, half of the targets first related and then unrelated to the prime and the other half in reverse order (counterbalanced between subjects). **Recognition**. All pictures within one display always belonged to the same higher-level category (i.e., all animals or all plants) and, if possible, also to the same lower-level category (e.g., all birds).

Rating of previous knowledge. At the end of the experiment, participants were asked to indicate how well they had known both the putatively known and unknown items prior to the experiment. If a rating of >= 4 was given on a 6-point Likert scale (1 = *had not known the item at all before the experiment*; 6 = *had known the item very well before the experiment*), participants were asked to type in the item's name at the subordinate category (e.g., hawk instead of bird).

7.2.1.4 Analyses

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org). Semantic priming effects were calculated by subtracting response times for correct responses to related targets from response times for correct responses to unrelated targets. Trials were removed from all analyses if the individual rating of previous knowledge was incongruent with the expected knowledge, that is, ratings of <= 3 for putatively known items and ratings of >= 4 for putatively unknown items, leading to a mean dropout rate of 11.39 % of correct trials. We then excluded individual outlier data points, defined as trials with response latencies of 1.5 inter-quartile ranges below the first and above the third quartile (Tukey, 1977), which resulted in a final mean dropout rate of 13.59 % of correct trials. Outlier participants with regard to the semantic priming effect were determined for each group separately and participants were excluded if they were defined as outliers in at least one discrimination condition (1.5 inter-quartile ranges below the first and above the third quartile Tukey, 1977). Sixteen outlier participants were removed from the analyses (incidental group: 7, intentional group: 9), which resulted in a final sample size of $n = 32$ participants in the incidental learning group (i.e., FMHO and IE conditions) and $n = 31$ participants in the intentional learning group (i.e., intFMHO and EE conditions) for the semantic priming analyses. Accuracy in the forced-choice recognition test was defined as the proportion of correct responses. Seven participants had to be excluded from the recognition analyses due to list errors (incidental group: 5, intentional group: 3). The factor object discrimination was included as within-subjects factor in all models, with the levels *discrimination* and *no discrimination*. The factor learning intention was included as between-subjects factor with the levels *intentional* and *incidental*. If not noted differently, all t tests were one-tailed. Significance level for all tests was set to $\alpha = .05$. If the criterion of homogeneity of variances between groups was not fulfilled, t test statistics were reported according to Welch's modification to degrees of freedom. Effect size η_p^2 reflects the ratio of the sum of squares of the effect to the sum of squares associated with the effect plus the residual sum of squares. Effect size d for the between-subjects difference of the semantic priming effects between groups was calculated as difference of the mean semantic priming effects, divided by the pooled standard deviation of the effects. Effect size d for the deviation of the semantic priming effects and recognition accuracy from zero was calculated as the mean priming effect or recognition accuracy divided by the standard deviation of the priming effect or recognition accuracy.

7.2.2 Results

Encoding. The average proportion of correct responses at encoding was $M = .95$ ($SD = .24$) trials. A 2 x 2 factorial mixed analysis of variance revealed a marginally significant main effect of object discrimination, $F(1,77) = 3.69$, $p = .059$, $\eta_p^2 = .05$, on

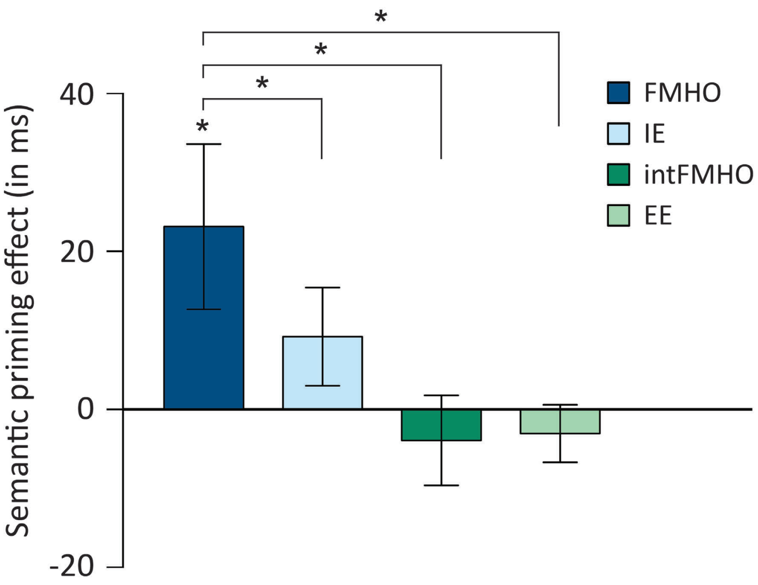

Figure 7.2 Results of the semantic priming task of Experiment 1. The semantic priming effect was calculated by subtracting response times to related targets from response times to unrelated targets. FMHO = fast mapping, high overlap; IE = incidental encoding; intFMHO = intentional fast mapping, high overlap; EE = explicit encoding. Error bars represent the standard error of the mean. *$p < .05$

the proportion of correct responses, and a marginally significant Object Discrimination x Learning Intention interaction, $F(1,77) = 3.87$, $p = .053$, $\eta_p^2 = .05$. This was mainly driven by the difference between the intentional learning conditions, $t(39) = -2.54$, $p = .015$, $d = 0.40$, two-sided ($M_{\mathrm{intFMHO}} = .94$, $SD_{\mathrm{intFMHO}} = .06$; $M_{\mathrm{EE}} = .97$, $SD_{\mathrm{EE}} = .04$), whereas no such difference was found between the incidental encoding conditions, $t < 1$ ($M_{\mathrm{FMHO}} = .93$, $SD_{\mathrm{FMHO}} = .14$; $M_{\mathrm{IE}} = .93$, $SD_{\mathrm{IE}} = .13$).

Semantic Priming. Accuracies in the semantic priming task were above chance in all conditions (all $ps < .001$) and separately for all subjects ($p < .05$, binomial test). In order to investigate the effects of the factors object discrimination and learning intention, a 2 x 2 factorial mixed ANOVA was conducted, revealing a main effect of learning intention, $F(1,61) = 5.09$, $p = .028$, $\eta_p^2 = .22$, with greater priming effects for incidental compared to intentional learning (see Table 7.1). Neither the main effect of object discrimination was significant, $F(1,61) = 1.95$, $p = .168$, nor the Object Discrimination x Learning Intention interaction, $F(1,61) = 2.41$, $p = .125$. The semantic priming effect in the FMHO condition was significantly larger than in the IE condition, $t(31) = 1.98$, $p = .029$, $d = 0.41$ (see Table 7.1 for descriptive statistics). Within the object discrimination conditions, the semantic priming effect was larger for the FMHO condition compared to the intFMHO condition, $t(47.78) = 2.27$, $p = .014$, $d = 0.57$.

The semantic priming effect for the FMHO condition was greater than the effect for the EE condition, $t(38.38) = 2.37$, $p = .012$, $d = 0.59$. Importantly, our previous findings (Chapter 5, Experiment 2) were replicated, that is, there was a significant semantic priming effect for the FMHO condition, $t(31) = 2.21$, $p = .017$, $d = 0.39$, but not for the EE condition, $t < 1$. There was no significant priming effect in the IE condition, $t(31) = 1.48$, $p = .149$, $d = 0.26$, two-tailed, or the intFMHO condition, $t < 1$ (see Figure 7.2).

Recognition. There were no significant differences in recognition accuracy between encoding conditions, with neither a main effect of learning intention, $F(1,69) = 1.03$, $p = .313$, nor an effect of object discrimination or their interaction, both Fs < 1 ($M_{\text{FMHO}} = .47$, $SD_{\text{FMHO}} = .13$; $M_{\text{IE}} = .48$, $SD_{\text{IE}} = .14$; $M_{\text{intFMHO}} = .49$, $SD_{\text{intFMHO}} = .16$; $M_{\text{EE}} = .51$, $M_{\text{EE}} = .14$) but accuracy was above chance level for all groups, all ps $< .001$.

