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Neurocognitive Mechanisms underlying Incidental Associative Learning

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Summary / Zusammenfassung

Summary (English)

The human being has an impressive capacity to identify and integrate different perceptual pieces of information into coherent contextual representation, even under incidental situations. The human episodic memory system can be viewed as a network of associations between multimodal environmental features and episodic events that continuously processes new incoming information. Within this dissertation project, I aimed to investigate incidental memory processing and related neurocognitive mechanisms under both uni- and crossmodal perceptual associative learning conditions. The aim of the presented studies was to extend previous knowledge on the human episodic memory system.

To date, core functions of the episodic memory are frequently attributed to the hippocampus, which operates independently from the involvement of awareness. Contrary to the traditional awareness-based theory, modern theories challenged the assumption of a direct link between consciousness and hippocampus-dependent learning. Accordingly, memory systems should not be systematized by consciousness but on the basis of functional processing. This topic has been directly addressed within my first study on implicit sequence learning. Furthermore, perception is multimodal and operates in terms of contextual information provided by multiple sensory modalities. While the essential involvement of the hippocampus in episodic memory formation has been frequently confirmed, it is also known that multisensory integration is not restricted to the involvement of a single region, but requires the recruitment of a network of cortical regions. In particular, some regions have been consistently related to high-level multimodal processing, such as the ventral part of the posterior parietal cortex, including the angular gyrus. Recent theories highlighted that the angular gyrus is not only involved in processes of attention or perceptual decision-making but also serves functions related to the integration and representation of multimodal information in relational memory. From this perspective, the hippocampus and the angular gyrus seem to contribute to memory processing of perceptually rich representations even under incidental learning conditions. Incidental learning paradigms are well suited to investigate neural correlates of implicit and explicit associative memory as they reflected more real-life memory performances. Based on the principle of ecological validity, learning from multiple senses is indeed more effective than unimodal learning. Hence, on the behavioral level, in fMRI study 1 and study 3, I examine the effect of the incidental learning process and related acquired implicit unimodal and crossmodal perceptual memory, while study 2 addressed whether crossmodal perceptual representations could be incidentally learned but explicitly recollected. Building up on prior imaging findings, in the fMRI studies 1 and 2, I investigated the neural correlates underlying incidental learning using unimodal and crossmodal perceptual associations.

Based on a prominent implicit associative learning paradigm, the aim of study 1 was to test whether the nature of learned associations rather than explicit instructions determine the specific involvement of the hippocampus. Within this study, I was able to relate bilateral hippocampal activation exclusively to purely perceptual associations, which is consistent with other imaging results indicating hippocampal engagement in implicit memory processes of perceptual associations. The presented projects not only provided additional evidence for a functional involvement of the hippocampus in the organization of relational (episodic) memory. The presented findings further support the assumption that memory systems should not be specified in terms of consciousness but by the characteristics of the learned material. Using a traditional paired-associate learning paradigm, the study 2 focuses on neural integration processes of semantically-incongruent, novel audiovisual associations under incidental learning conditions. Across the literature, it has been shown that different cognitive functions are attributed to different subregions of the posterior parietal lobe. However, the precise difference among ventral and dorsal parietal regions in associative memory processing of multimodal representations has yet to be determined. Using one experimental paradigm, I showed that the angular gyrus was specifically engaged when relational content had to be integrated, whereas a dorsal region of the parietal lobe was specifically activated when the demand for attentional control processes increased.

In conclusion, I propose that both the hippocampus and the angular gyrus have an important functional role during relational memory processing of perceptual associations. The presented studies provided evidence for a critical functional role for the hippocampus in both implicit and explicit memory processing of episodic representations. Further, I extended previous knowledge regarding the functional role of the angular gyrus in episodic memory processing of multimodal information. Taken together, the presented findings demonstrate that both regions contribute functionally to memory processing of pure perceptual associations, even under incidental learning conditions.

Zusammenfassung (German)

Das episodische Gedächtnis kann als ein Netzwerk von Assoziationen zwischen einzelnen Umweltgegebenheiten und Sinnesmodalitäten betrachtet werden. Das episodische Gedächtnissystem besitzt die Fähigkeit, Beziehungen zwischen multisensorischen Informationen zu erkennen und das neu erworbene Wissen in eine kohärente und kontextuelle Repräsentation zu integrieren. Die vorliegende Dissertation besteht aus drei Studien, deren Ziel es war, den inzidentellen Erwerb von unisensorischem und multisensorischem Wissen zu untersuchen, und die damit verbundenen neuronalen Korrelate zu identifizieren.

Kernfunktionen des episodischen Gedächtnisses werden häufig dem Hippocampus zugeschrieben, der weitgehend losgelöst vom Bewusstsein arbeitet. Im Gegensatz zum traditionell-bewusstseinsbasierten Erklärungsansatz, nehmen neueste Erklärungsansätze keine direkte Verbindung zwischen dem Bewusstsein und dem Hippocampus-abhängigem Lernen an. Moderne Erklärungsansätze für Gedächtnissysteme schlagen vor, dass ein Hippocampus-abhängiges Lernen auf Basis der funktionellen Verarbeitung unterteilt und spezifiziert werden sollte. Studie 1 erforschte das implizite Erlernen einer akustischen Sequenz, mit dem Ziel, den Zusammenhang zwischen einem Hippocampus-abhängigem Lernen und dem Bewusstsein zu untersuchen, und die Beteiligung des Hippocampus zu spezifizieren. Während die Beteiligung des Hippocampus an der Bildung des episodischen Gedächtnisses belegt ist, ist es ebenfalls bekannt, dass die multisensorische Verarbeitung nicht auf die Einbindung einer einzelnen kortikalen Region beschränkt ist, sondern die Einbindung eines kortikalen Netzwerks erfordert. Aktivierungen in unterschiedlichen multimodalen kortikalen Regionen, wie zum Beispiel des ventralen posterioren-parietalen Kortex, sind oft mit komplexen integrativen Prozessen von multimodalen Informationen in Verbindung gebracht worden. Diese Regionen scheinen nicht nur an Prozessen der Aufmerksamkeit oder der perzeptuellen Entscheidungsfindung beteiligt zu sein, sondern scheinen auch Funktionen im Zusammenhang mit der Integration und Repräsentation multimodaler Informationen zu erfüllen. Folglich kann angenommen werden, dass ein Netzwerk unterschiedlicher kortikaler Regionen zur Generierung von wahrnehmungsreichen Gedächtnisrepräsentationen beiträgt, die inzidentell erworben werden können. Inzidentelle Lernparadigmen sind insofern besonders geeignet, da sie realitätsnahe Gedächtnisleistungen widerspiegeln.

In den dargelegten Studien wurde der inzidentelle Erwerb von assoziativem Wissen und den damit verbundenen impliziten und expliziten assoziativen Gedächtnisstrukturen untersucht. Hierfür wurden unimodale (Studie 1) bzw. multimodale (Studie 2 und 3) und rein perzeptuelle Assoziationen verwendet. Aufbauend auf früheren Erkenntnissen haben die vorliegenden fMRI- und Verhaltensstudien darauf abgezielt, den inzidentellen Lernprozess und die zugrunde liegenden neuronalen Korrelate zu untersuchen. In Übereinstimmung mit anderen Studien mit bildgebenden Verfahren konnte die Aktivierung im Hippocampus ausschließlich mit rein perzeptuellen Assoziationen in Verbindung gebracht werden. Die vorliegenden Ergebnisse unterstützen somit die Annahme, dass Gedächtnissysteme nicht in Bezug auf das Bewusstsein, sondern durch die Eigenschaften des gelernten Materials spezifiziert werden sollten. Mit dem Fokus auf den inzidentellen Erwerb von neuartigen, semantisch-inkongruenten, audiovisuellen Assoziationen wurde in Studie 2 der zugrunde liegende neuronale Verarbeitungsprozess bei der Bildung von episodischen Gedächtnisinhalten im hinteren Parietallappen erforscht. Da bereits unterschiedliche kognitive Funktionen verschiedenen parietalen Unterregionen zugeschrieben werden konnten, war das primäre Ziel der Studie, den funktionellen Unterschied zwischen der ventralen und der dorsalen parietalen Region zu spezifizieren. Die vorliegenden Ergebnisse zeigen, dass die ventrale Region, der Gyrus angularis, spezifisch für die Verarbeitung von assoziativen, regulären Gedächtnisinhalten ist, wobei die dorsale Region mit Aufmerksamkeitsprozessen assoziiert werden konnte. Folglich kann geschlussfolgert werden, dass der ventrale Parietallappen eine bedeutende Rolle bei der inzidentellen multimodalen Verarbeitung von Wahrnehmungsassoziationen spielt. Studie 3 zeigte abschließend auf, dass nicht nur unimodale, sondern auch multimodale Assoziationen aus rein perzeptuellen Stimuli implizit erworben werden können.

Die hier dargestellten Ergebnisse beschreiben eine gerichtete Verbindung zwischen der funktionellen Rolle von zwei wichtigen kortikalen Regionen, dem Hippocampus und dem Gyrus angularis, und der inzidentellen Verarbeitung von episodischen Gedächtnisinhalten. Somit unterstreichen die erwähnten Ergebnisse die funktionelle Rolle des Hippocampus bei der Bildung und Organisation von implizitem als auch explizitem, episodischem Wissen. Andererseits zeigen die Resultate den wichtigen funktionellen Beitrag des Gyrus angularis bei der Verarbeitung von multimodalen, episodischen Gedächtnisinhalten. Folglich kann vermutet werden, dass diese beiden Regionen signifikant zur Verarbeitung von kontextreichen Informationen und der Generierung episodischer Repräsentationen im Gehirn beitragen.

List of Abbreviations

AnG	Angular Gyrus
AGL	Artificial Grammar Learning
ATL	Anterior Temporal Lobe
DMN	Default Mode Network
MTL	Medial Temporal Lobe
PPL	Posterior Parietal Lobe
dPPL	Dorsal Posterior Parietal Lobe
vPPL	Ventral Posterior Parietal Lobe
SPL	Superior Parietal Lobe
SRT	Serial Reaction Time
STG	Superior Temporal Gyrus
STS	Superior Temporal Sulcus
vATL	Ventral Anterior Temporal Lobe

List of Publications

Jablonowski, J., Taesler, P., Fu, Q., & Rose, M. (2018). Implicit acoustic sequence learning recruits the hippocampus. Plos one, 13(12), e0209590.

Taesler, P., Jablonowski, J., Fu, Q., & Rose, M. (2019). Modeling implicit learning in a cross-modal audio-visual serial reaction time task. Cognitive Systems Research, 54, 154-164.

Jablonowski, J., Fu, Q., & Rose, M. Exploring the functional role of the posterior parietal cortex in multimodal memory formation (in prep)

“People never learn anything by being told,

they have to find out for themselves.”
[Paulo Coelho]

1. Introduction

1.1. Scientific background and research question

The human brain has an impressive capacity to extract knowledge from experiences and to store relevant information over short and long periods. I was able to acquire knowledge not only about specific objects or events, but also about common features, differences, and relationships between objects and events. Memory enables us to categorize objects and to select an appropriate response in order to interact optimally with our environment. Certainly, the acquisition, integration and retrieval of the tremendous amount of environmental features and regularities are important characteristics of the human memory system (Kandel & Squire, 2000).

1.1.1. The declarative and the non-declarative memory system

To date, it is widely known that the human memory system is not a single unit, but can be classified into different memory systems which are regulated by different neural networks (Kandel, 2012; Squire, 1992b; Squire & Zola-Morgan, 1991; Tulving, 1985). Several memory (sub-) systems have been introduced which can be in general subdivided into short-term, or working memory, and long-term memory (Kandel, 2012; R.C. Atkinson & Shiffrin, 1968). Accordingly, short-term memory is involved in the storage of a limited amount of information for a short period of time. In contrast, long-term memory enables us to store a huge amount of information for a very long time, such as years or decades. One of the most influential approaches to classify memory is the traditional hierarchical memory taxonomy for long-term memory, differentiating declarative and non-declarative memory systems (Squire & Zola-Morgan, 1991). As the term "declarative" already implies, this type of memory allows information to be consciously acquired, accessed and intentionally declared by humans (N. J. Cohen & Squire, 1980). Declarative memory content is further differentiated into episodic and semantic memory (Tulving, 1972, 1985). Episodic memory refers to the memory of autobiographical episodes and personal events while relying on specific spatial-temporal contextual information. For instance, the memory of a specific birthday party in childhood is an episodic memory. Semantic memory refers to factual knowledge, such as the conceptual knowledge of mathematics, which is acquired independently of specific contextual information of the learning event itself. The differentiation between these two systems is not always obvious as both systems are likely to interact with each other. The present dissertation project mainly focused on memory processing which relies on spatial-temporal contextual information, i.e. episodic memory.

This important breakthrough in science based on critical evidence from amnestic patients with selective lesions in the medial temporal lobe (MTL), such as the prominent case of H.M. (Scoville & Milner, 1957). In 1957, the patient H.M. underwent surgery of the bilateral hippocampi, a structure within the MTL, as a treatment for his epileptic seizures. Although the epilepsy abated, the patient was left with a severe case of anterograde amnesia (Scoville & Milner, 1957). Anterograde amnesia is the condition in which a patient is impaired in the explicit acquisition of new memories and the explicit recollection of personally experienced events or impersonal factual knowledge (Squire, 1997). Despite the amnesia, an amnestic patient is, in general, still able to acquire a variety of skill-based kinds of learning, such as riding a bicycle. However, the knowledge of having acquired these skills remains without the involvement of awareness (Scoville & Milner, 1957; Squire, 1992a). The impaired memory performances observed in amnestic patients lead to the early assumption that there might be a functional relation between the involvement of the MTL and the memory functions associated with declarative memory (Squire, 1992b). Neurobehavioral studies of amnestic and healthy patients, and related animal studies with selective lesions in the MTL, accentuated the critical functional role of the hippocampus in memory formation of personal events and impersonal factual knowledge (H. Eichenbaum, Schoenbaum, Young, & Bunsey, 1996; Squire, 1997; Squire & Zola-Morgan, 1988, 1991). In contrast, it was suggested that specific other cognitive functions, such as motor skill learning, operate independently from hippocampal involvement but depend on multiple brain systems (Squire, 1992a).