7.2.3 Discussion

We aimed to investigate effects of learning intention and object discrimination in rapid semantic integration by means of FM, expecting the discrimination between the unknown and the known item to be a prerequisite for successful FM learning and incidental learning to be beneficial if object discrimination is required. Using a fully crossed design in which object discrimination and learning intention were manipulated orthogonally allowed to disentangle the effects of both factors. A main effect of learning intention was found, that is, greater semantic priming effects were observed when encoding was incidental. Whereas in the intentional learning group, object discrimination did not affect semantic integration, the semantic priming effects in the incidental learning group differed depending on object discrimination. A semantic priming effect was only found in the FMHO condition, in which highly similar objects needed to be discriminated, but not in the IE condition, in which only one picture was presented. In addition, the results of our previous findings were replicated, that is, rapid semantic integration of novel associations was found in the FMHO condition but not in the EE condition (see Chapter 5, Experiment 2) and was larger in the FMHO condition than in the EE condition. Although rapid semantic integration was observed in the FMHO condition (and thus the finding of Chapter 5, Experiment 2, was replicated), the results are not clear-cut with respect to the effect of discrimination. We found neither a main

Table 7.1 Mean Response Times (in ms), Semantic Priming Effect (i.e., Response Times Unrelated – Response Times Related), and Accuracies (in % Correct) by Condition

		Discrimination	No discrimination
Response times (in ms)			
Incidental		FMHO	IE
	Related	638.85 (57.49)	651.60 (78.24)
	Unrelated	661.97 (92.71)	660.79 (86.59)
Semantic priming effect		**23.11 (59.13)**	**9.19 (35.17)**
Intentional		intFMHO	EE
	Related	643.72 (73.12)	646.91 (77.60)
	Unrelated	639.79 (79.11)	643.84 (72.50)
Semantic priming effect		**-3.93 (31.71)**	**-3.06 (20.25)**
Accuracies (% correct)			
Incidental		FMHO	IE
	Related	91.69 (53.10)	90.99 (54.52)
	Unrelated	90.77 (53.78)	89.11 (68.79)
Intentional		intFMHO	EE
	Related	90.48 (73.44)	90.87 (79.18)
	Unrelated	90.61 (73.97)	91.68 (63.95)

Note. FMHO = fast mapping, high overlap; IE = incidental encoding; intFMHO = intentional fast mapping, high overlap; EE = explicit encoding. Standard deviations in parentheses.

effect of discrimination nor a significant interaction between discrimination and learning intention. We attribute this to the incidental encoding condition showing a numerical tendency towards a semantic priming effect. This was not expected as (Coutanche & Thompson-Schill, 2014, Experiment 2) did not find any effect of integration for their IE condition already for the labels on an item level. Moreover, we did not expect a semantic priming effect in an IE condition as we previously did not observe a priming effect even in an FM condition in which feature overlap was low (and thus, discrimination was less demanding) but object discrimination was still required (Chapter 5, Experiment 2). In exploratory post-hoc analyses we found that the IE condition was the only condition, in which the semantic priming effect was marginally significantly affected by the order of the encoding conditions, that is, the priming effect was larger for participants who started the encoding phase with the FMHO condition, and thus, the IE condition had been preceded by the FMHO condition, compared to the IE priming effect for participants who started with the IE condition, $t(19.98) = -1.98$, $p = .062$, $d = 0.26$, two-tailed. Moreover, recent results by Coutanche and Koch (2017) revealed that the typicality of the known item in the encoding phase modulates rapid lexical integration of the label by means of FM. We did not assess typicality ratings in Experiment 4 but can imagine that the manipulation of typicality could affect semantic integration in a similar manner. Just as the presence of a highly similar known item increases the demands on object *discrimination*, the presence of a highly atypical known item might increase the demands on semantic *integration*, which are both part of FM learning. We therefore conducted a typicality rating after a second experiment, in which the FMHO condition was compared to the IE condition in a between-subjects design by which we could exclude any order effects in the IE condition and validate the results of Experiment 4.

7.3 Experiment 5

As clearly no semantic priming effects were found in Experiment 4 if learning was intentional, encoding was always incidental in Experiment 5. In contrast to Experiment 4, encoding condition (i.e., FMHO, IE) was manipulated between subjects to prevent order effects. In addition, recent findings by Coutanche and Koch (2017) suggested that the typicality of the previously known item might affect rapid learning through FM, with known items that were atypical for their category fostering rapid lexical integration of the label. Therefore, we collected individual typicality ratings after participants had completed Experiment 5. Coutanche and Koch (2017) argued that atypical known items might boost cortical integration of associations as atypical items are better represented in the ATL, a structure relevant for FM learning (see e.g., Atir-Sharon et al., 2015) than typical exemplars (Rogers et al., 2015). We would additionally assume that atypical known items pose higher demands on the integration of the unknown item into existing semantic networks as these networks should be made better accessible by a very typical exemplar. This could be based on a similar rationale as our assumption that higher demands on object discrimination fosters rapid FM learning. By presenting atypical known items, the semantic category of the unknown item might be less accessible and thus more effort is required in order to integrate the unknown item into similar existing knowledge structures, which has already been defined as a requirement for successful FM learning by Sharon et al. (2011). At the end of the experiment, participants completed the Survey of Autobiographical Memory (SAM; Palombo, Williams, Abdi, & Levine, 2013) as Coutanche and Koch (2017) found that selectively participants with a high score on a semantic memory trait benefit from atypical known items. Such a high score on the semantic memory trait is assumed to indicate that individuals tend to draw on the semantic memory system in everyday life (see Sheldon, Farb, Palombo, & Levine, 2016). These individuals seem to recruit similar networks as those involved in FM retrieval by Merhav et al. (2015). Following the idea that higher demands on object discrimination lead to better semantic integration in FM learning, it was expected that larger semantic priming effects should be found after encoding in the FMHO condition, in which object discrimination was demanding, compared to the IE condition, in which no object discrimination was required. Within the FMHO condition, semantic priming effects for learned items should be larger the less typical the corresponding known item was rated if atypical known items indeed foster rapid semantic integration through FM.

7.3.1 Methods

7.3.1.1 Participants

Eighty students from Saarland University took part in the experiment and were randomly assigned to one of two groups in which encoding was always incidental. In the FMHO encoding group, participants ($n_{\mathrm{FMHO}} = 40$) were presented with two pictures, whereas in the IE condition ($n_{\mathrm{IE}} = 40$), they were presented with only one picture at a time. All participants were German native speakers and had normal or corrected-to-normal vision. They gave written informed consent prior to the experiment and were compensated for their participation with course credit. The experiment was approved by the local ethics committee of Saarland University in accordance with the declaration of Helsinki.

7.3.1.2 Materials

Stimulus material of Experiment 5 was the same as in Experiment 4. The SAM was translated to German by a native German speaker and back-translated to English by a native English speaker. Two native German speakers and one native English speaker then independently agreed on the equivalence of the back-translation with the original English version.

7.3.1.3 Design and Procedure

The experimental setting was as in Experiment 4.

Encoding. As object discrimination was manipulated between subjects, participants did not encode the items in four blocks with alternating conditions but this time, all 60 trials (including 12 filler trials) were encoded within one block of one encoding condition only (see Figure 7.3). Half of the participants were always presented with one picture at a time (IE) and the other half was presented with two pictures (FMHO). Everything else was as in Experiment 4.

Filler task, semantic priming, recognition, and rating of previous knowledge. After a 4-minute filler task, a semantic priming task was administered, followed by a three-alternative forced-choice recognition test, and a rating of previous knowledge. Design and procedure of these tasks was the same for both experimental groups and did not differ from Experiment 4 (see Figure 7.3).

Typicality. After the rating of previous knowledge, a typicality rating was administered, in which participants were presented with all items of the encoding phase in random order. At the beginning of each trial, participants assigned an item to one of six categories (i.e., mammals, birds, fish, fruit, vegetables, and plants) and they then

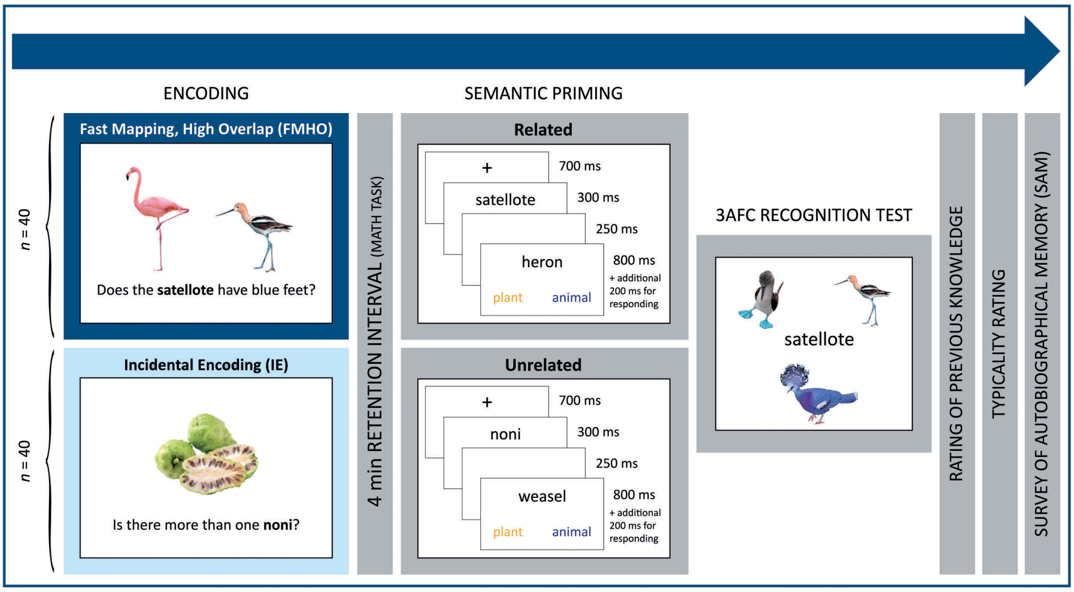

Figure 7.3 Experimental design and procedure of Experiment 5. **Encoding**. After the question had been presented for 2000 ms, either one or two pictures were inserted and presented together with the question for 3500 ms. Response options (*yes*/*no*) were provided after picture(s) and question had disappeared. Feedback was provided after a response had been made. **Semantic Priming**. Each prime appeared four times, twice related to the target, twice unrelated (order counterbalanced). Each target appeared twice, half of the targets first related and then unrelated to the prime and the other half in reverse order (counterbalanced between subjects). **Recognition**. All pictures within one display always belonged to the same higher-level category (i.e., all animals or all plants) and, if possible, also to the same lower-level category (e.g., all birds).

rated how typical the item was for the chosen category on a 6-point Likert scale (1 = *not at all typical*; 6 = *very typical*).

SAM. Lastly, participants were asked to indicate their agreement with items of the SAM, measuring memory traits for episodic, semantic, and spatial memory types, as well as future prospection.

7.3.1.4 Analyses

Analyses were conducted using R (R Core Team, 2016, https://www.r-project.org). The computation of the semantic priming effects, outlier exclusion, and the exclusion of trials due to incongruence of the individual knowledge with the expected knowledge was the same as in Experiment 4. The exclusion of knowledge-incongruent trials resulted in a mean dropout rate of 16.46 % of correct trials per participant. After the exclusion of individual outlier trials with regard to response latencies, the average percentage of trials remaining for the analyses was 80.95 % of correct trials. Three participants

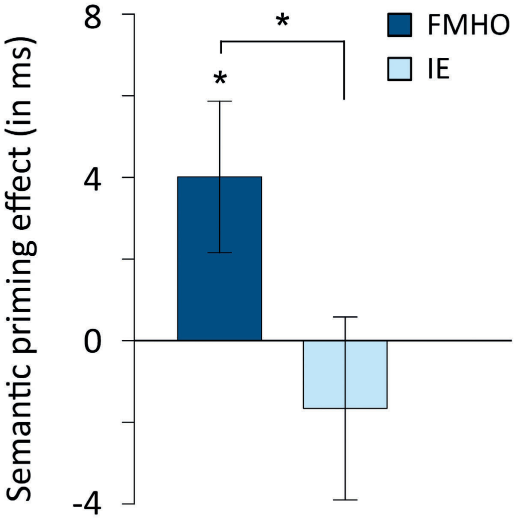

Figure 7.4 Results of the semantic priming task of Experiment 5. The semantic priming effect was calculated by subtracting response times to related targets from response times to unrelated targets. FMHO = fast mapping, high overlap; IE = incidental encoding. Error bars represent the standard error of the mean. $^*p < .05$

were excluded from the semantic priming analyses as they were outliers with regard to the semantic priming effect for their group, two in the FMHO group and one in the IE group, resulting in a final sample size of $N = 77$ ($n_{\text{FMHO}} = 38$, $n_{\text{IE}} = 39$). Recognition accuracy was defined as the proportion of correct responses. Unless noted differently, t tests were one-tailed and significance level was set to $\alpha = .05$. Effect sizes were calculated as in Experiment 4.

7.3.2 Results

Encoding. On average, participants correctly answered $M = 97.50$ % ($SD = 3.03$ %) of the encoding questions, with a marginally significantly better performance in the IE group ($M = 98.14$ %, $SD = 2.44$ %) than in the FMHO group ($M = 96.87$ %, $SD = 3.44$ %), $t(78) = -1.91$, $p = .059$, two-sided.

Semantic Priming. All participants performed above chance in the semantic priming task; see Table 7.3 for mean accuracies). As expected, there was a significant semantic priming effect for the FMHO group, $t(37) = 2.16$, $p = .019$, $d = 0.35$, and no priming effect was found for the IE group, $t < 1$ (see Table 7.3 for mean response times). In line with our hypothesis and the results of Experiment 1, semantic priming effects between the FMHO and the IE group were significantly different, $t(75) = 1.94$, $p = .028$, $d = 0.44$ (see Figure 7.4).

Table 7.3 Mean Response Times (in ms), Semantic Priming Effect (i.e., Response Times Unrelated – Response Times Related), and Accuracies (in % Correct) by Condition

	Discrimination	No discrimination
Response times (in ms)		
Incidental	FMHO	IE
Related	619.05 (50.14)	628.80 (48.79)
Unrelated	623.05 (48.72)	627.14 (50.60)
Semantic priming effect	**4.01 (11.45)**	**-1.66 (13.99)**
Accuracies (% correct)		
Incidental	FMHO	IE
Related	88.11 (32.37)	89.65 (30.47)
Unrelated	88.57 (31.82)	90.16 (29.79)

Note. FMHO = fast mapping, high overlap; IE = incidental encoding. Standard deviations in parentheses.

In order to control for potential confounds that might have provoked the semantic priming effect in the FMHO condition due to the usage of very atypical items, we explored if typicality of the known item could have influenced the semantic priming effect in the FMHO condition. Participants generally rated the known items as highly typical ($M = 5.01$, $SD = 0.70$), which should work against a semantic priming effect according to the results reported by Coutanche and Koch (2017). Typicality was not confounded with prior knowledge as both ratings were not correlated, $r = .03$, $t < 1$, $p = .196$. We calculated the correlation between the individual typicality ratings of the previously known items and the semantic priming effect on the unknown items with which they had been paired (i.e., mean response time of a prime's two presentations followed by an unrelated target minus mean response time of the two presentations followed by a related target) separately for each participant. Across participants, there was no correlation of the individually rated typicality of the known items and the semantic priming effect, r = -.01, $t < 1$, neither in participants who scored low on the SAM semantic scale, r = -.01, $t < 1$, nor in those who scored high, r = .00, $t < 1$.

Recognition. Participants recognized the associations above chance level in both the FMHO group (M = 44.90 %, SD = 8.54 %) and the IE group (M = 45.21 %, SD = 11.58 %), both ps < .001. Recognition accuracy did not differ between groups, $t < 1$.

7.3.3 Discussion

In Experiment 5, we investigated the effect of object discrimination given that learning is incidental and manipulated object discrimination between subjects, comparing semantic priming effects in an FMHO group and an IE group. As expected, there was a significant effect of object discrimination, with a greater semantic priming effect for the FMHO group compared to the IE group, in which no semantic priming effect was found. This replicates the semantic priming effect in the FMHO condition of Experiment 4 and Chapter 5 (Experiment 2). As in Experiment 4, no priming effect occurred in the IE condition, in which no discrimination was required. This is analogous to Chapter 5, Experiment 2, where an immediate priming effect was only found if the demands on object discrimination were high but not if they were low (operationalized by differential feature overlap). In the encoding phase in Experiment 5, participants showed a marginally significant difference in accuracy of their responses to the perceptual questions, with higher accuracies in the IE condition than in the FMHO condition. This could be due to a higher cognitive load in the discrimination condition, which makes sense as an additional picture needs to be processed. However, the semantic priming effect in the FMHO group cannot be attributed to encoding accuracy as encoding accuracy did not correlate with the priming effect in this group, r = -.02, $t < 1$. In addition, there were no differences in encoding accuracies between the FMHO and IE condition in Experiment 4, in which the same pattern of semantic priming effects was observed. In contrast to Coutanche and Koch (2017), Experiment 5 did not reveal any effects of typicality of the known items, irrespective of participants' semantic memory traits. However, our stimulus material did not allow for an a priori manipulation of typicality and we therefore used individual post-hoc ratings of typicality for our analyses.

7.4 General Discussion

The aim of this work was to investigate the role of object discrimination and the intention of learning in FM learning. In two experiments, a semantic priming effect as a measure of semantic integration was found immediately after learning only in an FM condition (Experiments 4 and 5) but not if learning was intentional (Experiment 4) and not in a condition in which learning was incidental but no object discrimination was required (Experiments 4 and 5). Importantly, in the FM condition used here, feature overlap between the unknown and known item was high, which is necessary for semantic integration through FM (Chapter 5, Experiment 2). Therefore, we conclude that the presence of a highly similar known item is a prerequisite for successful rapid semantic integration through FM. The bottom-up idea of the manipulation of object discrimination was based on the assumption that PrC engagement might essentially drive FM learning, which has recently been confirmed in an fMRI experiment (Chapter 6). When the demands on object discrimination were high in this experiment, that is, when items shared many features, the PrC contributed to FM learning more strongly. This is in line with the functional characteristics of the PrC as it is especially involved in the discrimination of highly similar objects (such as the unknown and the known item; e.g., Barense et al., 2007; Mundy et al., 2012). However, by providing a known item that shared many perceptual features with the unknown item, we inevitably provided a semantically related context as well. Thus, the FMHO group might not only have benefitted from higher demands on object discrimination but also from the availability of a known item that was semantically strongly related, which is what Sharon et al. (2011) suggested to be a criterion for successful learning through FM. So far, it is unclear if the semantic or perceptual similarity of the items is the crucial factor that boosts rapid FM learning. However, we can imagine that both is beneficial but for different parts of FM learning. It is conceivable that a more demanding discrimination between the pictures (e.g., operationalized by a higher perceptual overlap) is important in order to initially trigger perirhinal processing, whereas, in a next step, a higher semantic overlap might possibly facilitate integration. A strong semantic relation between the items might also be of more relevance for the integration process than the typicality of the known item in isolation. We assumed that the beneficial effects of atypical known items as reported by Coutanche and Koch (2017) might be based on a similar rationale as the beneficial effects for high feature overlap pairs: Higher demands on a cognitive operation relevant for FM learning might be advantageous. Whereas a high feature overlap between items poses higher demands on the discrimination process, a very atypical known item might increase the demands on the integration into semantic networks. However, we can imagine that the typicality of the known item is not sufficient to determine the demands on semantic integration. Even though the flamingo is an atypical exemplar of the bird category (which should be beneficial), integration of the satellote might be less demanding if presented together with a flamingo since they share many (semantic and perceptual) features. Vice versa, if the satellote had been encoded together with a highly typical sparrow, integration might have been more demanding due to a lower similarity between the items. Hence, we suggest that the semantic relation between the items might foster FM learning rather than the typicality of the known item per se. This remains to be clarified in future experiments.