Subsequent imaging studies on memory processing provided additional evidence for a crucial role of MTL structures, including the hippocampus, in encoding and retrieval of declarative memory (for a review, see Eichenbaum, 2017; Eichenbaum, Yonelinas, & Ranganath, 2007). A crucial function of the declarative memory system is not only to consciously learn and remember impersonal facts and personal events (Tulving, 1972), but also to detect the relationship between previously unrelated pieces of information (Clark & Squire, 1998; Squire & Zola-Morgan, 1991). In particular, this includes the extraction of similarities among different episodic events, and the fast acquisition of relational representation of multiple stimuli (Squire & Zola-Morgan, 1991). Relational memory allows us to flexibly use the acquired knowledge and to transfer this knowledge to different tasks or situations in order to optimally perform under different environmental conditions (Clark & Squire, 1998; Squire, 2004; Squire & Zola-Morgan, 1988). To sum up, there is a great deal of evidence that the hippocampus plays a key role in the schematic or associative organization of memories (H. Eichenbaum, 2017).

In contrast, skills that remained intact in amnestic patients, were classified as non-declarative memory which results from the unconscious acquisition of knowledge and skills which can be measured through performance optimization, such as a decrease in reaction times (Clark & Squire, 1998; Squire, 1992a; Squire & Zola-Morgan, 1988, 1991). To be specific, the acquisition of non-declarative memory is based on a certain regularity and is formed independent of awareness (Squire & Zola-Morgan, 1991), such as skill learning abilities (including motor, perceptual and cognitive skills), the formation of habits, conditioning, and priming (N. J. Cohen & Squire, 1980; Squire, 1992b, 2004; Squire & Zola-Morgan, 1991). More complex kinds of learning abilities, such as artificial grammar learning or probability learning, were also suggested to rely on non-declarative memory processes (A. S. Reber, 1967; Squire & Zola-Morgan, 1991). As these skills were not affected by lesions to the MTL, it was argued that the formation of non-declarative memory depends on a different network of brain regions than those which are formed by the declarative memory system. Taken together, much evidence revealed that non-declarative memory processes can be related to the acquisition of relational and more abstract information in term of rules and associations between features and categories, which can be acquired without the learner's awareness (A. S. Reber, 1967; Arthur S. Reber, 1989). These "memory processes without the involvement of awareness" are particularly addressed in the research field of "implicit memory". The focus of this dissertation project will be on these "unintentional" or unconscious learning processes, which will be elaborated in more detail in the following section.

1.1.2. The implicit memory system

As already introduced, an additional research focus was set on incidental learning which describes the process of unintentional (unplanned) or intuitive learning, which improves from experiences over a period of time (Watkins & Marsick, 1992). Incidental learning has been frequently observed in studies with children on natural language acquisition. Studies revealed that children were able to select correct linguistic symbols (i.e. following a hidden rule structure) without explicit instructions, while not being able to verbalize this knowledge (Braine, 1963). Interestingly, they only reported that their responses were based on intuition or a sensation that "it feels right" (1963, Braine). The interesting research question is here: How could this be?

Not only during childhood but throughout life, humans constantly extracts regularities and contingencies from incoming environmental input. Thus, incidental learning and the related acquisition of "unconscious memory" reflects real world experiences. In fact, incidental learning becomes the focus in the research field of "implicit memory". The terms "implicit memory" and "implicit learning", were first introduced by Arthur Reber (A. S. Reber, 1967; Arthur S. Reber, 1989) who investigated whether a person can unconsciously learn an artificial (finite-state) grammar. He described that implicit memory results from an automatic learning process which relies on implicitly formed associations (A. S. Reber, 1993; A S Reber, Allen, & Reber, 1999). A fundamental feature of the acquired implicit memory is the intuitive knowledge about a specific rule structure, which allows for an effortless adaptation to regularities inherent in the environment. In line with the traditional memory taxonomy of two separate memory systems, implicit learning can be clearly differentiated from a (conscious) explicit learning mechanism (A. S. Reber, 1967; Squire, 1992a). In contrast, the process of explicit learning, or hypothesis-driven learning, allows to flexibly transfer the acquired knowledge to a different situation and to intentionally control the decision making (Z. Dienes & Perner, 1999).

However, the basic research on implicit memory is still a central theoretical challenge. On the one hand, there are conceptual difficulties on how to classify consciousness. On the other hand, there are methodological difficulties on how to measure the conscious state of a learner. Furthermore, subsequent behavioral studies on implicit memory revealed that not all participants remained unconscious about the acquired knowledge, but that a variable number of participants actually gained awareness about the underlying regularity, i.e. gained explicit memory (Rünger & Frensch, 2008; Wessel, Haider, & Rose, 2012). However, the present dissertation does not focus on the neural correlates underlying this specific transition process from implicit to explicit memory. The focus is to investigate the specific neural correlates involved in the acquisition of episodic memory within and across modalities under an incidental learning condition. In the first place, an overview over the classical methodological principles used to investigate incidental learning and the formation of implicit and explicit memory is required. An overview is provided in the following.

1.1.2.1. Paradigms on implicit memory

Reber provided first evidence for implicit learning effects by empirical studies using an Artificial Grammar Learning (AGL) task (A. S. Reber, 1993; A S Reber et al., 1999; Arthur S. Reber, 1989). In an AGL task, participants were exposed to a set of letter strings, which, unbeknownst to the participants, followed a specific artificial probabilistic grammar rule. After the memorizing phase, a different set of letter strings composed of the same or the new vocabulary was shown. Participants were unable to verbally report the underlying grammar rule, although they were able to apply the acquired grammatical knowledge with an accuracy above chance level (Altmann, Dienes, & Goode, 1995; Z. Dienes & Altmann, 1995; Arthur S. Reber, 1989). Subsequently, it has been assumed that the acquisition of implicit memory can be assumed when knowledge could be expressed through modifications of a person's performance, and the lack of conscious access to the acquired knowledge based on the fact that no verbal report could be given (A. S. Reber, 1967; Arthur S. Reber, 1989).

However, within this research field, there are several conceptual and methodological difficulties. On the one hand, there is disagreement on how to explain the behavioral performances in an incidental learning task observed in healthy participants and amnestic patients. These explanatory approaches differed in their core assumption, while assuming that this processes results from a single learning system (Shanks & St John, 1994b, 1994a) or from at least two separate learning systems (Haider & Frensch, 2005; P. J. Reber & Squire, 1994; Paul J Reber & Squire, 1998). Proponents of the single system view argue that both verbal and nonverbal learning rely on the same knowledge representation (Shanks & St John, 1994a), while some even questioned the existence of an implicit knowledge system (Searle, 1992). In contrast, proponents of a multiple system view argue that there are at least two learning systems which contribute to the formation of implicit and explicit memory (Zoltán Dienes & Berry, 1997; Haider & Frensch, 2005; Haider & Rose, 2007; Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; P. J. Reber & Squire, 1994; Paul J Reber & Squire, 1998). Proponents of a multiple system view support the general assumption of two memory systems. However, related accounts further differ in how the systems are related (P. A. Frensch & Rünger, 2003). On the one hand, it has been suggested that the implicit and explicit memory systems are functionally independent and do not interact (P. J. Reber & Squire, 1994; Paul J Reber & Squire, 1998). On the other hand, there are more "modern" theories arguing that incidental learning might first result in the formation of implicit memory but does not operate independently from the explicit memory system (Peter A. Frensch et al., 2003; Haider & Frensch, 2005). According to the latter account, the generation of implicit memory can trigger the development of explicit memory representations, so that new acquired memory can be accessed by consciousness over time (Peter A. Frensch et al., 2003; Haider & Frensch, 2005; Rünger & Frensch, 2008). On the other hand, it is still controversially discussed if implicit memory is of abstract nature or is rather based on more simple associations (Z. Dienes & Altmann, 1997; Perruchet & Pacteau, 1990). While using different stimulus configurations there is much evidence for both accounts, however, further studies also revealed that participants were able to learn a probabilistic sequence implicitly (Cleeremans & McClelland, 1991; A. Cohen, Ivry, & Keele, 1990). Accordingly, it has been reported that participants became in particular sensitive to the temporal context of previous stimulus of the sequence. Using a connectionist model, it has been suggested that the underlying implicit memory process might operate associatively, by selectively attending to small fragments or units (chunks) of a sequence (Cleeremans & McClelland, 1991; Arnaud Destrebecqz & Cleeremans, 2001). Furthermore, it has been suggested that the learned material in an classical AGL task might not rely on complex rule abstraction processes, but might result from chunking mechanisms or simple associative learning (Cleeremans & McClelland, 1991; Fu, Bin, Dienes, Fu, & Gao, 2013; Jiménez, Méndez, Pasquali, Abrahamse, & Verwey, 2011; Perruchet, Gallego, & Savy, 1990; Perruchet & Pacteau, 1990; Schlaghecken, Stürmer, & Eimer, 2000).

While particularly addressing associative learning, a prevalent paradigm in neuroimaging studies on implicit memory is the serial reaction time (SRT) task which was first introduced by Nissen and Bullemer (Nissen & Bullemer, 1987). In this sequential learning task participants are instructed to match a set of (e.g. visual) stimuli to a (visual) target by pressing a corresponding response (button press) as fast as possible. Unbeknownst to the participants, both stimuli and the corresponding motor responses follow a deterministic regular sequence. Thus, participants can learn a hidden regularity implicitly. The typical outcome of implicit learning is a significant change in reaction times. To illustrate, when a regular (learned) and an irregular (control) sequence was learned, participants' reaction times decreased (Abrahamse, Van Der Lubbe, & Verwey, 2008; Goschke & Bolte, 2012; Remillard, 2003). Further, when the underlying (learned) regularity suddenly changed or an unexpected stimulus was presented, participants' reaction times increased significantly (Eimer & Goschke, 1996; Willingham & Goedert-Eschmann, 1999). Thus, while being unaware about this behavioral performance, a significant change in reaction times has been frequently reported to be one sensitive indicator for an implicit learning effect (Haider, Eberhardt, Kunde, & Rose, 2012; Haider & Rose, 2007). As previous SRT studies mostly used visual stimuli as perceptual inputs, the aim of our first fMRI study was to examine (1) whether those behavioral and related neural findings are "general effects" of implicit memory processing, or whether those effects may be specific for implicit visual learning. Thus, I investigated implicit sequential learning using *auditory stimuli* (study 1). Noteworthy, these questions are addressed in more detail in a later section, because, at first, the classical measurements used to assess and differentiate between implicit and explicit knowledge has to be introduced. In fact, the existence of an implicit system has even be called into question early on, resulting in a growing demand for objectively valid measurements for implicit and explicit knowledge (Shanks & St John, 1994a, 1994b).

1.1.2.2. Methods to measure the conscious state

The dissociation between accurate above chance level knowledge and expressive knowledge has been frequently used as an indicator for implicit memory (Nissen & Bullemer, 1987; A S Reber et al., 1999). While above chance performance can be used as an reliable indicator for knowledge, it has been argued that participants' verbal report is not a sensitive objective measurement to both indicate whether participants' knowledge is conscious and to differentiate between implicit and explicit knowledge (Shanks & St John, 1994a, 1994b). The inability to verbally report the acquired knowledge might underestimate the acquisition of (partial) explicit memory. However, a sensitive indicator for the conscious state of the learner is required, since the amount of the acquired knowledge does not reflect whether memory is of implicit or explicit nature. As already discussed previously, incidentally acquired knowledge usually has an impact on the learner's behavioral performance, even if knowledge is acquired implicitly.

Taken these points into consideration, classical studies on implicit learning have been characterized by three aspects (Cleeremans, Destrebecqz, & Boyer, 1998). First, participants are incidentally exposed to a complex regularity or sequence, and attention is payed to the "to-be-learned stimulus" within several learning trials (P. A. Frensch & Rünger, 2003; Haider et al., 2012; Nissen & Bullemer, 1987). Second, learning task are followed by a forced-choice task, a method for measuring participants' memory sensitivity. Third, each of these test trials is accompanied by an additional measurement for the assessment of the conscious state about the acquired knowledge. A classical measure for the conscious state of the learner has been introduced by Persaud et al (Persaud, McLeod, & Cowey, 2007). Using a "post-decision wagering" task, the participant is instructed to evaluate each response (i.e. the decision) by placing a high or a low wager (Zoltán Dienes & Seth, 2010; Persaud et al., 2007). Each wager should reflect whether the response was made with or low confidence reflecting whether memory is implicit and explicit, respectively. Thus, the combination of a forced-choice task and a post-decision wagering task is at present the most sensitive approach to assess both the amount of acquired knowledge and the conscious state of the learner (Zoltán Dienes & Scott, 2005; Fu et al., 2013; Fu, Fu, & Dienes, 2008; Haider et al., 2012; Haider, Eichler, & Lange, 2010; Rose, Haider, & Büchel, 2010). Therefore, the fMRI studies included in this dissertation are based on these methodological principles.

1.1.2.3. Challenging the traditional memory taxonomy

Different studies on implicit memory provided an essential foundation for the research on consciousness. Those included not only behavioral studies (P. J. Reber & Squire, 1994; Robertson, 2007) and computational approaches (Axel Cleeremans & Dienes, 2008), but also lesion studies with amnestic patients and healthy controls (Knowlton, Ramus, & Squire, 1992; Nissen & Bullemer, 1987) and related imaging studies (Rose, Haider, Salari, & Büchel, 2011; Rose, Haider, Weiller, & Büchel, 2004). Early lesion studies with amnestic patients and healthy controls seemed to support the traditional awareness-based account of memory suggesting that memory systems are differentiated by the involvement of the MTL (Nissen & Bullemer, 1987; P. J. Reber & Squire, 1994; Paul J. Reber, 2008; Squire, 1992b). Amnestic patients revealed qualitative "near-normal" performances on implicit learning task, compared to healthy controls (Knowlton et al., 1992; Knowlton & Squire, 1994, 1996; Nissen & Bullemer, 1987). The findings of intact implicit performances of amnestic patients were in line with SRT studies with healthy controls using brain imaging techniques, as effects of implicit learning were particularly found in the basal ganglia and the cerebellum (A Destrebecqz et al., 2005; Grafton, Hazeltine, & Ivry, 1995; Peigneux et al., 2000; Rauch et al., 1997). Thus, these findings supported the traditional assumption that only explicit memory formation requires the engagement of the medial temporal lobe including the hippocampus (P. J. Reber & Squire, 1994).

Subsequent controversial findings on implicit memory challenged the assumed relation between consciousness and MTL-dependent learning. For example, an early study found impaired performances on an implicit visual search task in amnestic patients with damage in the MTL (including the hippocampus) in contrast to healthy controls (Chun & Phelps, 1999). Thus, findings appeared to be inconsistent with the traditional memory account. While performing the implicit perceptual learning task, controls were able to implicitly acquire relevant contextual information and benefit from their acquired knowledge in subsequent test trials. Surprisingly, patients did not show this behavioral benefit. This finding was indeed inconsistent with the traditional awareness-based account of memory. However, a follow up study conducted by Manns and Squire directly addressed these conflicting results and provided an explanation which should still support this memory model. On the one hand, as in the study by Chun and Phelps the exact location of the damage of the amnestic patients was not specified, a reasonable interpretation could not be made. Accordingly, the impaired performances could be due to damages exclusively in hippocampal structures or within MTL structures. Thus, using the same implicit perceptual learning test as in Chun and Phelps, eight amnestic patents who differed in the location of the damage were tested. While the findings revealed that only damage to the MTL resulted in impaired performances in implicit learning task, it was concluded that the involvement of hippocampal structures might be exclusively related to explicit memory formation (Manns & Squire, 2001). However, this interpretation has also been challenged by several neuroimaging studies, in which effects of implicit learning were related to activation within the MTL which included the hippocampus proper (Degonda et al., 2005; Henke, Mondadori, et al., 2003; Henke, Treyer, et al., 2003; Rose, Haider, Weiller, & Büchel, 2002). One study even found activation in MTL structures during both implicit and explicit SRT learning (Schendan, Searl, Melrose, & Stern, 2003). Consequently, it has been suggested that several different learning mechanisms might account for the controversial behavioral findings reported in studies on implicit memory (Abrahamse, Jiménez, Verwey, & Clegg, 2010; Rose et al., 2011; Stöcker, Sebald, & Hoffmann, 2003; Ziessler, 1994). To address this, different modified versions of the classical SRT task were used, in which e.g. the stimulus modality (e.g. visual, auditory, and tactile), the stimulus character (e.g. letter, number, and location), or the stimulus regularity (deterministic, probabilistic) has been changed (Abrahamse et al., 2010). In fact, associative learning might result from learning the regularities employed in the sequence of responses (response-response; R-R) (Willingham & Goedert-Eschmann, 1999; Willingham, Greeley, & Bardone, 1993). On the other hand, SRT learning might also result from learning the relation between the stimulus and the response (stimulus-response, S-R) (Willingham, Nissen, & Bullemer, 1989), or the response and the stimulus (response-stimulus, R-S) (Ziessler, 1994; Ziessler & Nattkemper, 2001). Interestingly, several SRT studies also suggested that participants might have learned the relation between the stimuli (S-S learning) (Abrahamse, Van Der Lubbe, & Verwey, 2009; Abrahamse & Verwey, 2008; A. Cohen et al., 1990; Goschke & Bolte, 2007; Remillard, 2003, 2009; Rose et al., 2011). Taken together, it was shown that the effects of implicit learning, observed in the classical SRT task, might not be unambiguously assigned to one particular learning mechanism. The fixed stimulus-response mapping employed in the classical SRT task implies that participants could have been learned both sequences, the perceptual and the motor response sequence, or even a combination of both modalities, because the two sequences are structurally identical and thus obviously correlated (Rose et al., 2011). Therefore, an unambiguous interpretation about the underlying learning mechanisms ("what was learned") and, thus, related neural correlates cannot be drawn. Based on this interpretation, the studies of this dissertation aimed to examine the neural correlates, which are specific for incidental learning of pure perceptual associations. However, could this aspect be implemented within one SRT paradigm?

A ground-breaking fMRI study directly addressed the functional assignment of the neural systems involved in the different learning mechanisms, i.e. learning the association of motor responses versus the association of stimuli (Rose et al., 2011). In a modified version of the SRT, participants were instructed to react to either a purely perceptual or a purely motor response sequence (motor modality). This approach allowed to disentangle the motor and perceptual learning system within one task and provided significant insight into the functional characterization of MTL-related learning processes (Rose et al., 2011). Activations in bilateral hippocampus were exclusively related to implicit learning of perceptual contingences, whereas activations in the basal ganglia and motor cortex regions were exclusively related to motor sequence learning. This study and other imaging studies provided evidence for the engagement of the MTL in implicit memory processes when the acquired memory relied on perceptual contingences (Gheysen, Gevers, De Schutter, Van Waelvelde, & Fias, 2009; Gheysen, Van Opstal, Roggeman, Van Waelvelde, & Fias, 2011; Grafton et al., 1995; Peigneux et al., 2000; Rauch et al., 1997). In contrast, the involvement of the basal ganglia and the motor cortex has been frequently related to the learning of motor responses, consistent with previous reported studies using the SRT. Further fMRI studies on implicit learning supported the assumption that the hippocampus has an important function in the implicit binding process between perceptual associations, while revealing that the sequential material is not a mandatory factor for its involvement (Degonda et al., 2005; Henke, Treyer, et al., 2003). Finally, studies suggested that neither awareness nor intentional retrieval is a reasonable account for the role of the hippocampus in memory formation (Degonda et al., 2005; Konkel & Cohen, 2009). In fact, a recent imaging study revealed that activations in the MTL were not affected by whether retrieval of word pairs occurred intentionally or incidentally (Wang & Giovanello, 2016).

Consistent with both nonhuman and human (lesion) functional neuroimaging data, the assumed function of the hippocampus in perceptual associative learning is in line with the key features of the declarative human memory system (DeVito & Eichenbaum, 2011; H. Eichenbaum, 2000; Ranganath, 2010; Squire, Genzel, Wixted, & Morris, 2015). In fact, on the level of single neuron recordings, additional evidence revealed a significant hippocampal involvement in perceptual associative learning in human beings (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005) as well as in the flexible integration of spatial and non-spatial information into an organized unified representation (Terada, Sakurai, Nakahara, & Fujisawa, 2017). Thus, its key function should be rather specified in terms of perceptual relational representation (Duss et al., 2014; Henke, 2010; Konkel & Cohen, 2009), in both sequential and non-sequential material. In fact, the hippocampal functional role in memory formation of relational, domain-general information has been widely confirmed, which occurs independent of conscious retrieval (see review (H. Eichenbaum, 2017; Hannula & Ranganath, 2009; Rose et al., 2011)). In line with the notion of the declarative human memory system, hippocampal function were related to binding processes of spatiotemporal information and/or the encoding of event sequences (N. J. Cohen, Poldrack, & Eichenbaum, 1997; H. Eichenbaum, 1997, 2000; Squire & Zola, 1996). However, new explanatory approaches suggested that those functions could also operate without the involvement of awareness (Duss et al., 2014; Henke, 2010). Hence, episodic recollection may involve different kinds of neurocognitive processing, while several studies confirmed that not only explicit but also automatic and implicit processing occur in the hippocampus (Duss et al., 2014; H. Eichenbaum, 2017; Hannula & Ranganath, 2009; Henke, Reber, & Duss, 2013; Rose et al., 2011; Voss, Lucas, & Paller, 2012). Taken together, not only the assumption that basal ganglia are exclusively related to implicit memory formation had been challenged, but also the traditional memory taxonomy which assumes that human memory systems can be differentiated by consciousness.

Current theories on memory proposed that a distinction should be made between retrieval processes, which are generally relevant for episodic memory, and neural activations which are frequently found in recollection-related processes (Voss et al., 2012). Interestingly, functional connectivity analysis on neuroimaging data revealed that the hippocampus is functionally highly correlated with a network of several regions, such as the posterior parietal cortex, the anterior temporal cortex, the precuneus and the frontal cortex (Buckner, Andrews-Hanna, & Schacter, 2008; H. Eichenbaum, 2017; Moscovitch, 2008; Ranganath, 2010; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Vincent et al., 2006). However, these regions are differently modulated by different cognitive functions. The hippocampus has been classified as a significant component to memory processes, which acts as a linking hub or convergence zone required for the acquisition and retrieval of memories. Furthermore, an additional cortical network might significantly contribute to the subjective (conscious) state of the recollected memory (Moscovitch, 2008; Rose et al., 2010). As already addressed within previous theories, such as the relational memory account (N. J. Cohen et al., 1997) and the processing account of memory systems (Henke, 2010), it has been frequently stated that memory systems are not divided by consciousness, as in the traditionally manner, but on the basis of functional processing (N. J. Cohen et al., 1997; Henke, 2010).

From this perspective, memory processing has been classified into three different modes according to their cognitive features (Henke, 2010). Accordingly, memory may results from (a) rapid or slow encoding, (b) associative or single items encoding, and may relate to (c) flexible or rigid representations (Henke, 2010). The hippocampus is related to rapid encoding of new and flexible associations, while inflexible (including non-relational information) memories are rather related to neocortex involvement. Thus, the hippocampus has been suggested to specifically contribute to the flexible representation of a memory, which can easily be reactivated by associations containing remotely related (i.e. different from the encoding event) retrieval cues (Duss et al., 2014; H. Eichenbaum, 2017; Henke, 2010; Nyberg, 2017). Thus, the hippocampal functional role has to be differentiated by the properties of the learned material, i.e. by "what has been learned". To sum up, the hippocampus is suggested to be a critical component in memory formation, irrespectively of whether knowledge was processed implicitly or explicitly, while interacting with neocortical structures involved in memory processes (Z. Dienes & Altmann, 1997; Duss et al., 2014; H. Eichenbaum, 2017; Nyberg, 2017; O'Reilly & Rudy, 2000). These critical findings motivated my research on examining the cortical regions which are specific for *integration processes of perceptual associations within* (study 1) and *across modalities* (study 2 and study 3, see below) using an incidental learning paradigm.

1.1.3. Neural integration and associative processing across modalities

Although traditional studies on incidental learning examine the various senses independently (unimodal learning), perception is usually multimodal. Clearly, perception usually operates in terms of contextual information, which is provided by multiple sensory modalities (multimodal learning). Across literature, however, it is widely known that learning from multiple senses is not only more realistic but also more effective than unimodal learning (Shams & Seitz, 2008; Shams, Wozny, Kim, & Seitz, 2011).

Theoretically, the integration or binding of multisensory information improves the ability to detect, discriminate and to categorize incoming information (Calvert, Spence, & Stein, 2004). This notion implies that the human memory system is able to identify which unisensory inputs belong together and which has to be bound into a single unitary object or event. To be specific, the memory system is somehow able to determine which sensory inputs belonged together, and which should be treated separately. The unity assumption addressed some of these aspects, such as the multisensory integration of auditory and visual information (Spence, 2007). Accordingly, important informative components, such as temporal and spatial coincidences or a sequence of events, have an effect on the strength of the acquired associations (Damasio, 1989; Jensen, Merz, Spence, & Frings, 2020). To illustrate, for laboratory studies, learning of arbitrary associations can be triggered by presenting stimuli together on a regular basis (Jensen et al., 2020). Of course, prior or emerging explicit knowledge (due to instructions or incidental learning, respectively) can also affect associative integration processes (Evans et al., 2020; Rose et al., 2010; Wessel et al., 2012). Hence, the interaction between non-cognitive (temporal and spatial coincidence) and cognitive (prior knowledge and expectations) factors are assumed to have a significant impact on multisensory integration (Y. C. Chen & Spence, 2017).

Considering all these aspects within both fMRI studies, I focused on *perceptual associative learning under incidental conditions*, i.e. the memory processes in which knowledge is acquired without prior knowledge about the to-be-learned content. In particular, within study 2, I aimed to identify the neural correlates that are specifically involved in multimodal processing and explicit memory formation acquired under incidental conditions. To be specific, I aimed to examined which neural correlates are (1) specific for the *associative processing of multiple sensory inputs into a unified representation*, (2) or mostly required during attentional control processes, particularly involved when unimodal sensory inputs are (or have to be) processed separately. In contrast, within the additional study 3, I addressed the question whether incidentally acquired crossmodal perceptual representation could also be learned implicitly without being accessible to consciousness. Interestingly, across current theories, there are different view on crossmodal implicit learning. Most theories support the view that implicit learning relies on statistical learning of a *single* transition (Howard, Howard, Dennis, & Kelly, 2008; Remillard & Clark, 2001). Accordingly, this process occurs with the absence of consciously accessible high-level regularities or rule-sets. Furthermore, it implies that the implicit learning process occurs only within uni-modal modules. According to a recent model by Keele and colleagues (2003), the dual system account of implicit learning, stated that the implicit system allows for multiple unimodal learning systems, but it has been argued that those processes only work in parallel and without the involvement of consciousness. Hence, multimodal learning is only possible when explicit awareness is involved. To be specific, it has been suggested that a different system is responsible for the related multimodal integration process of unimodal information into a unified association, which can be accessed by consciousness. However, recent studies challenged and extended this view, suggesting that crossmodal or multimodal representation of the stimulus input can be acquired implicitly within a common module (Haider, Esser, & Eberhardt, 2020; Hommel, Müsseler, Aschersleben, & Prinz, 2001). As those theories focused on the binding between stimulus and response modalities, the additional behavioral study presented in this dissertation (study 3) addressed the question of whether crossmodal perceptual representations of *different pure perceptual modalities* can be learned and acquired implicitly.