Apart from the involvement of the PrC in object discrimination, it is also involved in the binding of an item's features (e.g., color, shape, and the label) to a coherent feature conjunction (Barense et al., 2005; Barense et al., 2007; Cowell et al., 2006). If no such intra-item binding mechanisms are triggered and participants are instead instructed to intentionally bind the picture and the label to an association (as in the EE condition), one would typically expect the picture-label association to be created by hippocampal relational binding. Hippocampal binding without additional object discrimination should not lead to rapid semantic integration, which might be reflected in the data of Experiment 4, in which no priming effect was found for the EE condition (see also Atir-Sharon et al., 2015, for supporting fMRI data). It has been unclear if rapid semantic integration is possible by means of an intentional FMHO condition, in which hippocampal relational binding is triggered but perirhinal involvement is also required in order to discriminate between highly similar items. Experiment 4 revealed that if learning is intentional, no rapid semantic integration is possible even if highly similar objects have to be discriminated. It has been shown previously that the ATL (Atir-Sharon et al., 2015, Chapter 6), the PrC, and anterior parts of the hippocampus (Chapter 6) contribute to FM learning. There is evidence that the functional characteristics of the hippocampus differ along its longitudinal axis (Brunec et al., 2018; Brunec et al., 2019; see Poppenk et al., 2013, for a review) and anterior parts of the hippocampus are assumed to belong to an anterior temporal system (together with the PrC and the temporal poles) that is involved in semantic processing and the representation of objects (Ranganath & Ritchey, 2012). According to their framework, especially the posterior hippocampus would be recruited in relational binding of associative contents. Although speculative, it might be possible that such posterior hippocampus activation deactivated the contribution of anterior hippocampal regions and the PrC, which are both involved in FM learning (Chapter 6). Even though there is so far no data on potential inhibitory mechanisms in FM learning, there is evidence for antagonistic activation-deactivation patterns between anterior and posterior regions in the hippocampus in spatial memory tasks (Duarte et al., 2014). However, our behavioral data do not allow for such strong conclusions and the data we reported previously (Chapter 6) cannot speak to that as encoding was always incidental. Irrespective of the underlying neural mechanisms, it can be said that the main effect of learning intention together with a lack of a semantic priming effect for the intFMHO and EE conditions indicate that incidental learning is a prerequisite for successful FM learning, as was suggested by Sharon et al. (2011). One could further raise the concern that instead of object discrimination, the mere presence of the known item or the requirement of an inferential conclusion could have fostered semantic integration. However, based on data from our previous experiment (Chapter 5, Experiment 2), in which rapid semantic integration was observed by means of an FM condition in which feature overlap between the items was low, even though an inferential conclusion was required, we can exclude that the effects were based on the inferential conclusion alone. The mere presence of a known item is also not sufficient to evoke and immediate semantic priming effect, as a known item was also displayed in the low-overlap overlap condition in Chapter 5, in which no priming effect was found. Moreover, it can be excluded that simply answering a perceptual question can account for the results, as this was required in all conditions of both experiments. Thus, if learning is incidental, the presence of a highly similar known item is necessary for rapid semantic integration by means of FM, which might either be driven by the highly demanding object discrimination or the availability of a strongly related semantic context.

7.4.1 Conclusions

Within two experiments, it was shown that incidental learning and object discrimination are essential determinants for successful rapid semantic integration by means of FM. It has not been clear until now if FM encoding needs to be incidental in healthy young adults in whom the hippocampal route is functionally intact. As long as all other criteria for FM learning are fulfilled, an additional learning intention might not have impeded FM learning in healthy adults even though it might additionally trigger a hippocampal-neocortical consolidation process. However, Experiment 4 revealed that there is no rapid semantic integration as soon as encoding is intentional. In line with previous findings, it was again confirmed that the discrimination between the unknown and the known item is necessary for successful FM learning. For future experiments, we recommend that FM encoding should always be incidental and the demands on object discrimination should be high, operationalized by, for example, a high feature overlap between the unknown and the known item.

7.4.2 Acknowledgments

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Chapter 8

General Discussion

Although there is evidence that rapid and direct cortical integration is possible by means of FM (e.g., Himmer et al., 2017; Korenic et al., 2016; Merhav et al., 2014, 2015; Sharon et al., 2011), contradictory findings have been reported (e.g., Greve et al., 2014; Smith et al., 2014; Warren & Duff, 2014; Warren et al., 2016) and it has recently been discussed if rapid learning through FM should be considered a distinct memory phenomenon at all (see Cooper et al., 2018, and the respective commentaries). This thesis aimed to identify moderating factors that could potentially resolve these contradictions. Sharon et al. (2011) suggested three criteria that need to be fulfilled for successful learning through FM: (1) Learning must be incidental, (2) the link between the unknown item and the label needs to be actively discovered by the participant through the recognition and rejection of the known item, and (3) an already existing semantic context must be available, into which the novel associations can be integrated. Atir-Sharon et al. (2015) later added that (4) the new associations must not overlap with previously learned associations in order to prevent catastrohpic interference. However, apart from the fourth criterion (see Merhav et al., 2014), the necessity of these criteria had not been investigated. Therefore, we examined if and under which conditions rapid, direct cortical integration of novel, arbitrary associations is possible by means of FM. In order to do so, we asked which neurocognitive processes might be involved in learning through FM and how they could be fostered.

Previous literature points to the ATL as a structure that might essentially contribute to FM learning. Indeed, Atir-Sharon et al. (2015) found that ATL engagement at encoding is predictive for subsequent recognition memory for associations acquired through FM (but not EE). Moreover, in the study by Sharon et al. (2011), lesions to the ATL differentiated best between patients who benefitted from FM and those who did not. Correspondingly, the ATL has been dubbed a semantic hub, in which modality-specific information converges to a semantically meaningful conceptual unit (Lambon Ralph et al., 2017; Patterson et al., 2007, see also Section 1.1). However, the patient groups in Sharon et al. (2011) did not only differ with regard to residual ATL but also PrC volumes. Due to its neurofunctional characteristics, the PrC seems to be predestined to contribute to FM learning. In the FM paradigm, the pictures of the previously unknown and the previously known item have to be *discriminated* and the unfamiliar label and the unknown item need to be *bound* to associations until they can finally be *incorporated* into cortical networks. The PrC is especially qualified to bind single features to distinct intra-item associations on a highly complex representational level (e.g., Barense et al., 2005; Bussey et al., 2002; Cowell et al., 2006, see also Section 1.1). It further supports the orthogonalization of such intra-item associations or units in order to prevent interference through overlap. Thereby, perirhinal processing is supportive for the discrimination between complex objects. Perirhinal engagement also contributes to the binding of arbitrarily matched items (e.g., a word and a picture that are unrelated) as long as they can be processed as a single unit (see Section 1.4.2.2). Hence, increasing the feature overlap between the unknown and the known item in the FM task might increase the recruitment of the PrC as it requires object discrimination on a highly complex representational level, which would not be possible in more posterior visual regions. This might in return foster the binding of the picture and the label to an intra-item feature conjunction that can then be rapidly incorporated into cortical networks. Therefore, unintended variations in feature overlap between the unknown and the known item across previous studies might possibly have contributed to contradictory findings. Identifying the role of feature overlap in learning by means of FM might have the potential to resolve these contradictions.

As expected, we found that a high feature overlap is a requirement for rapid semantic integration of picture-label associations by means of FM (Chapter 5, Experiment 2). Lexical integration of the labels on an item level, however, was not affected by feature overlap (Chapter 5, Experiment 1). In addition, rapid semantic integration was not found in conditions in which only one picture was presented and in a condition in which feature overlap is high but learning is intentional (Chapter 7, Experiments 4, and 5). The idea that a high feature overlap between the unknown and the known item might be beneficial due to increased PrC involvement was further supported by an fMRI experiment. Structures of an anterior temporal system (i.e., PrC, ATL, anterior hippocampus) were found to contribute to learning through FM and this contribution depends on the feature overlap between the pictures (Chapter 6, Experiment 3).

In Experiments 1, 2, and 3, we compared a condition in which the unknown and the known item shared many features (FMHO) with a condition in which they shared few features (FMLO). Experiment 1 showed that rapid lexical integration of the labels on an item level is generally possible through FM, which is in line with findings by Coutanche and Thompson-Schill (2014). Lexical integration was measured by means of lexical competition effects, with the idea that the unique identification of a real word should take longer if this word has gained an additional lexical neighbor (i.e., words that deviate in only one letter) at encoding. If the label *satellote* has successfully been integrated into lexical networks, response times to identify the real word *satellite* should be slowed as it competes with its novel lexical neighbor. Thus, such competition effects indicate if a new label has been successfully integrated. We found lexical competition in Experiment 1 for labels acquired within an FM paradigm. Contrary to our expectations, this effect was observed across feature overlap conditions and was not different between the FMHO and FMLO condition. However, by using a lexical competition paradigm, we did not capture the *semantic* integration of the complete *picture-label asscoiation* but rather the *lexical* incorporation of the label on an *item level.* The integration of the label is a prerequisite for the integration of the association but can be achieved without perirhinal intra-item binding processes as only one feature (i.e., the label) needs to be integrated. Thus, triggering perirhinal involvement by increasing the demands on object discrimination might not be beneficial for lexical item-level integration.