Early on, it has been assumed, that incoming information is first processed in modality-specific cortical regions independently (Treisman & Gelade, 1980), while multisensory interactions and resulting binding process occur in later associations areas of the brain (Jones & Powell, 1970). Neurophysiological research challenged this view and revealed that automatic multisensory processing may already be initiated in primary sensory cortices, and hence occur much earlier than previously assumed processing (Calvert, 2001; Rouiller & Durif, 2004; Rutkowski, Miasnikov, & Weinberger, 2003). Thus, the integration process comprises a set of different processing stages while interacting with different (unisensory) information arriving from different sensory modalities (e.g. visual, auditory, or tactile). Noteworthy, this dissertation project focused on the higher-order association areas that are classified as being crucial components in episodic memory processing.

Early computational memory models hypothesized that one or more specific multimodal cortical regions, or so called convergence zones, are responsible for the integration of different unisensory elements into a conjunctive memory representation (Damasio, 1989; H. Eichenbaum, 2000; Marr, 1971). To date, the existence of such cortical regions is generally agreed upon, however, the role and the anatomical basis of such multimodal representation in episodic and semantic memory is still controversially discussed. Physiological data from single neurons in animal models revealed that information could indeed be combined together at relatively early cortical stages, which were previously assumed to operate only as unisensory sensory cortices (Budinger, Heil, Hess, & Scheich, 2006; Calvert et al., 1999; Noesselt et al., 2007; Schroeder & Foxe, 2005). They identified specific neurons which were multisensory in nature as they receive and respond to input from more than one sense (Alais, Newell, & Mamassian, 2010; Werner & Noppeney, 2010b). While "primary sensory" association areas are involved in enhancing the stimulus salience (Seitz, Kim, & Shams, 2006; Shams et al., 2011), "higher-order" association areas are considered to be involved in the extraction of relevant features and the formation of conjunctive multimodal representation (Binder, Desai, Graves, & Conant, 2009; Noesselt et al., 2007; Tanabe, 2005; Werner & Noppeney, 2010a). Thus, multisensory integration relies on a distributed neural network including primary and higher-order association areas, while the various areas differ in their functional role in multimodal integration (Murray, Lewkowicz, Amedi, & Wallace, 2016; Werner & Noppeney, 2010a). The convergence of multisensory information is not only required during perceptual processing (Singer, 1999) but also during (episodic and semantic) memory formation (H. Eichenbaum, 2001), which allow memory representations to be accessed and retrieved as a whole (O'Reilly & Rudy, 2000; Tulving, 1972). On the neural bases, a convergence zone has been defined by its conjunctive coding and significant interconnectivity with other brain regions (Damasio, 1989; Marr, 1971). Evidence from human imaging studies (Chadwick, Hassabis, & Maguire, 2011; Larocque et al., 2013) and neuroimaging connectivity methods (C. M. Lewis, Baldassarre, Committeri, Romani, & Corbetta, 2009; Vincent et al., 2006) provided early evidence for the formation of conjunctive representations and convergent connectivity in hippocampal structures. Indeed, the crucial functional role of the hippocampus in episodic and semantic memory formation is widely confirmed (see previous sections). However, it is also known that multisensory integration is not restricted to the involvement of a single region, but also requires the involvement of a network of other regions, such as the posterior parietal cortex, the anterior temporal cortex, the precuneus and the frontal cortex (H. Eichenbaum, 2017; Moscovitch, 2008; Ranganath, 2010). While differentiating between episodic and semantic memory processing, it is controversially discussed which additional multimodal regions might specifically contribute to these multimodal integration processes (Humphreys & Ralph, 2015; Lambon Ralph, Jefferies, Patterson, & Rogers, 2016; M. R. Uncapher, Otten, & Rugg, 2006). However, as mentioned previously, this differentiation is not always obvious. With respect to the focus of this dissertation, the next sections will present state-of-the-art scientific evidence on the neural processes underlying multimodal integration within higher-order association areas required for multimodal memory formation.

Activations within several multimodal cortical regions, including regions of the parietal lobe through the entire length of the temporal lobe, have been consistently related to high-level integrative processes of multimodal input and the formation semantic and episodic memory (Binder et al., 2009; Humphreys & Ralph, 2015; Kim, 2010; Koenig & Grossman, 2007; Patterson, Nestor, & Rogers, 2007; Spaniol et al., 2009). Accordingly, these region are centered at the convergence of numerous modality specific pathways and are assumed to be highly suitable to perform multimodal integration processes by feedforward and feedback activation within a distributed memory network (Binder et al., 2009; Patterson et al., 2007; M. R. Uncapher et al., 2006; Xue, 2018). Building on current theories, two cortical regions were particularly associated with multimodal integration processes: the anterior temporal lobe (ATL) (Chiou & Lambon

Ralph, 2019; Patterson et al., 2007; Visser & Lambon Ralph, 2011), and the inferior part of the posterior parietal lobe (PPL), in particular the angular gyrus (AnG) (Humphreys, Ralph, & Simons, 2021; Ramanan & Bellana, 2019; Shimamura, 2011). While these two cortical regions are assumed to reveal similar functional features in general, they might differ in their functional specificity in multimodal memory processes (Davis & Yee, 2019; Desai, Reilly, & Van Dam, 2018; Patterson et al., 2007; Ramanan, Piguet, & Irish, 2018; Shimamura, 2011). Since episodic and semantic memory is often difficult to differentiate, to identify which cortical regions are specific for multimodal integration, episodic and/or semantic memory formation remains challenging in research. As this dissertation mainly focused on the neural correlates of episodic memory, the functional specification of these two associative cortical regions in memory processing will be introduced in the following section.

1.1.3.1. The anterior temporal lobe

The hub-and-spoke theory is a prominent account for the underlying neural network underlying semantic memory processing. Accordingly, this network has been classified into two key components: a) The anterior (ventral) portion of the human temporal lobe (the anterior temporal lobe; ATL) described as an domain-general (i.e. modality invariant) integrative *hub* (Patterson et al., 2007) and b) multiple modality specific regions described as spokes (Patterson et al., 2007). Accordingly, the ATL is assumed to significantly contribute to semantic processing by combining incoming modality specific information and forming amodal semantic representation (Patterson et al., 2007). An amodal representation is characterized as being generated from any individual modality (e.g. auditory modality) which can be expressed in any individual other modality (e.g. visual modality). These features are important for the formation of modality-invariant conceptual representations, as it allows not only to generalize across conceptually similar instances which differing in their modality, but also to differentiate between entities, which share the same modality. This theory relies originally on patients' studies with semantic dementia (SD) revealing impaired performances in multimodal processes. Across different types of neurological patients, patients with SD have a brain atrophy in the vicinity of different subregions of the temporal lobe, which might also cover anatomically distinct regions including the fusiform gyrus. Although basic perception in each modality remained intact, these patients revealed impaired performances in semantic knowledge, such as naming and recognizing of objects and their functions (Hodges & Patterson, 2007; Lambon Ralph et al., 2016; Lambon Ralph & Patterson, 2008; Wong & Gallate, 2012).

Using various methods to study semantic processing in SD patients and healthy controls, the ATL activation in multimodal integration processes and, in particular, semantic processing has been widely confirmed (Binder & Desai, 2011; Hung, Wang, Wang, & Bi, 2020; Koenig & Grossman, 2007; Patterson et al., 2007; Wong & Gallate, 2012; Xu, He, & Bi, 2017; Xu, Lin, Han, He, & Bi, 2016). While functional activation has also been found in emotional processing and social cognition or even modality specific processing (Olson, McCoy, Klobusicky, & Ross, 2013; Simmons & Martin, 2009; Wong & Gallate, 2012), both the left and right ATL has been mainly related to verbal and no-verbal (language-based) semantic processing. The ATL can be divided into different subregions to which major white matter pathways from different unisensory cortical regions converge (Friederici, 2009; Pascual et al., 2015). While contributing to (language-based) semantic processing of both verbal and no-verbal material, it has been found that the functional role of ATL subregions varies in a graded manner across the temporal subregions (Binney et al., 2012; Chiou & Lambon Ralph, 2019; Hein & Knight, 2008; Pascual et al., 2015; Brodmann, 2005). Accordingly, significant activations where found in semantic processing relative to non-semantic processing task, irrespective of the modality input and stimulus category (Chiou & Lambon Ralph, 2019; Lambon Ralph et al., 2016; Patterson et al., 2007; Visser & Lambon Ralph, 2011). Based on these neuroimaging and physiological findings, it becomes clear why the ventral and the superior region of the ATL has been frequently reported to be specific for the integration of meaningful semantic information within and across modalities (Beauchamp et al., 2004; Calvert, 2001; Calvert et al., 2001; Chiou and Lambon Ralph, 2019; Davis and Yee, 2019; Deroy et al., 2016; Duffau, 2011; Noesselt et al., 2007; Werner and Noppeney, 2010b). Taken together, the ATL might be a critical cortical region in the semantic processing network of language, including speech comprehension and production (Chiou and Lambon Ralph, 2019; Hickok and Poeppel, 2007). With respect to this dissertation project, I were particularly interested in the neural integration processes of semantically-incongruent, novel audiovisual associations. This means, within study 2, the critical factor that might allow that binding/learning had occurred is based on the temporal coincidences of these two unimodal inputs. These findings will be important for my work, because they allow to specify hypotheses concerning the functional involvement of the ATL and the ventral/inferior part of the posterior parietal lobe (vPPL).

Indeed, the hub-and-spoke theory clearly differentiated between the functional involvement of the ATL and the IPL, in particular the AnG (which is will be discussed in detail in the following section). Accordingly, the ATL has been clearly classified as an "amodal" hub which allows to integrate sensory inputs and to from so called amodal representations (Lambon Ralph & Patterson, 2008; Patterson et al., 2007). Amodal knowledge has been classified as a representation that is not bound to any specific modality. This function has been related to the generation of taxonomic knowledge including the formation of taxonomic relations and categorization, such as superordinate "label" (e.g. a dog is an animal), or taxonomic concepts (e.g. the smell, the sound, the color of a dog), known as feature-based knowledge. To sum up, the ATL has a specific role in the identification and discrimination between (highly) similar (and confusable) objects, e.g. coffee and tea, orange and apple (Binder et al., 2009; Clarke & Tyler, 2015; Davis & Yee, 2019; Kalénine et al., 2009; A. G. Lewis, Poeppel, & Murphy, 2015; Schwartz et al., 2011). In contrast, within this framework, it has been argued that the AnG does "only" combine crossmodal information arising from different sensory modalities (similar to the function of the ATL), but does not generate these amodal representations (Patterson et al., 2007). In relation to other related studies on conceptual knowledge, the functional role of the IPL, in particular the AnG, has been frequently related to the formation of thematic relationships (Binder & Desai, 2011; Binder et al., 2009; Davis & Yee, 2019). Thematic relationships are formed by considering event-based information, such as temporal and spatial coincidences of objects in an event ("what objects belong together"). For example, imagine you assume that your partner might need milk and sugar when you make coffee for breakfast. This reflects a thematic/relational representation between the mild and the suger when making coffee.

To sum up, the IPL, in particular the AnG, is assumed to be somehow involved in the formation of thematic relational representations while being sensitive to episodic details and contextual details. Hence, its precise functional role in multimodal memory processing has yet to be determined. As already implied, the aim of fMRI study 2 was to investigate the neural correlates underlying the processing of semantically-incongruent audiovisual information. I assumed that the ventral/inferior part of the PPL, including the AnG, serves critical functions related to memory-related associative processing.

1.1.3.2. The posterior parietal lobe

According to their connectivity pattern and functional responses across a variety of cognitive processes, the parietal lobe has been anatomically and functionally segregated (i.e. anterior vs. posterior, dorsal vs. ventral) processes (Binder & Desai, 2011; Bzdok et al., 2013; Caspers et al., 2011, 2006; Gilmore, Nelson, & McDermott, 2015; Nelson et al., 2010; Rushworth, Behrens, & Johansen-Berg, 2006). While anterior parietal region contains primary somatosensory areas, the posterior end of the parietal lobe (PPL) has been associated with several higher-order functions related to episodic memory processing. This is why, this dissertation project focused on the PPL. Across the literature, it is now controversially discussed whether the functional role of the PPL can be limited to processes of attention or perceptual decision making, as previously suggested (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). However, to date, there are several studies and meta-analyses, that revealed that the PPL does also serve a critical function in episodic memory processing (Humphreys & Ralph, 2015; Kim, 2010; Rugg & King, 2018; Sestieri, Corbetta, Romani, & Shulman, 2011; Sestieri, Shulman, & Corbetta, 2017; Vilberg & Rugg, 2009a). Across the literature, it has been stated that some parts of the PPL were reported to scale simply with the repeated exposure of objects (Gilmore et al., 2015). However, several studies revealed that the PPL, in particular ventral and medial regions of the PPL, are functionally related to successful memory processing rather than perception (Binder et al., 2009; Daselaar et al., 2009; Favila et al., 2018; Kim, 2011, 2010).

Based on its functional diversity, the PPL has been further subdivided into different subregions revealing different cognitive functions (Caspers et al., 2006; Humphreys & Ralph, 2015; Hutchinson et al., 2014; Nelson, Arnold, Gilmore, & Mcdermott, 2013; Nelson et al., 2010). To illustrate, the PPL can be anatomically and functionally classified along the intraparietal sulcus (IPS) into a dorsal and a ventral region. The dorsal (i.e. superior) parietal region (dPPL) includes the IPS and the superior parietal lobe (SPL), whereas the ventral (i.e. inferior) parietal region (vPPL) includes the angular gyrus (AnG) and the supramarginal gyrus (SMG) (Caspers et al., 2006; Humphreys & Ralph, 2015; Nelson et al., 2013, 2010).

In general, it has been suggested that the ventral and dorsal PPC operate in a dynamic interaction and competition during memory formation, while differing in their encoding and retrieval-related effects (Gilmore et al., 2015; Humphreys & Ralph, 2017; Sestieri et al., 2017). However, there is one prominent theory that specified the distinctive functional role of ventral and dorsal region in episodic memory processes. The dorsal region is suggested to mainly reflect the involvement of a “top-down” attention network, which involves memory reinstatement and memory-based decisions (Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008). Thus, retrieval-related activity in the dorsal PPL might not reflect a memory signal, but might be rather related to executive control processes, such as the detection of behaviorally relevant information and the preparation of goal-directed (top-down) behavior (Kim, 2010; Koenigs, Barbey, Postle, & Grafman, 2009; Spaniol et al., 2009; Wager & Smith, 2003). In contrast, the ventral region was classified as the “bottom-up” attention network, which mainly involves the allocation or reorientation of attention to internal sensory representations (Cabeza, 2008; Cabeza et al., 2008; Corbetta & Shulman, 2002). Alternative theories argued that the functional involvement of the vPPL cannot be fully explained by an attentional reorienting account alone (Humphreys et al., 2021; Ramanan et al., 2018; Maureen Ritchey & Cooper, 2020; Seghier, 2013; Shimamura, 2011). In fact, meta-analytic and within-study evidence argued against such a strict “co-activation” of dorsal and ventral regions in attention-reorienting memory processes (Humphreys & Ralph, 2015; Hutchinson et al., 2014; Regenbogen et al., 2018; Sestieri et al., 2011; Sestieri, Shulman, & Corbetta, 2010; M. Uncapher & Wagner, 2009; Vilberg & Rugg, 2012).

Taken together, the posterior parietal cortex has been frequently shown to be involved for these memory functions, whereas ventral and dorsal regions revealed differences in their functional recruitment for several cognitive functions. However, the precise functional difference in multimodal memory processing ween the ventral and the dorsal region of the PPL has yet to be determined, using an incidental multimodal learning task (study 2). Based on previous findings, I assumed that there is a precise functional difference between the ventral and the dorsal PPL regions during associative processing of information that have contextual meaning in terms of previously acquired knowledge (Baldassano et al., 2017; Branzi et al., 2021, 2020; Brodt et al., 2016; Ritchey et al., 2020).

1.1.3.2.1. The angular gyrus and its role in associative processing

In fact, the ventral posterior parietal lobe is a structurally and functionally heterogeneous system, which interacts with various cortical regions in frontal, occipital and temporal lobe (Desai et al., 2018; Hutchinson et al., 2014; Lee, 2018; Rushworth et al., 2006). As the vPPL reflects hemisphere-specific functionality (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002), an additional functional segregation between the left and the right hemisphere has been suggested (Caspers et al., 2006; Friederici, 2009; Vincent et al., 2008; Xu et al., 2017, 2016; Zhang & Li, 2014). Spatial and non-spatial attention, motor preparation and conflict-related activations were mostly related to the right hemisphere (Corbetta & Shulman, 2002; Seghier, 2013; Sestieri et al., 2011; Ye & Zhou, 2009). Thus, the right hemisphere was classified to be an important component of the so called “ventral attention network” (Corbetta et al., 2000; Corbetta & Shulman, 2002). Importantly, memory-related parietal activity has been frequently related to the left rather than the right hemisphere (Hutchinson et al., 2014; Rugg & King, 2018; M. Uncapher & Wagner, 2009). Indeed, across the literature on the integration of episodic features, the left vPPL has been frequently described as an associative region (or “convergence zone”) that can be related to a variety of different processes (Binder et al., 2009; Nelson et al., 2010; Seghier, 2013; Seghier, Fagan, & Price, 2010). Noteworthy, both the assumed function and the anatomical location strengthen the hypothesis that the vPPL is a key component of the (episodic) posterior memory network (PMN) involved in multimodal information integration (Gilmore et al., 2015; Humphreys et al., 2021; Ramanan & Bellana, 2019; Maureen Ritchey & Cooper, 2020; Rugg, Johnson, & Uncapher, 2015; Rugg & King, 2018; Shimamura, 2011).

Consistent with the left-right asymmetry observed in the ventral part of the posterior parietal system describes previously (Caspers et al., 2006), subsequent reviews also suggested a functional distinction both within and across the left and the right angular gyrus (AnG) (Nelson et al., 2010; Seghier, 2013). However, there is still little evidence for a structural and functional segregation of the right hemisphere. While right AnG activations were typically associaited with processes of attentional reorientation (Cappelletti, Lee, Freeman, & Price, 2010), increased activations in the left AnG were frequently related to a variety of different memory processes. With respect to study 2, this section provides an overview of the available evidence for the functional role of the left AnG, in particular during memory-dependent processing of multimodal encoding and retrieval.

Early on, in 1965, the angular gyrus has already been proposed to be a central component in the formation of relational representations (Geschwind, 1965). In this proposal, Norman Geschwind originally worte: “the angular gyrus is important in the process of associating a heard name to a seen or felt object, it is probably also important for associations in the reverse direction”(Geschwind, 1965). As already discussed, integrating a set of features, which classify a unique episodic event (such as items, living creatures, places or other contextual details), into a coherent relational representations is a significant cognitive function that constitute episodic representations (Squire, 2004; Tulving, 1985). Studies on episodic memory revealed that hippocampal activations were frequently reported to be accompanied by activation of a large brain network across the temporal, parietal and the frontal lobe (Addis, Wong, & Schacter, 2007; H. Eichenbaum, 2017; Rugg & Vilberg, 2013; Vilberg & Rugg, 2014). Consistent with these early proposals, functional and structural connectivity studies revealed dense polysensory connections between the AnG and both modality-specific cortical regions and modality-general areas, such as the hippocampus, the temporal lobe and regions of the frontal cortex (Nelson et al., 2010; Seghier, 2013; Uddin et al., 2010).

Based on the traditional notion of episodic memory, it is further assumed that the construction of complex relational representations correlates with a sense of vivid re-experiencing or so called "mental time travels" (Tulving, 1985). Further studies provided evidence for a strong relation between activation in the AnG and recollection strength of information (Bellana, Ladyka-Wojcik, Lahan, Mosocovitch, & Grady, 2019; Hutchinson, Uncapher, & Wagner, 2009; Vilberg & Rugg, 2007; A. D. Wagner, Shannon, Kahn, & Buckner, 2005). In line with these findings, further studies also demonstrated that the activity in the AnG scaled with memory performance (Humphreys & Ralph, 2015; Van Opstal, Verguts, Orban, & Fias, 2008; Vilberg & Rugg, 2009b, 2009a). Interestingly, studies on memory indeed underlined a moderate left-hemisphere lateralization in the AnG during episodic and semantic recollection. The relation between AnG and recollection performances has been even more pronounced by studies using multivoxel pattern classification, which found a relation between AnG activation and the specific "content" of the retrieved memory (Kuhl & Chun, 2014; Lee, Chun, & Kuhl, 2017). Interestingly, a relation between increased activity and encoded informational content was found not only during successful retrieval but also during recollection (Janice Chen et al., 2017; Kuhl & Chun, 2014; Kuhl, Johnson, & Chun, 2013; Lee et al., 2017). With regard to the subjective feeling in episodic experiences, activation in the left AnG activity was also associated with the coherent and vivid re-experiencing of memory details in several studies (Kuhl & Chun, 2014; Tibon, Fuhrmann, Levy, Simons, & Henson, 2019; Yazar, Bergström, & Simons, 2017). While investigating recollection effects when participant had to maintain retrieved relational information in memory, studies revealed that the left AnG indicated sustained activation for a variable delay period, whereas hippocampal structures revealed transient activation (Vilberg & Rugg, 2012, 2014). According to their interpretation, the left AnG plays an important role in the network responsible for binding processes. This and other studies suggested that this region specifically operates on internally generated memory representations of highly relational, multimodal content (Bonnici, Cheke, Green, FitzGerald, & Simons, 2018; Ramanan & Bellana, 2019; Rugg & King, 2018; van der Linden, Berkers, Morris, & Fernández, 2017). In particular, it has been pointed out, that the functional involvement of the left AnG might be sensitive to whether detailed contextual material or rather homogenous material, i.e. containing less contextual-rich and complex features, was retrieved (Bellana et al., 2019; Bellana, Liu, Diamond, Grady, & Moscovitch, 2017; Bonnici, Richter, Yazar, & Simons, 2016; Ramanan & Bellana, 2019; Rugg & King, 2018). In line with the assumption of a functional role of the AnG in contextual integration processes, increased activation in the left AnG was frequently related to learning and recollection processes of relational material (Bellana et al., 2019; Ramanan & Bellana, 2019; van der Linden et al., 2017). This functional role has been further supported by studies on multimodal integration, indicating that increased activations in the left AnG were more sensitive to multimodal than unimodal information during both retrieval (Bonnici et al., 2018, 2016; Yazar, Bergström, & Simons, 2014; Yazar et al., 2017) and encoding processes (Tibon et al., 2019). Based on both resting-state functional connectivity analyses and meta-analyses, the left AnG, in particular the ventral AnG, has been classified as the "connector (crossmodal) hub" which is specific for the integration of information within and across memory processing networks (Binder et al., 2009; Patterson et al., 2007; Seghier, 2013; Xu et al., 2017, 2016). Novel frameworks thus classified the left AnG as a key region of a large-scale neocortical network that might be coactivated with hippocampal structures during the processing of multimodal information (Humphreys et al., 2021; Maureen Ritchey & Cooper, 2020; Seghier, 2013; Shimamura, 2011; Xu et al., 2016). To be specific, AnG has been regarded as a necessary precursor to the formation of "situation models" (Ranganath and Ritchey, 2012) and "schemata" (Schwartz et al., 2011; van der Linden et al., 2017; Wagner et al., 2015), as those are specific for the acquisition of “thematic relationships” (Davis and Yee, 2019; Lewis et al., 2019) and “event concepts” (Binder and Desai, 2011). Consistent with the assumption that the AnG is particularly engaged during contextual-related processing, there are few studies that tested its activation across episodic and semantic contexts within the same individual (Bellana et al., 2019; Bonnici et al., 2016). These studies found that the recollection of sensory details of both episodic and semantic memory recruited the left AnG (Bonnici et al., 2016). Furthermore, it has been pointed out that the activity in the left AnG region might not be limited to a specific memory alone (e.g. encoding, retrieval). Assuming that memory is an integral component of information processing, its memory-dependent processing should be thus classified by the nature of this left hemisphere dominance during memory-dependent processing in general (Hasson, Chen, & Honey, 2015; Maureen Ritchey & Cooper, 2020).

Nevertheless, there are also studies that questioned the specific functional role of the AnG in memory processes (Buckner et al., 2008; Kim, 2019; Vatansever, Manktelow, Sahakian, Menon, & Stamatakis, 2017). Accordingly, this region might be rather a component of the default mode network, in which increased activation are mainly found during resting states compared to cognitive task (Buckner et al., 2008). In contrast, further studies revealed that the default mode network has been positively enaged during different task performances, such as episodic memory processes or imaging future events (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Benoit & Schacter, 2015; Kim, 2011; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). Furthmore, it has been found that activations across default mode regions are differently sensitive to both specific memory processes and conscious/unconscious memory retrieval (Bellana et al., 2017; Daselaar, Prince, & Cabeza, 2004; Legostaeva et al., 2019; Seghier, 2013; Shannon & Buckner, 2004; Wheeler & Buckner, 2004; Yang, Weng, Zang, Xu, & Xu, 2010). Accordingly, the default mode network not only reflects a task-negative network, but related regions might also operate in a more complex manner as previously thought. Considering these and previously discussed findings, related regions might exhibit both positive and negative activations which are assumed to be differently sensitive to current task requirements (Andrews-Hanna et al., 2010; Bellana et al., 2017). Consistent with recent spatial parcellation frameworks for the left AnG, it has been suggested that different subregions of the left AnG might support different cognitive mechanisms (Caspers et al., 2006; Seghier, 2013; Uddin et al., 2010), accounting for its functional activation or deactivation across a variety of different task.

Taken together, as the functional role of the left AnG has been frequently related to associative rather than perceptual processes, novel frameworks reasonable proposed that the left AnG reflects a domain-general role during the generation or reactivation of relational and representations containing contextual meaning. Furthermore, the functional role of the AnG might not be classified in isolation, but in combination with other cortical regions involved in the construction and representation of episodic information (Humphreys et al., 2021; Ramanan & Bellana, 2019; Maureen Ritchey & Cooper, 2020; Seghier, 2013).