We addressed this issue in Experiment 2, in which rapid semantic integration of the picture-label associations was assessed by means of semantic priming effects. Participants were first presented with the unknown label as a prime, followed by a real target word that was either semantically related or unrelated to the prime. If the prime had been successfully incorporated into semantic networks, this should have facilitated access to semantically related but not to unrelated targets. Such a semantic priming effect can only occur if the complete picture-label association has been semantically integrated. Rapid semantic integration of the picture-label associations was observed and, in line with our hypotheses, only if feature overlap was high but not if it was low. Moreover, no semantic priming effect was observed in an EE condition, in which encoding is expected to rely on the hippocampus. Unexpectedly, the semantic priming effect of the FMHO condition vanished after 24 hours and turned even in a negative direction, indicating that response times to related targets were slower rather than faster after a longer delay. This might provide further insights into the robustness of associations acquired by means of FM, which will be discussed in Section 8.3.

Although the manipulation of feature overlap was based on the idea that the PrC would be recruited more strongly in the FMHO compared to the FMLO condition, our behavioral data could not speak to that. Making use of fMRI, Experiment 3 confirmed that this manipulation of feature overlap elicited differential PrC involvement at encoding, with stronger PrC activation in the FMHO condition compared to the FMLO condition. Most importantly, PrC recruitment during the encoding in the FMHO condition was a better predictor for subsequent memory than PrC activation during encoding in the FMLO condition. Apart from the PrC, greater subsequent memory effects in the FMHO compared to the FMLO condition were observed especially in the left ATL, the anterior hippocampus bilaterally, the lateral orbitofrontal cortex, the mPFC, and in the right putamen. According to the AT-PM framework suggested by Ranganath and Ritchey (2012, see also Section 1.3), regions within the ATL, the anterior hippocampus, the lateral orbitofrontal regions, and especially the PrC as key component are part of an anterior temporal system. This anterior temporal system is involved in the processing of items or units and their semantic representation and abstraction to categories and concepts. It might be possible that multiple components of the AT system and their interaction support learning by means of FM, each of them to the extent of their specialization. While the PrC might foster the discrimination between feature conjunctions (i.e., between the pictures) and the binding of the label to the feature conjunction of the unknown item, the ATL might support the processing of the newly bound picture-label feature conjunction as a coherent, semantically meaningful whole (for a discussion on differential contributions of a discrimination versus integration process to learning, see Section 8.1). Together with the results of Experiment 2, this experiment provided evidence for the contribution of the PrC as part of an anterior temporal system to rapid semantic integration by means of FM, given that the unknown and the known item share many features.

Although the demands on object discrimination seem to affect rapid cortical integration by means of FM, it still had not been shown if object discrimination in general plays a role, that is, if rapid semantic integration could also be achieved if only the unknown picture is presented. After all, one could argue that in the FMLO condition, the known item might not only have no effect on rapid cortical integration but that it might even be distracting since object discrimination is required but is not helpful in order to boost perirhinal involvement. Thus, it might have been possible that the semantic priming effect in the FMHO condition is not a boost through PrC involvement but rather that the low-overlap known item in the FMLO condition might have inhibited semantic integration, leading to the absence of an effect that might be generally observable. In order to clarify this issue, an incidental encoding (IE) condition was needed, in which only one picture was presented. In addition, Sharon et al. (2011) suggested that learning by means of FM must be incidental. However, this criterion had not yet been tested and by comparing the typical FM condition with an EE condition, the influence of a learning intention is not assessed in isolation but is conflated with many other differences between these paradigms. Within a fully crossed design in Experiment 4, we investigated the effects of a learning intention and object discrimination on rapid semantic integration in healthy young adults. In line with our hypotheses, a semantic priming effect shortly after learning was only observed if the associations had been encoded in an FMHO condition, in which learning was incidental and highly similar objects had to be discriminated. No semantic priming effects were found in an intentional FMHO condition and in the (intentional) EE condition, suggesting that a learning intention prevents from rapid semantic integration through FM. In the (incidental) IE condition, in which no object discrimination was required, there was no significant semantic priming effect but a numerical tendency towards such an effect that might have led to the absence of an interaction of object discrimination and learning intention. In order to rule out potential carry-over effects, which might underlie this tendency, we compared the FMHO condition and the IE condition again in a between-subjects design (Experiment 5). In addition, we took new results by Coutanche and Koch (2017) into account, which suggested that rapid learning by means of FM might be influenced by the typicality of the known item. Analogously to an increase in the demands on a discrimination process, atypical known items might increase the demands on the integration of the novel associations and thus be beneficial in a similar vein. As in Experiment 4, a significant semantic priming effect was found for the FMHO group but not for the IE group. Contrary to the findings reported by Coutanche and Koch (2017), the typicality of the known item did not affect these results. We explain this by the notion that the typicality of the known item in isolation might play a minor role compared to the semantic relation between the unknown and the known item.

8.1 Fast Mapping From a Representational Perspective

From a representational perspective, one would assume that each of the congitive operations required in order to solve the FM encoding task (e.g., discriminating between pictures, binding the picture to the label, semantically integrating the association) are supported by regions that are qualified to process the respective representational content. Whereas more posterior regions along the ventral visual stream are capable of processing single, elemental features, the identification of complex feature conjunctions would require perirhinal processing. The discrimination between two complex pictures in the FM task would require their perceptual and conceptual orthogonalization. Just as the hippocampus uniquely codes complete episodes (i.e., items within their contexts) on distinct, pattern-separated memory traces, the PrC is qualified to orthogonalize highly overlapping information on an item level (Burke et al., 2011; Kent et al., 2016). In the FM task, the discrimination between the unknown and the known item by means of perirhinal pattern separation might enable their unique identification. The participant can then infer that the label must belong to the unknown item, thereby linking the label to the picture. As the PrC is also qualified to bind distinct elements to units, it is reasonable to assume that by means of FM, the PrC might not only support the discrimination between pictures (through the binding of visual features to intra-item associations) but also the binding of the arbitrarily matched label and the picture of the unknown item to a coherent unit. Therefore, perirhinal contribution to memory in an FMHO condition, which was observed in Experiment 3, might not only be an expression of object discrimination but might, in a second step, also reflect its contribution to the binding of the picture and the label to a unitized intra-item association. Besides discrimination and binding, it is unclear what drives the final storage of the newly bound intra-item associations into cortical networks. Considering the functional characteristics of the ATL, it is conceivable that ATL engagement supports the incorporation of the new intra-item associations into semantic memory networks as abstracted, gist-like, conceptual representations. ATL-mediated integration processes might possibly be fostered by the previous perirhinal binding of inter-item associations to units. Additionally, the presence of a not only perceptually but also semantically similar known item in the FMHO condition might also support ATL involvement. This might have smoothed the way to the incorporation of the units into semantic memory networks in the FMHO condition to a greater extent than in the FMLO condition. One could argue that the absence of a correlation between recognition accuracy and ATL volumes in older adults, as reported by Greve et al. (2014), contradicts the contribution of the ATL to learning. However, the absence of such a correlation in their study could be attributable to the assumption that their item pairs might not have triggered the anterior temporal system (including PrC and ATL) sufficiently as feature overlap might not have been high enough (judged from the provided example item pairs). Therefore, neither PrC nor ATL processing might have been recruited. In addition, Greve et al. (2014) did not report correlations between memory outcome and volumes of other anterior temporal or anterior medial temporal structures that might be involved in learning through FM, such as the PrC.

I suggest that increasing the task demands on an early process in the FM task (e.g., perirhinal binding of visual features to distinct units, i.e., pictures) might trigger structures relevant for successful binding of items to units (e.g., perirhinal binding of the picture and the label) and structures that might foster the integration of the novel associations into semantic memory networks (e.g., the ATL). This might possibly be beneficial in order to achieve successful rapid semantic integration through FM. With regard to the representational view, triggering processes other than those of anterior temporal and anterior medial temporal structures, such as (especially posterior) hippocampal binding of items and their contexts or processing in early visual areas, might not be beneficial for rapid learning through FM as they would operate on inappropriate representational levels. In addition, hippocampal inter-item binding processes would likely trigger the storage of the picture and the label as inter-item association, which would be cortically integrated by means of slow hippocampal-neocortical consolidation. Triggering hippocampal binding might be achieved by instructing participants to explicitly remember the (inter-item) association between the picture and the label. This fits with the results of Experiments 2 and 4, in which no semantic priming effects were found immediately after encoding by means of EE or an intentional FMHO condition.

8.2 The Contribution of the Hippocampus

In the earlier literature on FM in adults, a strong focus was set on the question if the hippocampus can be bypassed in learning by means of FM. The findings by Sharon et al. (2011) indicate that hippocampus-independent learning is possible as the amnesic patients with predominantly hippocampal lesions showed normal recognition accuracy if associations had been encoded through FM. However, the discussion of hippocampus-independent learning by means of FM holds two important issues with the potential to raise misunderstandings: 1) The hippocampus might have been defined too broadly as its representational gradient along its longitudinal axis has so far been neglected in the FM literature and 2) the question if FM learning is hippocampus-independent might not be equally appropriate to ask for all samples.

8.2.1 Longitudinal Axis of the Hippocampus

Apart from anterior temporal structures and the PrC, Experiment 3 of this thesis revealed the contribution of hippocampal processing to FM learning and the predictive value of hippocampal involvement at encoding was greater if feature overlap was high than if it was low. Hippocampal contribution to learning by means of FM has also been reported previously in a sample of healthy young adults similar to ours (Atir-Sharon et al., 2015). Based on these findings, it might be even more reasonable to assume that the hippocampus is involved in learning by means of FM than that it is not, as long as it is functionally intact. Interestingly, in Experiment 3 we found hippocampal involvement selectively in anterior portions of the hippocampus. There is evidence that different regions along the hippocampal longitudinal axis are involved in different processes (Section 1.3). The anterior portion of the hippocampus is assumed to belong to an anterior temporal system (Ranganath & Ritchey, 2012) and has been more strongly associated with semantic processing and memory for items and their abstraction to generalized concepts (Poppenk et al., 2008; see Poppenk et al., 2013, for a review). The processing of relational information, in contrast, has been ascribed to the posterior hippocampus (Wang & Giovanello, 2016). Brunec et al. (2018) posit that there is a representational gradient from coarse- to fine-grained representations from anterior to posterior hippocampal regions, at least for spatiotemporal processing. Based on the functional characteristics of the anterior hippocampus and the respective AT system, it seems reasonable that especially the anterior hippocampus supports rapid cortical integration through FM. Carefully speaking, it might be possible that greater demands on perirhinal processing in the FM task might not only trigger involvement of the ATL but also other components of the AT system, such as the anterior hippocampus. Once the label and the picture are bound to an intra-item assciation, the engagement of several components of this system might be supportive for rapid storage in different ways. Ranganath and Ritchey (2012) propose that the anterior portion of the hippocampus essentially contributes to sharpening processes on an item level, that is, several mallard ducks that slightly look different are merged to one gist-like, sharpened concept of *mallard duck*. Although speculative, it might be possible that in a similar vein, the anterior hippocampus could be preferably involved in any other cognitive operations on an item-level (rather than a level of relational representations of items and their contextual features, such as the posterior hippocampus).

Critically, previous FM literature has only been concerned with hippocampal involvement in general, without differentiating between subregions along its longitudinal axis. Atir-Sharon et al. (2015) found that in the hippocampus, a trained subsequent memory classifier (i.e., a model of the relationship of multi-voxel encoding acvitity patterns and memory outcome) was predictive for both learning by means of FM and EE. However, they used a standard brain atlas template of the complete hippocampus in order to assess hippocampal classification accuracy. It would be interesting to know if anterior and posterior hippocampal contribution to learning differ between the FM and EE condition. Greve et al. (2014) reported a positive relationship between hippocampal volume and recognition accuracy irrespective of the encoding paradigm but volumes were not determined separately for anterior and posterior parts of the hippocampus. In that way, a differential correlation between hippocampal subregions and recognition accuracy might have been masked, such that anterior hippocampal volume might have been better related to FM learning whereas posterior hippocampal volume might have correlated more strongly with learning by means of EE. Furthermore, reanalyses of lesion studies that take into account differential morphology along the hippocampal longitudinal axis would be informative. Despite the evidence by Sharon et al. (2011) and Merhav et al. (2014) that rapid learning of arbitrary associations by means of FM is possible in patients with severe lesions to the hippocampus, the assumption that they cannot functionally rely on their hippocampus has been implied from severe damage to the hippocampus in general. However, although they all exhibit severe damage to the hippocampus, at least some residual hippocampal volume is spared. Localizing such residual volume in re-analyses would be supportive for our findings if patients who benefitted from FM in Sharon et al. (2011) and those who showed catastrophic interference in Merhav et al. (2014) had lesions especially to the posterior hippocampus with spared matter in the anterior hippocampus, which would be a prerequisite to functionally rely on particularly anterior parts.

8.2.2 Redefining ”Bypassing the Hippocampus”

Even if individuals who cannot functionally rely on their (both anterior and posterior) hippocampus benefitted from FM learning, this would not allow for the reverse conclusion that FM must necessarily always be hippocampus-independent. After all, Experiment 3 of this thesis revealed anterior parts of the hippocampus to be involved in successful FM learning in healthy young adults. However, the reverse conclusion that its involvement is necessarily always required is also not valid. Before interpreting the necessity of hippocampal involvement to FM learning, the function of the anterior hippocampal involvement (which we found in Experiment 3) needs to be identified. Although the present data only allow for speculations, one could argue from a representational perspective that the most anterior parts of the hippocampus might potentially be involved in pattern separation on an item level. This does not contradict Poppenk et al. (2013) who suggested that the anterior hippocampus has a bias for pattern completion whereas the posterior hippocampus is predominantly involved in pattern separation. They consistently referred to separation and completion of complete episodes and thus, they argued on a constant representational level. It could still be possible that the anterior hippocampus is involved in pattern separation but on a different representational level that is closer to intra- compared to inter-item representations. In contrast to perirhinal pattern separation, anterior hippocampal pattern separation in learning through FM might go beyond on-line perceptual object discrimination and also keep items at least temporarily orthogonalized during storage. This would resemble hippocampal pattern separation of item-context or inter-item associations but on a more generalized item level. Very carefully speaking, it might be possible that such anterior hippocampal pattern separation might at least partly reduce interference in FM. Although speculative, this might potentially be an approach to explain the results on interference effects reported by Merhav et al. (2014). In young and healthy adults, who can rely on anterior hippocampal processing (and possibly item-level pattern separation), catastrophic interference only occured if the association of the picture A and the label C was studied 22 hours after studying the picture A together with the label B. Given that the anterior hippocampus might be involved in the initial acquisition (and pattern separation) of the new associations at least for a short period of time, anterior hippocampal pattern separation might have prevented interference that is induced shortly after AB encoding (since AB and AC might have been processed simultaneously in the anterior hippocampus). As a consequence, AB and AC pairs that had been presented shortly after one another (and thus, experienced pattern separation) might be less susceptible to interference. If there was no need to keep simultaneously processed associations apart (i.e., if the AC pair had been encoded after a 22-hours delay), catastrophic interference might occur due to the lack of an at least temporary item-level pattern-separation process. If (anterior) hippocampal functioning is not intact, this might lead to catastrophic interference irrespective of the time of interference induction, as in the patients with severe hippocampal lesions reported by Merhav et al. (2014). If the anterior hippocampus has such a temporary item-level pattern-separation function, hippocampal processing might be helpful if the associations are exposed to interference but not necessarily required for successful learning through FM. It needs to be emphasized again that this is only a very vague post-hoc explanation of existing data and it would need extensive research in order to confirm this thought. Volumetric data of the healthy elderly in Merhav et al. (2014) would be helpful to shed more light on this assumption. As long as the role of the (anterior) hippocampus is not finally identified, I would suggest not to emphasize hippocampus independence in future experiments but the phenomenon should rather be reframed as ”rapid cortical integration by means of FM independent of the posterior hippocampus and with the possibility to also bypass anterior hippocampal processing”.

8.3 Stability of Associations Acquired by Means of Fast Mapping

The characteristics of memory representations acquired by means of FM are yet unclear. As outlined above, the novel associations seem to be susceptible to interference under some conditions, possibly if the hippocampus is completely bypassed. However, even without the induction of interference, it is not yet clear how the stability and strength of the new memories develop over time. It needs to be further clarified to what extent the memories acquired by means of FM resemble hippocampally-neocortically consolidated declarative memory representations.

It is generally difficult to draw conclusions on the stability of associations acquired through FM from the current literature. Study-test delays vary greatly across studies, regarding the duration of the delay (from no delay to a one-week delay) and the nature of the filler task (e.g, vocabulary tests, conversation, math tasks, intelligence tests). In some studies, the picture-label associations were recalled twice between the encoding and recognition phase (Warren & Duff, 2014; Warren et al., 2016), and thus, it cannot be disentangled to what extent recognition accuracy reflects learning through FM or is rather based on the reactivation through recall prior to the recognition test. This problem also occurs in longitudinal designs as they require multiple testing of the same associations. In previous FM literature, in which the novel associations were typically tested once immediately after encoding and once after a longer delay, it was often emphasized that memories acquired by means of FM remain robust over time. Sharon et al. (2011) considered the memory representations as stable since both the healthy participants and the amnesic patients with severe lesions to the hippocampus performed above chance level even one week after encoding. Moreover, the associations they remembered after a week were the same as the ones they remembered at the immediate test. Himmer et al. (2017) found that associations encoded through FM are even more stable than associations encoded through EE over a 24-hours delay as they were not susceptible to increased interfering information during a period of wakefulness compared to sleep.[1] This can be explained through fast integration of associations acquired through FM, as there is less opportunity for exposure to interfering information than it would be during a slow consolidation process. Hence, the protective effect of sleep is not necessary for the retention of associations acquired through FM. In line with that, Merhav et al. (2015) found in an fMRI experiment that associations which have recently been acquired through FM evoked the same activation pattern as associations learned the day before. In an EE condition, however, they observed increased widespread neocortical activation for remotely compared to recently encoded associations (see also Figure 2.2). This indicates rapid cortical integration by means of FM and underscores the findings by Himmer et al. (2017).