1.2. Aims and hypotheses of the dissertation

Humans frequently acquire knowledge under incidental situation that enables them to adapt as fast and accurate as possible to regularities and contingencies inherent in their environment. Across psychological and neuroscientific studies, this unintentional learning process is traditionally investigated in incidental learning situations. In these tasks, participants were instructed to react to a set of perceptual stimuli, which, unbeknownst to the participants, follow a specific underlying regular pattern of stimulus events. The fMRI studies included in this dissertation aimed to investigate the neural correlates underlying the incidental acquisition of associative knowledge using unimodal (study 1) and multimodal (study 2) associations. Furthermore, within an additional behavioral study (study 3), my colleagues and I aimed to examine whether the pure perceptual implicit learning effect could also occur across modalities, the auditory and the visual modality.

Study 1

While previous SRT studies have only examined unimodal sequence learning, it is unclear whether a series of auditory stimuli could also lead to implicit learning. With respect to the first study, previous studies have frequently demonstrated that the functional role of the medial temporal lobe, in particular the hippocampus, is not exclusively linked to explicit memory, but is also involved in the acquisition of implicit memory (Duss et al., 2014; Henke, 2010; Rose et al., 2011, 2004). Accordingly, hippocampal involvement particularly relies on the nature of learned associations and not on the involvement of awareness. Building up on prior findings, this first fMRI study addressed the hypothesis of an assumed generalized functional role of the hippocampus for the implicit formation of sequenced perceptual representations (Rose et al., 2011). To test this hypothesis, I used a modified version of the SRT task with auditory stimuli. This is of particular interest, as previous studies on implicit pure perceptual learning have mostly used visual stimuli as perceptual inputs.

As studies on incidental learning traditionally examine the various sensory modalities independently (unimodal learning), it is noteworthy that perception is actually multimodal. Clearly, perception usually operates in terms of contextual information that is provided by multiple sensory modalities. Across the literature, it has been widely shown that learning from multiple senses is not only more realistic but also more effective than unimodal learning (Shams & Seitz, 2008; Shams et al., 2011). The involvement of some cortical regions in episodic memory processes has been generally agreed, whereas the functional involvement of the parietal cortex in memory processes is still controversially discussed. Based on the assumption that the posterior parietal cortex could be anatomically and functionally segregated into a ventral and dorsal subregion, the precise difference in activation between these two regions during associative memory-dependent processing remains unclear.

Study 2

Thus, in the second fMRI study, I investigated the differentiation of the neural processing networks during the acquisition of multimodal associations, which is a crucial functional in episodic memory. Crucially, I put particular focus on the functional role of dorsal and ventral regions of the posterior parietal lobe (PPL) during both learning and recollection of new multimodal associations under an incidental learning condition. To test this, I used a paired-associate learning task in which volunteers incidentally acquired memory for new semantically incongruent audiovisual stimulus pairs with different underlying binding regularities. As explicit memory could be acquired incidentally over time, this approach reflected a more real-life associative learning experience than using unimodal stimuli. To illustrate, within one condition, there were multimodal associations that were repeatedly presented together (“constant” condition). The other condition contained different audiovisual stimulus pairs that were rearranged throughout learning sessions (“variable” condition). Importantly, the amount of unimodal stimuli and related presentation was identical in both conditions, but the only difference was the constant or variable pairing of the unimodal stimuli. This specific multimodal paradigm allowed us to investigate the diversity in functional involvement among PPL regions being both critically recruited during constant and variable processing, respectively. I assumed that constant audiovisual associations could be automatically acquired over time, and thus successfully retrieved in a subsequent recollection test (“constant” condition). Based on previous findings, I hypothesized that the ventral PPC was specific for automatic, constant processing of consistent multimodal stimulus pairs. In contrast, for the variable multimodal condition, I assumed that more attentional control processes are required when different unimodal stimuli has to be processed separately or “in isolation”. I thus expected increased activation within the dPPC in attentional, control processing of multimodal stimulus pairs. Finally, in the subsequent recollection test, the amount of explicit multimodal knowledge acquired under an incidental condition was assessed. Crucially, in contrast to the learning phase, the pairs were presented in a sequential order, i.e. as two successive unimodal stimuli. This was important for investigating whether the new acquired multimodal knowledge could also be accessed when only unimodal information were presented. I thus hypothesized a clear functional difference in PPC activation during recollection. From this perspective, I suggested that the angular gyrus critically contributes to constant processing of episodic, consciously-accessible knowledge incidentally acquired over time, independently of the memory stage. Furthermore, I expected hippocampal involvement during episodic memory processing of newly, explicitly learned multimodal associations (H. Eichenbaum, 2017; Henke, 2010).

Study 3

The aim of the additional behavioral study was to address the question of whether crossmodal perceptual representations could also be learned and acquired implicitly. Focusing on stimulus and response modalities, recent studies suggested that crossmodal or multimodal representation of the stimulus input can be acquired implicitly within a common module (Haider et al., 2020; Hommel et al., 2001). Taken together, this study examined crossmodal learning of *different pure perceptual modalities* under incidental learning conditions.

To sum up, in all presented studies, I tested whether *pure perceptual associations* can be learned under *incidental conditions*, i.e. without the explicit instruction to focus on the underlying stimuli regularities. The aim of study 1 was to test whether the nature of learned associations - rather than explicit instructions – are specific for the involvement of hippocampal activation during incidental associative learning and related implicit memory formation. The aim of study 2 was to test whether multimodal perceptual associations can also be learned incidentally, while being consciously accessed (explicit memory) throughout learning trials. Furthermore, this study aimed to investigate whether the ventral posterior parietal lobe significantly contribute to associative processing of multimodal information. Finally, the aim of the additional behavioral study 3 was to test whether an audio-visual (crossmodal) sequence could also be learned implicitly without the involvement of explicit guided attentional processes.

2. General Material and Methods – All Studies

2.1. Participants

All volunteers who participated during piloting or the presented experiments were recruited by online advertisements and had no history of psychiatric or neurological illness. Across all studies, the general exclusion criteria were medical reports, such as neurological or psychological disorders, substance abuse, current medication, or technical difficulties during fMRI measurements.

Based on the research question of the respective study, participants were further excluded from subsequent analyses if they gained explicit memory about the underlying hidden regularity (i.e. studies on implicit memory: study 1 and 2), or if they did not noticed any regularity (i.e. study on incidentally acquired explicit memory: study 2).

All presented studies were approved by the ethics committee of the "Deutsche Gesellschaft für Psychologie" (DGPs). The methods were conducted in accordance with the relevant ethical guidelines and regulations of the Declaration of Helsinki. Each volunteer war instructed to sign an informed consent before participating in the fMRI experiment.

2.2. Stimuli and experimental set-up

Behavioral and imaging data collection was performed at the University Hospital of Eppendorf in Hamburg. The volunteers, who participated in an fMRI study, were first familiarized with the experimental set-up before entering the scanner. Each participant was thus trained how to respond or react within a corresponding practice session prior to the scanning.

For both fMRI studies, the stimuli were presented onto a white background screen controlled by a computer that ensured synchronization on a MR scanner using the Presentation software package (Neurobehavioral Systems Inc, USA; www.neurobs.com/). An LCD projector displayed the visual stimuli to the participants via a mirror system (10 x 15° field of view) inside the scanner. Auditory stimuli were presented via MR-compatible headphones. Due to scanner noise, the level of sound pressure was individually calibrated to a comfortable level for each participant. The responses of the participants were recorded using MRI-compatible response devices (one device for each hand).

2.3. Paradigms on incidental associative learning

With respect to the presented research questions of this dissertation project, I was particularly interested in whether incidental associative memory can be acquired within the auditory modality (study 1) and across two different modalities (study 2 and 3). To be specific, in all presented studies, I tested whether perceptual associations can be learned without the explicit instruction to do so. While the focus of study 1 and 3 was to examine the behavioral (study 3) and neural indicator (study 1) underlying implicit associative memory, the focus of study 3 was to investigate the behavioral and neural indicators underlying explicit crossmodal memory which had been acquired under an incidental learning condition.

Traditionally, studies on incidental learning are traditionally composed of three critical components (Cleeremans et al., 1998).

- First, the learner has to be exposed to a complex regularity or sequence in an incidental learning condition (P. A. Frensch & Rünger, 2003; Haider et al., 2012; Nissen & Bullemer, 1987). For example, the serial reaction time (SRT) task is a classical used parameter for measuring implicit sequence learning (for more details, see "Introduction").

The other two measurements are then employed in the subsequent recollection phase:

- The second measure (an objective measure) relies on how well the acquired knowledge can be expressed (learning vs guessing),
- The third measure (an subjective measure) is used to assess to what extend the learner was aware of the acquired associative knowledge (implicit vs explicit memory).

Based on these classical principles, all three presented studies of this dissertations project employed both an incidental learning task and a recollection task in order to assess implicit and explicit memory as well as to investigate the underlying memory processes related to encoding and retrieval of the acquired associative memory, respectively. To do this, I have designed three different incidental learning paradigms, in which participants acquired associative knowledge

- within a single perceptual modality: study 1: the *Auditory Serial Reaction Time Task*
- across two different perceptual modalities: study 2: *Incidental Paired Associative Learning Task* and study 3: *Crossmodal Audio-Visual Serial Reaction Time Task*

Furthermore, to test whether associative knowledge was acquired and to assess whether the acquired memory is of implicit or explicit nature, adapted versions of the traditional force-choice tasks were used in combination with a confidence rating (for more details, see below). Furthermore, within all studies, participants performed post-experimental questionnaires and received an appropriate debriefing after participants within these studies.

2.4. Method for measuring the learners' sensitivity and conscious state

The assessment of the relative contribution of implicit and explicit knowledge on associative learning is an important issue in the literature on incidental learning (Cleeremans & Destrebecqz, 2003; Cleeremans & Jiménez, 2002; Jacoby, 1991). As already introduced in the beginning, the combination of two sensitive methods, an objective and a subjective measure, is frequently used as a sensitive measurement for the acquired knowledge and the conscious state of the learner. These measures are employed in various different forced-choice tasks, such as the generation (or completion task), the recollection task, or the free recall task. With respect to the research questions of this dissertations project, implicit and explicit associative memory were assessed by using modified versions of the traditional force-choice tasks, which are introduced briefly in the following (for a detailed description, see "Study Methods and Results").

The generation task (also known completion task) is a well-established method for measuring the amount of the acquired knowledge and the conscious state of the learner. Within this test, a stimuli is presented to the participants, and he or she is then asked to predict the identity of the next stimulus as well as to indicate their confidence about their decision. Based on these principles, for fMRI study 1, I used a modified version of a classical generation task while employing an almost identical experimental set-up as in the corresponding acoustic SRT task. After the presentation of each stimuli the sequence paused and a question mark appeared in the center of the screen. Participants were then instructed to indicate the "next" response or stimulus via button presses. Unbeknownst to the participants, all visual stimuli were presented in the same presentation sequence (i.e. same sequential order) as in the learning task. Furthermore, each response was followed by a confidence rating that indicated the confidence in their response.

Within a classical recollection task, participants are generally confronted with a variety of "known or learned" (i.e. old) and "new" stimuli about which a judgement - based on a specific classification criterion- has to be made (Cleeremans & Destrebecqz, 2003; Cleeremans & Jiménez, 2002; Jacoby, 1991). For example, a participant is instructed to classify a stimulus as being an “old” or a “new” stimulus or as belonging to “category A” or “category B”. For fMRI study 2, the test phase based on the principles of a classical recollection forced-choice task following an incidental learning task. Critically, the aim of study 2 was not only to assess the amount of explicit memory, but also to test for participants’ ability to differentiate between presented stimuli inputs, i.e. differentiate between (the learned) constant multimodal pairs and those which “varied” across trials (for a detailed description, see “Study Methods and Results). Interestingly, in contrast to the learning task, I presented audiovisual pairs in a sequential order, i.e. as unimodal stimuli. This specific approach allowed to test if explicit knowledge of the multimodal associations (a) was actually acquired and (b) could further be controlled by the participant while being able to transfer the acquired knowledge under unimodal experimental conditions. These two criteria would additionally confirm that the acquired knowledge is of explicit and not implicit character. Finally, as implemented in all presented studies, each response of the participant was followed by a confidence rating.

Within a classical free recall task, are first asked if they if they recognized any regularity or any specific structure within the learning task. If so, participants are then instructed to indicate as much as possible of their acquired knowledge. For the additional behavioral study 3, participants were asked Furthermore, they were asked to identify any stimuli combinations (i.e. audiovisual pairs) which they thought had been presented regularly together, i.e. as audiovisual stimuli combinations or transitions. However, if they were unsure about their response, they were still motivated to make any guesses. Each response was made via button presses and, as in study 1 and 2, followed by a confidence rating.

To sum up, each of the three studies consisted of two phases, an associative learning phase and a test phase. For an overview over the specificities of the three incidental learning paradigms, see Table 1.

Table 1. Overview over the specificities of the incidental learning paradigms in the three studies

Study	**Study 1**	**Study 2**	**Study 3**
Learning phase	Auditory Serial Reaction Time Task	Incidental Paired Associative Learning Task	Crossmodal Audio-Visual Serial Reaction Time Task
Stimuli modality during learning	Unimodal	Multimodal	Crossmodal
Stimuli type	Tones (sine wave samples)	Images and sounds (natural)	Colored squares and tones (sine wave samples)
Number of stimuli	Six	16 images and 16 sounds	four
Type of learned associations	Auditory sequence	Audiovisual stimulus pairs	Audiovisual sequence
Implicit / explicit memory	Implicit	explicit	implicit
Control condition	No	Yes	Yes
Test phase	Classical completion task	unimodal forced-choice task	Free recall of crossmodal combinations

2.5. Behavioral data acquisition and analyses

Data acquisition is described in the following, if not stated otherwise. All studies were performed at the University Hospital of Eppendorf in Hamburg. In cooperation with my supervisor Michael Rose, I designed and programmed the fMRI study 1 and 2. Furthermore, I conducted the experiment, analyzed the data and wrote the corresponding final manuscript on my own, but under the supervision of Michael Rose. Throughout my PhD time, I further contributed to other additional behavioral studies, such as study 3, which was designed, programmed, conducted and analyzed in cooperation with Michael Rose and Philipp Taesler.