It is important to note that even if recognition accuracy for associations acquired through FM seems to be as stable as for associations acquired through EE, at least those behavioral data that are collected within a period of 24 hours in healthy young adults are likely based on different retrieval mechanisms (i.e., cortical retrieval for associations acquired through FM; initially hippocampal but later cortical retrieval for associations acquired through EE), which makes their comparison even more complicated. Using implicit tests, however, increases the likelihood that non-hippocampal

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[1] Please note that by interference in this context I refer to random interfering information during wakefulness that might simply aggravate consolidation. This is not to be confused with the explicit induction of interference in an AB-AC paradigm in which highly overlapping, contradictory information is presented. In the latter case, one would also expect interference effects after learning by means of FM (see Merhav et al., 2014, and Section 8.2.2).

retrieval is equally addressed in all encoding conditions. In order to assess stability of associations acquired by means of FMHO, we conducted a priming phase twice in Experiment 2, once four minutes after encoding and again after one day. Although we found above-chance recognition performance on Day 2, the semantic priming effect for associations acquired by means of FMHO on Day 1 turned into a negative direction. We suggested that a center-surround approach might be able to explain this, that is, the newly acquired memories might possibly not be forgotten (as in that case, no priming effect would have occurred) but they might rather have become more difficult to access. Thus, in order to retrieve the novel associations, surrounding, closely related nods in the semantic network might be inhibited. This would lead to slowed responses to related compared to unrelated target items. This is not contradictory to the findings by Coutanche and Thompson-Schill (2014), who report lexical competition effects even after 24 hours, as they only captured item-level lexical integration of the labels. We propose that associations acquired by means of FM might remain stable, in a sense that, once integrated, they can be successfully recognized even up to one week after learning. However, semantic access to the picture-label combination might still become weakened, that is, accessing the semantic meaning of the label might take more time and effort. It has been discussed in previous literature that associations acquired through FM might be in a ”hypothetical status” in order to allow for modifications after future exposures, such that associations remain integrated only until participants are exposed to contradictory information (e.g., Merhav et al., 2014, 2015). In such a hypothetical status, memories might be more susceptible to interference and if conflicting information is encountered, the associations can be adapted. This is compatible with our idea that, although novel associations are successfully integrated, they might be more difficult to access and their representations might be weaker than associations acquired through EE. However, the exact development of associations acquired by means of FM over time needs further investigation.

8.4 Other Ways to Rapid Semantic Integration

Theories assuming hippocampal-neocortical system-level consolidation imply that semantic memory predominantly is a result of the semanticization of episodic memory representations (e.g., McClelland et al., 1995; Nadel & Moscovitch, 1997; Squire & Alvarez, 1995). Therefore, the semantic integration of new memories into cortical networks is a slow and time-consuming process. A different approach is taken by Tulving's (1995) SPI theory, which assumes that new memories are sequentially passed from a perceptual to a semantic and finally to an episodic system and thus, the acquisition of episodic memories depends on the semantic memory system. This model needed an addendum in order to account for evidence for episodic but not semantic memory in patients with semantic dementia, which suggests parallel instead of sequential routes to semantic and episodic memory (Graham et al., 2000). Such an extension of the SPI theory weakens the boundaries to the hippocampal-neocortical consolidation theories named above, which assume that semantic memories are created by the abstraction of repeatedly experienced episodes. These theories, vice versa, experienced problems explaining how patients with hippocampal lesions can still acquire semantic knowledge even though they cannot rely on hippocampal-neocortical consolidation. Some argued that this is possible by means of sparse coding through some residual episodic memory (Squire & Zola, 1998). Others, like McClelland (2013), extended their framework by a route to rapid cortical integration if the new memories can be embedded into prior knowledge structures. Although different theories are approaching each other by addenda suggesting exceptions to the theories, they all would struggle with explanations for rapid and direct cortical integration of associations by means of FM versus EE. If semantic memories are always created through episodic memory, FM would constitute an exception even to the addendum by McClelland (2013), suggesting accelerated semantic integration if new information can be related to prior knowledge. This model does not explain how a new label that is unrelated to prior knowledge on the two pictures in the FM task can be rapidly integrated. In contrast, if all new memories are initially processed in a semantic store (as in the SPI model), it is unclear why there are no effects of rapid semantic integration in the EE condition.

One could speculate that memory formation is generally possible via both routes but with a preference for one or the other depending on the task. For example, triggering hippocampal inter-item binding processes might support the slow consolidation of novel items within their contexts whereas triggering the perirhinal binding of features to intra-item associations might access direct routes to semantic memory. Ultimately, both frameworks share the view that either way is possible under certain (exceptional) conditions. As outlined in Section 1.4, rapid integration into cortical networks is not a phenomenon unique to the FM paradigm. One exception to hippocampal-neocortical consolidation theories is that time-consuming consolidation processes can be bypassed if the to-be-integrated information is congruent with an already existing schema (Section 1.4.2.1) or if the task requires to merge two items to a unit (Section 1.4.2.2).

8.4.1 Schema-Based Learning

By means of an extension to the CLS theory (McClelland et al., 1995), McClelland (2013) showed that the pace of learning in the neocortical system strongly depends on the availability of prior knowledge, with faster learning rates for information congruent with prior knowledge structures or schemas and slower learning for incongruent information. According to the SLIMM model (Van Kesteren et al., 2012), new information that is congruent with a pre-existing schema can directly and rapidly be embedded into this schema. Their co-activation through conceptual information to which they are both related elicits "resonance" that evokes an mPFC-mediated creation of new, direct links between the schema and the new information. Thereby, the hippocampal route is assumed to be bypassed or even suppressed (Van Kesteren et al., 2012; but see e.g., McKenzie et al., 2014; Preston & Eichenbaum, 2013, see also Section 1.4.2.1). For example, a previously unknown plastic duck can be directly integrated into the neocorctical system if it is presented in the context of a bathroom as they are both related to a rubber duck bath toy. One could argue that our data might also have been driven by schema-based learning. It is indeed plausible to assume that a bird schema, which is activated by a flamingo, might provide an environment into which the satellote can be integrated more easily than if the satellote was encoded together with a guinea pig. Therefore, it can be assumed that the schema provided in the FMHO condition is more congruent with the unknown item compared to the schema provided in the FMLO condition. Correspondingly, Experiment 3 revealed greater contribution of the mPFC to learning in the FMHO condition compared to the FMLO condition. However, schema-based learning alone cannot explain similar patterns within the PrC, the anterior hippocampus, and the ATL. Most importantly, schema-based learning would only be able to account for the integration of the picture on an item level, such that the picture of the satellote would be better remembered if it had been encoded next to a flamingo. However, the schema approach does not provide an explanation for the binding of the picture and the label. In our experiments, the labels are previously unrelated to the pictures and thus per definition not congruent with the schema of any of the known items. According to the SLIMM model, the encoding of schema-congruent information is also selective, which means that distorting, arbitrary information (e.g., a ringing mobile phone in the bathroom) is inhibited in favor of the schema-congruent information (e.g., the plastic duck in the bathroom). One could draw the analogy to the labels in our experiment, suggesting that in the case of a schema-congruent known item (i.e., in the FMHO condition), the label would even be inhibited in order to facilitate the integration of the schema-congruent picture of the unknown item. Hence, schema-based learning might be additionally beneficial but cannot explain the integration of novel, arbitrary picture-label associations. Therefore, our data support the assumption that perirhinal binding rather than mPFC-mediated schema learning might be essential for the creation of the intra-item association of the picture and the label. Nevertheless, if such a binding process has been successful, as in the FMHO condition, this new unit might benefit from the presence of a schema-congruent known item.

8.4.2 Unitization

Apart from rapid learning that is supported by prior knowledge, it has been shown that different paradigms allow for the transformation from inter-item to intra-item associations, or, in other words, unitization. In typical unitization paradigms, the task requires to merge single items to a unit and/or the single items are related in some way. For instance, items can be unitized by a semantic relation (Tibon et al., 2014), they can be related perceptually by displaying items moving to or interacting with each other (e.g., D'Angelo, Kacollja, Rabin, Rosenbaum, & Ryan, 2015; Ryan, Moses, Barense, & Rosenbaum, 2013), or by creating newly defined compounds out of single unrelated words (e.g., Bader et al., 2010; Bader et al., 2014; Haskins et al., 2008). In the FM paradigm, in contrast, participants need to actively and implicitly create the associations themselves without any instruction to unitize the picture and the label. Morover, both the picture and the label are previously unknown and not related to each other. There is neurofunctional evidence that unitization relies on perirhinal processing (Haskins et al., 2008; Quamme et al., 2007), which is potentially necessary in order to transform inter-item to intra-item associations. In the FM paradigm, perirhinal binding processes seem to transform inter-item to intra-item associations in a similar vein. As outlined in Section 1.4.2.2, it needs to be differentiated between the unitization paradigm and the unitization process. I would propose that learning by means of FM also underlies a unitization process, even though unitization is not achieved by means of a classical unitization paradigm but through the FM paradigm that follows the criteria suggested by Sharon et al. (2011).

Limitations and Future Directions

Determinants of Learning by Means of Fast Mapping

It has already been shown that the absence of interfering information is a requirement for learning by means of FM (Merhav et al., 2014). The experiments reported in this thesis revealed that learning must also be incidental, that the presence of a previously known item is required, and that this known item should share many features with the unknown item. Experiments 2 and 3 showed that in order to rapidly integrate novel, arbitrary associations into semantic memory networks, feature overlap needs to be high. We inititally set out to manipulate feature overlap with regard to the visual commonalities of the unknown and the known item. However, we cannot finally say if it is an increase in perceptual or semantic overlap that drives rapid learning by means of FM as the stimulus material we used conflates both kinds of overlap. Although it would certainly be informative, disentangling perceptual and semantic overlap might not even be necessary as the intention behind the feature overlap manipulation was to increase the demands on perirhinal processing. This might be achieved no matter if the overlap was semantic or perceptual as the PrC represents a combination of both (Martin et al., 2018). While both semantic and perceptual overlap might make the *discrimination* process more demanding, an unique benefit of a high semantic overlap might be a facilitated *integration* process due to the presence of a semantically closely related known item. An eye-tracking experiment would be one possibility to shed light on the effects of (visual and/or semantic) object discrimination versus (semantic) integration. If the discrimination between the pictures has an incremental contribution to learning by means of FM, the extent to which participants' eye-movements switch between the pictures of the known and the unknown item should be predictive for subsequent memory. This is particularly promising as a recently published eye-tracking study revealed that the saccades in a task in which highly similar pictures needed to be discriminated are predictive for subsequent memory (Zhou et al., 2018). Interestingly, fMRI evidence of an experiment using the same task related this subsequent memory effect to the contribution of the PrC to learning if highly similar pictures needed to be discriminated at encoding (Chen et al., 2019).

Together with previous experiments such as Sharon et al. (2011), the data reported in this thesis strongly suggest that learning by means of FM requires that a perirhinal pathway to semantic integration is functionally available and triggered by, for example, increasing the demands on perirhinal processing. If our interpretation of the results of Experiment 4 (i.e., no rapid semantic integration through FM in intentional learning conditions) holds true, this route should also be the only one that is triggered. If (posterior) hippocampal inter-item binding processes are provoked by the instruction to explicitly bind the previously unrelated picture and the label, (posterior) hippocampal binding might possibly have a dominating role (see also Duarte et al., 2014, for an anterior/posterior antagonsim in the hippocampus). However, this assumption needs further testing as our behavioral data do not allow for conclusions on the underlying neurofunctional processes. One option could be to ask patients with damage to the posterior hippocampus to encode associations within an FMHO condition and an intentional FMHO condition. If patients who cannot rely on (posterior) hippocampal processing show rapid cortical integration of novel associations despite a learning intention (in contrast to our healthy participants in Experiment 4), this might indicate that (posterior) hippocampal binding might indeed have led to an absence of rapid semantic integration in the intentional FMHO condition in healthy young adults in Experiment 4.

Characteristics of Associations Acquired by Means of Fast Mapping

As outlined in Section 1.4, semantic memory representations of single conceptual units are assumed to be rigid, whereas hippocampally represented arbitrary inter-item associations are more elemental in nature, thereby enabling flexible recall (see e.g., Giovanello et al., 2009). Memory representations would be considered flexible if, for example, intact associations (e.g., *duck – bike*) can be remembered equally well or are based on the same neural mechanisms as reversed associations (e.g., *bike – duck*). If features are merged to a single intra-item association, however, they are processed as a unit in its exact configuration. Given that FM learning is based on a similar process than that underlying learning within unitization paradigms, one could propose that associations acquired through FM (i.e., “unitized” associations) are less flexible than associations acquired by means of EE (i.e., “non-unitized” associations; Bader et al., 2014; see also Henke, 2010). However, this needs further clarification, for example by studies investigating how rigidly the label is tied to exactly the picture of an item presented in the encoding phase.

There is evidence that associations acquired by means of FM are more susceptible to highly overlapping, explicitly induced interference than if they were encoded by means of EE (Merhav et al., 2014). At the same time, associations encoded through FM experience less forgetting as they are assumed to be immediately integrated and thus, less prone to random interference during wakefulness compared to sleep (Himmer et al., 2017; Merhav et al., 2015). Although I speculated on possible functions of the involvement of the anterior hippocampus in learning by means of FM, such as the prevention of interference, its contribution still needs to be investigated. One way to do so would be to re-analyze previous findings and relate them not only to the general residual volume of the hippocampus but to the anterior and posterior portions separately. In addition, an experiment similar to Merhav et al. (2014), potentially with a more fine-grained time course of interference induction and highly overlapping pictures in the FM encoding phase might clarify if the anterior hippocampus indeed has a temporary pattern-separating role in FM learning.

Conclusion

It has been extensively discussed if the FM ”phenomenon exists” (see Cooper et al., 2018, and the respective commentaries). Sharon et al. (2011) suggested that rapid learning through FM is possible if (1) learning is incidental, (2) the link between the unknown and the known item must be actively discovered by rejecting the previously known item, and (3) the picture-label associations must be learned in the context of previously known item, activating semantic knowledge structures into which the new information can be integrated. Based on Merhav et al. (2014), Atir-Sharon et al. (2015) added that (4) the new associations must not interfere with previous information. This thesis confirmed the requirement of incidental learning and subsumed the second and third criteria under the requirement of the presence of a previously known item. Our data further indicate that this known item must share many features with the unknown item. If all of these criteria are fulfilled within one paradigm, rapid and direct cortical integration should be found. It is important to mention that, to my understanding, the aim of research on FM learning is not to show that learning by means of FM is a completely new mechanism that is distinct from any other learning mechanism. I suggest that it should be considered what it is, that is, an encoding paradigm by which rapid cortical integration of novel, arbitrary associations is possible. With regard to the mechanisms underlying learning within this paradigm, the data point to the relevance of a unitization process that is triggered through increased involvement of the PrC. The potential role of anterior hippocampal involvement in pattern separation, the role of the ATL in semantic integration, and the role of potentially mPFC-mediated schema-based learning are to be investigated within future experiments.

I conclude with the notion that FM is an encoding paradigm that enables rapid cortical integration of novel, arbitrary associations, which challenges traditional theories that assume hippocampal-neocortical consolidation. Previous contradictions in the FM literatrue can largely be explained by choosing unfavorable samples (e.g., including patients with lesions to structures involved in FM learning) or by a too low or uncontrolled feature overlap. Future memory research might make use of the findings on FM learning in order to gain insights on more general questions of cognitive neuroscience of memory, such as the existence and characteristics of different routes to semantic memory formation, which is fundamental to our understanding of human memory.

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Appendix

Table A1 *Newly Created Lexical Neighbors to German Hermit Words, Used as Labels in Experiment 1 in Order to Evoke Lexical Competition*

Neighbor	Hermit	Translation	Neighbor	Hermit	Translation
Akroyat	Akrobat	acrobat	*Matralle*	Matratze	mattress
Albur	Album	album	*Menka*	Mensa	canteen
Borbe	Bombe	bomb	*Minuster*	Minister	minister
Brude	Bruder	brother	*Mored*	Moped	moped
Dontor	Doktor	doctor	*Murtel*	Murmel	marble
Eigel	Eigelb	egg yolk	*Muspel*	Muskel	muscle
Fabrek	Fabrik	factory	*Orfel*	Orgel	pipe organ
Famolie	Familie	family	*Palist*	Palast	palace
Flemme	Flamme	flame	*Pfalle*	Pfanne	pan
Förser	Förster	forester	*Pilor*	Pilot	pilot
Futo	Foto	photo	*Pistoke*	Pistole	pistol
Galanie	Galaxie	galaxy	*Plakal*	Plakat	placard
Globuk	Globus	globus	*Satellot*	Satellit	satellite
Gürmel	Gürtel	belt	*Schirk*	Schirm	umbrella
Honil	Honig	honey	*Schneel*	Schnee	snow
Kaisek	Kaiser	emperor	*Stiemel*	Stiefel	boot
Kalunder	Kalender	calendar	*Taifur*	Taifun	typhoon
Keramuk	Keramik	ceramic	*Torado*	Tornado	tornado
Kleiser	Kleister	paste	*Trator*	Traktor	tractor
Knoske	Knospe	bud	*Trelor*	Tresor	safe
Kondimor	Konditor	confectioner	*Trochel*	Trommel	drum
Künsler	Künstler	artist	*Tunnek*	Tunnel	tunnel
Lössel	Löffel	spoon	*Tursine*	Turbine	turbine
Magalin	Magazin	magazine	*Vulka*	Vulkan	volcano

Note. Participants were explicitly instructed to categorize persons or professions as *natural.* In the encoding phase, one third of the hermit neighbors were presented as labels in the FMHO (fast mapping, high overlap) condition, one third in the FMLO (fast mapping, low overlap) condition, and one third was not encoded, as in the lexical competition task, the respective hermit words served as non-neighbor hermits (i.e., hermit words which did not obtain a new neighbor at encoding).