Visual stimuli were presented onto a white background screen and motor responses were recorded using the Presentation software package (Neurobehavioral Systems Inc, USA; www.neurobs.com/). Auditory stimuli were presented via headphones. The level of sound pressure was individually calibrated to a comfortable level for each participant.

2.5.1. Behavioral analyses

Learning phase

For the behavioral analysis of the learning phase, I calculated the amount of incorrect responses for each participant and excluded those, which indicated a high level of errors (> 30% errors). For each included participant, additional single trials were excluded from further behavioral and fMRI analyses if they revealed incorrect or extraordinary slow responses (response latency above 2000ms). Furthermore, the effect sizes of the behavioral analyses using Cohen's *d* and eta squared (η2) were calculated and reported, if not stated otherwise (J. D. Cohen, 1969; Rosenthal, R., Robert, R., & Rosnow, 1985).

Test Phase

For each participant I first calculated the amount of correct responses in order to assess participants' performance. The number of correct responses were used as a performance score for the acquired implicit or explicit memory. A score above chance level would indicate that (1) participants actually learned the characteristics of the perceptual material (i.e. the sequence, stimuli combinations) throughout the learning sessions and (2) were able to express the acquired knowledge. Performance scores that were not significantly higher than chance level (i.e. 50% correct) were excluded from further analyses (and classified as guesses).

Among included participants (with a performance score above chance level), I then assessed whether the acquired knowledge was of implicit or explicit character. To assess this, I relied on the two criteria introduced previously:

- One criteria was the *verbal report,* which directly followed the test phase. After the experiment, participants were asked to verbally report the new acquired knowledge. If the underlying regular structure (i.e. a regular sequence or an audiovisual combination) was noticed and/or could be verbally reported, participants were classified as "explicit participants". Otherwise, I classified them as "implicit".
- With the other criterion (the test phase), I assessed the *relative contribution of implicit and/or explicit acquired knowledge*. In particular, this allowed me to detect a participant who might have acquired "total" or "partial" explicit knowledge but lacked the confidence to verbally report it. To do this, correct responses were grouped into "explicit" and "implicit" responses, according to their "high confidence" or "low confidence" ratings, respectively. The relative distribution of these two groups was used as an indicator for the conscious state of the learners' acquired knowledge (Wessel et al., 2012). Memory was classified as implicit if performances were above chance level with no significant difference between high and low correct responses, as in study 1 and 3. In contrast, memory was classified as explicit if performances were above chance level and, importantly, if there was a significant difference between the "high and low confidence" ratings (i.e. high > low confidence ratings) as in study 2.

Signal detection theory

Furthermore, for the presented fMRI studies, participants' performance of the recollection task was additionally used as a measure for participants' ability to differentiate between the newly acquired multimodal associations and the variable multimodal conditions. This allows assessing whether the acquired knowledge was of explicit nature. To do this, the analysis was based on the principles of the signal detection theory (Stanislaw & Todorov, 1999). The traditional theory addressed the ability to differentiate between relevant information, the "signal", and random or irrelevant information, the "noise", when being confronted with distinct information-bearing input. Using this theory, the question whether the learned stimuli can be differentiated from novel stimuli, which were not shown during the learning phase ("old versus "new" stimulus, was addressed. For the force-choice task, as in study 2, the aim was to test participants' ability to differentiate between constant and variable multimodal stimuli. Hence, to apply the signal detection theory to the data, responses had to be classified into four different types of outcomes: hits, misses, correct rejections, false alarms. With respect to study 2, the different types of outcomes were as follows:

- *Hits*: multimodal stimulus pairs that were correctly identified as being those which remained fixed / were continuously presented together throughout learning (i.e. constant pairs)
- *Misses*: multimodal stimulus pairs that were incorrectly judged as "not constant pairs" (i.e. variable pairs)
- *Correct rejections*: "variable" multimodal stimulus pairs that were correctly judged as those which were continuously recombined throughout the learning sessions
- *False alarms*: "variable" multimodal stimulus pairs that were falsely classified as constant multimodal pairs

To exclude a liberal response bias (Stanislaw & Todorov, 1999), both the hit rate (correct responses of the constant condition) and the false alarm (incorrect responses of the variable condition) has to be taken into account in order to reliably measure participants' memory sensitivity, i.e. the ability to differentiate between the two conditions. One of the most frequently used statistics to calculate the related memory sensitivity is the so-called sensitivity-index, or *d'* ("d prime") (Stanislaw & Todorov, 1999). Accordingly, the statistic *d'* is the standardized difference between the hit rate (of the constant condition) and the false alarm rate (of the variable condition). To calculate the *d'*, the following formula should be used:

$$d' = \mathrm{Z}(\text{hit rate}) - \mathrm{Z}(\text{false alarm rate}),$$

with $\mathrm{Z}(p)$, $p \in [0,1]$ which is the inverse of the cumulative distribution function of the Gaussian distribution (Stanislaw & Todorov, 1999). With respect to study 2, a high value of *d'* would reflect a high ability to discriminate between constant and variable multimodal stimuli, while a *d'* of zero would rather reflect pure chance performance, i.e. guessing. Therefore, for each participant, I computed the statistic *d'* and used this value as an additional objective measure for participants' memory performance. As in study 1, this memory sensitivity value was included as a covariate in later neuroimaging analyses in order to relate the acquired knowledge to the neural responses.

2.6. Functional magnetic resonance imaging

For both fMRI studies (study 1 and 2), I used functional magnetic resonance imaging (fMRI) in order to relate learning- and recollection-related effects to neural correlates in regions of interest. Stimulus presentation was controlled by a computer that ensured synchronization on the MR scanner. Participants' responses were recorded using MRI-compatible response devices (one device for each hand). An LCD projector displayed the visual stimuli to the participants via a 45° mirror system to the inside of the scanner. Auditory stimuli were presented via MR-compatible headphones.

2.6.1. Principles of functional magnetic resonance imaging

This noninvasive neuroimaging technique uses a strong magnetic field in combination with radio wave technologies which allows to detect changes within the magnetic properties of blood (Huettel, 2005; Smith, 2004). Neurons need energy and oxygen to function, thus activity in a specific brain region requires an increase in metabolism, such as an increase in oxygen uptake of the cell accompanied by a dynamic regulation of the blood flow. This is called the hemodynamic response. As oxygenated and oxygen-depleted hemoglobin have different magnetic properties, an increase in the oxygenated blood level results in a chance (a reduction) in the local magnetic field inhomogeneity. As a result, a stronger transversal magnetic signal is sent, which is known as the Blood Oxygenation Level Dependent (BOLD) signal. While BOLD effects can be acquired over time, with a rather poor temporal resolution of several seconds, effects can be acquired with a reliable spatial resolution. This enables to localize changes in the BOLD signal accurately on a millimeter scale and map these changes in activation on an array of 3D pixels, which are known as voxels, across the brain. As the presented studies aimed to examine the neural correlates involved in the incidentally acquisition of associative memory, I decided to use this noninvasive technique with a relatively high spatial resolution.

With respect to the analysis of imaging data, the most frequently used method is the general linear model (GLM) (Poline & Brett, 2012; Smith, 2004).The GLM is a method to model an observed signal, i.e. the individual BOLD of a single brain voxel (“Y“), in terms of (one or) multiple explanatory variables, i.e. called the regressors (“x“). Regressors are task-related, which means an input regressor might be the onset of a stimulus of a specific condition. Regressors are convolved with a hemodynamic response function in order to assess the average amplitude of the BOLD signal in response to each condition in the GML. For best model estimation, relative weights assigned to each regressor, the so called beta weights (“β“), reflecting the contribution of the regressor to the observed signal. Differences between the measured signal and the best fitted model, are called the residual error. For the best GLM fit for the timeseries of the measured signal in each single voxel Y, a linear combination of multiple scaled regressors $x1\ \beta1$ to $xn\ \beta n$ and a residual term ε is used. This can be expressed as:

$$Y = x1\ \beta1 + x2\ \beta2 + x3\ \beta3 + \ldots + xn\ \beta n + \varepsilon$$

As every voxel has its own time-series, the GLM analysis is performed separately for the fMRI data at each single voxel, thus it is a voxelwise analysis (Poline & Brett, 2012). Further, this procedure is a mass-univariate analysis, because beta weights for each voxel’s time-series are assessed. Hence, the best model fit can be approached by minimizing the difference between the measured signal and the fitted model, i.e. achieving the smallest residual error, and by finding the best value for each scaling parameters (beta) of each regressor. The result of this approach is a brain map which reveals for every voxel the contribution of every task variable to the observed signal. Research question of interest can be then expressed in the GLM by using contrasts (Poline & Brett, 2012; Smith, 2004). Contrast maps results from defining a set of weights to each beta. Due to this mass-univariate approach, i.e. performing the same analysis many times separately for each voxel in the brain, p-values have to be corrected for multiple comparisons in order to avoid false positive findings. On individual subject level, each contrast map is transmitted to the second level analysis for testing regional activation within a specific group. For each single voxel, across individual subjects, the second level model aims to find the best model fit to best explain the average effects, i.e. the beta, and the related variance of the group. This approach allows to investigate significant differences in activation between different conditions consistently within a group using statistical tests. The second level model and subsequent statistical tests were used in order to examine the functional involvement of brain regions of interest in specific task-related conditions. In addition to that, I tested for the effect of the covariate in order to identify the relation between memory performance and individual event-related blood oxygen level-dependent (BOLD) activations in regions of interest.

2.6.2. Functional magnetic resonance imaging analyses

For the first fMRI study, I tested whether there is a relation between implicit sequence memory of auditory association and hippocampal activation. For the second fMRI study, I tested whether there is a difference in activation between the ventral and dorsal region of the posterior parietal lobe when multimodal consciously-accessible knowledge was incidentally acquired over time. Furthermore, I tested whether there is a relation between the explicit associative memory of audiovisual associations and activation within the ventral posterior parietal lobe. Finally, I also tested for a functional involvement of the hippocampus for newly learned multimodal associations.

For both fMRI studies, I reported significant fMRI effects at a threshold of $p<.05$ corrected for familywise error (FWE) using whole brain analysis. Based on the a priori assumptions of hippocampal involvement during the flexible acquisition and organization of abstract information, I performed region-of-interest (ROI) analysis in order to examine learning-related activation in bilateral hippocampus (study 1 and 2). Furthermore, I further tested for a functional difference in neural response between ventral and dorsal regions of the bilateral parietal cortex using ROI analyses (study 2). The subsequent ROI sphere was based on peak activation coordinates from a large-scale, multi-domain meta-analysis of Humphreys and Ralph (2014), in which the functional role of the posterior parietal cortex in several different cognitive domains was addressed (Humphreys & Ralph, 2015). Finally, all significant fMRI results were reported at a voxel-level threshold of $p < .05$ FWE small volume corrected (SVC).

3. Study Methods and Results

3.1. Study 1 – Auditory sequence learning

3.1.1. Participants

Sixteen healthy individuals participated (between 18-36 years old, 6 females) within this fMRI experiment. All participants were right handed and had normal or corrected-to-normal vision. I had to exclude one participant who indicated a high level of errors (>30% errors), and was thus not included within behavioral and imaging analysis.

3.1.2. Study design and paradigms

Experimental set-up and stimuli

Within this fMRI study, I presented two black arrows on a white square (0.6° x 0.6°; distance 2.3°) against a grey background screen. The black arrows pointed either upwards or downwards on the white squares, as illustrated below (figure 1).These arrows corresponded to the two respective response buttons, i.e. left and right button. For stimuli presentation subsequent recording of the behavioral data, the "Presentation" software (http: //www. neurobs.com/) was used. The computer was synchronized with the MR scanner allowing for the manipulation of the experimental visual and auditory stimuli.

As the study investigated auditory sequence learning, I used sinusoidal tones as auditory stimuli. To be specific, I used five sinusoidal tones that differed in frequency (400 Hz, 600 Hz, 800 Hz, 1200 Hz, and 1800 Hz). Auditory stimuli were presented to the volunteers via MR-compatible headphones.

Experimental procedure

The employed experimental design consisted of two phases, a learning phase (auditory SRT task), and the test phase, as illustrated in Figure 1. As introduced previously, the test phase was divided into the completion task, a confidence rating. All included volunteers performed the learning task and the completion task within the MR scanner. The test phase was then followed by a free-recall task, a post-experimental interview and a debriefing outside the scanner.

The auditory serial reaction time (SRT) task

To study implicit sequence learning of auditory (i.e. unimodal) associations, I used a modified version of the serial reaction time task. This modified paradigm was adapted from a previous fMRI study on implicit sequence learning of perceptual associations conducted by Rose et al. (Rose et al., 2011). As in the study by Rose et al, I exclusively examined pure perceptual sequence learning by excluding motor response learning. Thus, the two modalities, the perceptual and the motor modality, were independently manipulated by implementing a trial-by-trial remapping of response buttons. This specific remapping allowed to exclude motor learning and thus the dissociation of the two modalities, since the motor sequence relied on an irregular, unpredictable variation of button presses. While the assignment of the stimulus to the response location changed in each trial, the perceptual sequence followed a systematic variation of auditory target stimuli. To sum up, this well-establish methodological approach allowed to identify the neural mechanism underlying pure auditory sequence learning.

Five different sinusoidal tones were used as auditory stimuli, which followed a determined sequence across trials. After each tone presentation, the task was to identify whether the current presented tone was higher or lower (in pitch) than the tone they heard previously (see Figure 1a). While not being informed about the determined order of the auditory sequence, participants were told to respond as fast as possible. As responses had to be given by button presses, each auditory stimulus was simultaneously presented with two visual stimuli consisting of two arrows either pointing upwards or downwards. Thus, the two arrows indicated the two response possibilities concerning the pitch rating ("higher tone" or "lower tone") of the current tone. To sum up, this specific SRT paradigm allowed that a pure perceptual sequence could be incidentally learned.

The completion task

For the completion task, I applied the logic of a generation task in order to identify the amount of implicit (and explicit) sequence knowledge (see "General Materials and Methods"). This means, unbeknownst to the participants, perceptual stimuli were presented in the same presentation sequence as in the learning task, and were instructed to predict the next response via button presses (see Figure 1b). To be specific, if they predicted the next auditory stimuli to be lower, they had to press the left key; if they predicted the next auditory stimuli to be higher, they had to press the right key. Each auditory stimuli was presented four times to the participant. Furthermore, each response was followed by a confidence rating about their last response (Left key: Low confidence, right key: high confidence). Importantly, only participants who acquired implicit multimodal knowledge were included. The criteria used to assess whether the new acquired knowledge is implicit or explicit is described in the next section. This specific method tested whether participants were able to express (implicitly) their acquired sequence knowledge, even if knowledge was only implicitly acquired. In particular, above chance performances and no significant difference between high and low correct responses were used as an indicator for successfully acquired implicit memory.

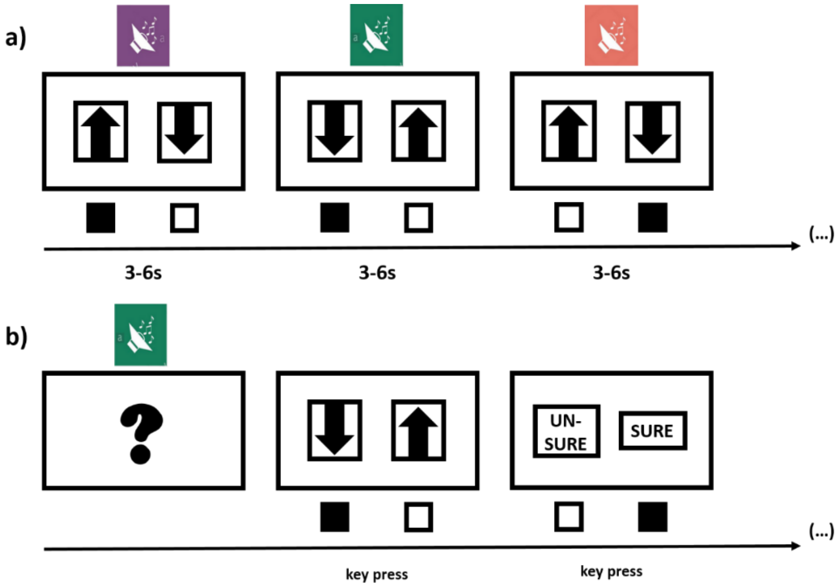

Figure 1: **Schematic illustration of the learning paradigm and the generation task of fMRI study 1.** (A) The auditory serial reaction time task was used to investigate pure perceptual sequence learning by excluding motor response learning. (B) The generation task was used to assess the acquired sequence knowledge and the conscious state of the learner. Note: Within this illustration, the colored sound icons were only used to indicate the auditory sequence, however they were not shown as visual icons to the participants.

3.1.3. Analyses

Statistical analyses of behavioral data

For both, the learning and the recollection phase, I only included correct responses in the subsequent fMRI analyses. The recollection phase was used to assess the amount and the status of multimodal knowledge by two criteria: the completion task performance in combination with the confidence rating, and the verbal report (please see "General Material and Methods").

First, for the behavioral data of the learning phase, I only included participants who performed above chance level on their correct responses. For each included participants, incorrect trials or trials with an extraordinary slow responses (i.e. with a latency above 2000 milliseconds) were excluded within further analyses. For the reaction time (RT) analyses, the mean RT across the learning trials (SRT task) with respect to the onset of the correct response were calculated for each single input.

For the test phase, the generation task was used to directly measure the implicit sequence knowledge, in which participants were instructed to indicate the pitch of the next auditory stimuli. To assess participants' performance score and awareness, I first subdivided the responses into correct and incorrect responses. Furthermore, correct responses were grouped according to their confidence rating, i.e. into "high confidence" or "low confidence" responses. This grouping allowed me to differentiate between correct responses with high confidence and correct responses with low confidence. Participants were classified as "explicit", if there was a high amount of correct responses and high confidence ratings. Participants were classified as "implicit", if there was a high amount of correct responses but an equal distribution between high and low confidence ratings.

As the presented study was on implicit memory, only participants with implicit memory were included within further analyses. For included participants, I then calculated the amount of the "implicit" correct responses for each individual tone-to-tone transitions (in percentage). This approach is based on the assumption that (implicit) sequence knowledge might develop from distinct parts of the sequence one by one. Thus, participants might first acquire chunks (Cleeremans & McClelland, 1991) before acquiring knowledge about the "complete" sequence. The outcome is referred to as the completion task score in the following passages. The completion task (CT) score was then used as an objective measure for implicit sequence knowledge acquired from the previous learning task. In the subsequent neuroimaging analysis, the CT score was included as a covariate in order to examine the different modulations of BOLD signal responses in relation to the acquired implicit memory. To be specific, testing for the effect of the covariate allowed the examination of the different tone-specific neural responses in relation to the acquired implicit knowledge for each tone-to-tone transition during the last session of the learning phase.

Finally, the free-generation test and the post- experimental questionnaire were included in order to additionally test for possible explicit knowledge. For the free-generation test, the amount of correctly recalled tone-to-tone was calculated. If a participant was able to transfer the acquired knowledge concerning the underlying sequence correctly within the free-generation task, he or she was excluded from further analyses. Another exclusion criteria was if a participant was able to verbally describe the underlying regularity within the post- experimental interview. Noteworthy, no participant was excluded from further analyses based on these two additional exclusion criteria.

Functional MRI acquisition and data preprocessing

At the University Hospital of Eppendorf in Hamburg, I used a 3 T MR Scanner (Siemens Trio) for imaging data acquisition. Furthermore, a standard gradient echo-planar imaging T2*-sensitive sequence was used with 36 contiguous axial slices, 2mm thickness, 1mm gap, and a repetition time (TR) of 2.178 s (echo time (TE) 25ms, flip angle 80°, field of view 216 mm^2). The high-resolution structural MRI was acquired for each participant (1x1x1 mm voxel size), while using a standard three-dimensional T_1-weighted FLASH sequence.

For pre-processing and statistical analyses of the functional MRI data, I used the statistical parametric mapping (SPM12; http://www.fil.ion.ucl.ac.uk/spm/; Welcome Department of Imaging Neuroscience, London, UK). Functional images were realigned and unwarped to the middle volume and spatially normalized to the standard EPI template image of the MNI (Montreal Neurological Institute). Furthermore, volumes were smoothed with a 6mm full width at half maximum (FWHM) isotropic Gaussian kernel.

Functional imaging data analysis

For the first level analysis, data was analyzed by an estimation of the BOLD signal for each tones and error response trials across the learning phase (session 1-3) convolved with a hemodynamic response function. Further, I used a high-pass filter with a cut-off period of 120 s and a low-pass filter (Gaussian envelope FWHM of 4 s). Regression coefficients were estimated for each regressor by using a general linear model. Then, a contrast for each tone-to-tone transition was performed, which were then transmitted to the second level.

For group level analysis, a flexible factorial design with inter-subject variability as random effects was used. The flexible factorial design included one factor for the subject and five additional factors for each tone-tone transition. The objective parameter for the acquired implicit sequence knowledge, the completion task score, was included as a covariate within the group level model for each tone and each subject, respectively. The aim was to test for the effect of the covariate. This allowed to examine the different modulations of BOLD responses in relation to the acquired implicit memory. Crucially, as only one completion score for each tone in one participant could be computed, the inclusion of a covariate at the first level was not possible. Therefore, the effect of the covariate could have only be examined at the group level across subjects. Relating participants' acquired implicit sequence knowledge to the different modulations of BOLD responses, the incidental learning effect could be investigated.

With respect to the a priori hypothesis, I defined the hippocampus as a Region of Interests (ROI). I centered the region of interest on coordinates of a previous conducted fMRI study on implicit learning of a pure perceptual sequence by Rose et al. (2011) [20]. Thus, the ROI was based on the following coordinates; left: $x = -34$, $y = -20$, $z = -18$; right: $x = 28$, $y = -24$, $z = -18$. For the a priori ROI analysis I corrected for multiple comparison (FWE threshold at $p < 0.05$) based on a search volume of $600mm^3$.

3.1.4. Results

With respect to the a priori hypothesis, I tested for hippocampal engagement in the implicit formation of sequence knowledge in the auditory modality, using an acoustic version of the SRT. I excluded four participants which did not met the criteria for implicit memory about the acquired sequencen knowledge.

Behavioral results

Within the remaining participants, the mean error rate was very low (7% error over 120 trials), and thus the accuarcy overall was high. For the reaction time (RT) analyses, a significant decreased in RT over time ($F(2,36) = 12.61$, $p < .001$) across included participants (mean: session 1 = 888.5 ms; session 2 = 792.4 ms; session 3 = 804.4 ms) was found.

While the presented findings suggested successful sequence learning, participants' memory sensitivity about the sequential consistencies was further assessed in the subsequent behavioral analyses of the generation task. The next step was to assess the amout of implicitly and explicitly acquired sequence knowledge. Within the group of implicit participants, performances were above chance level of 50%, while no significant difference between high and low confidence trials were found across correct responses.

To be specific, the CT performance (correct trials in percent), a significant difference between the amount of correct and incorrect trials (T(11) = 3.45, p = .005, *d* = 2.18) was found, with a mean score of correct responses of 13.75 (68.75 %), and incorrect responses of 6.25 (31.2 %). This significant difference in correct and incorrect indicated that a great amount of sequence knowledge had been acquired during the auditory SRT task. Importantly, among those correct responses, no difference between high and low confidence trials was found (T(11) = 1.84, p = .09, *d* = 1.11). This finding is of great importance, as this implies that participants' performance relied on implicit knowledge.

Noteworthy, none of the included participants noticed any regularity. However, there was one tone, i.e. the tone with the highest pitch, which particularly attracted participants' attention, even more than all the other tones presented during the SRT task. To be specific, participants reported "there was one specific tone which was especially noticeable and unpleasant". Consequently, related trials with this specific tone were excluded from further behavioral and imaging analyses. Taken together, I additionally tested whether there was a significant difference between correct and incorrect trials when the salient tone had been excluded from analysis. Interestingly, for the CT performance (correct trials in percent), the significant difference between the amount of correct and incorrect trials remained (T(11) = 3.3, p = .007, *d* = 1.99) when excluding the salient tone from analysis (mean scores: correct = 10.41 (65.1 %); incorrect = 5.58 (34.9 %)). To reliably ensure that the acquired implicit sequence knowledge was statistically significant, a one sample t-test was performed. I thus tested whether the summed value of 65% of the CT performance, i.e. the correct trials in percent, was above the chance level of 50% (T(11) = 3.29; p < .01, *d* = 1.99). In fact, across participants, the CT performance was above chance level of 50%. Hence, it can be assumed that the included participants had reliable implicit knowledge about the sequential auditory sequence. Crucially, there was also no significant difference between high and low confidence ratings (T(11) = 1.51, p = .16) among correct trials, see Figure 2. Taken together, even when the salient tone was excluded from analysis, the (almost) equal distribution between high and low confidence ratings remained. Consequently, possible explicit knowledge might not explain participants' above chance performances and the related acquired auditory sequence knowledge. In other words, these findings suggested that reliable implicit knowledge about the sequential consistencies was generated.

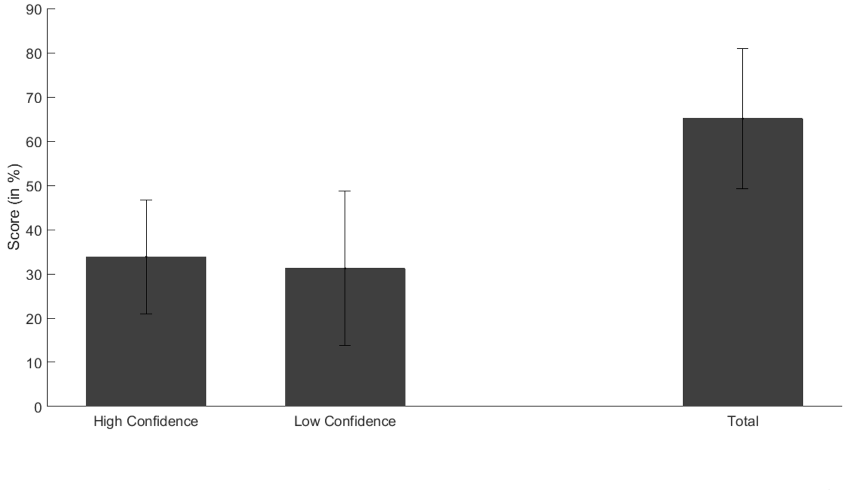

Figure 2. **Behavioral results.** Across included implicit participants, mean CT performance for correct responses is demonstrated in percentage. To be specific, the correct responses with high confidence, correct responses with low confidence, and the total amount of correct responses are shown from left to right. Note: the error bars indicate the standard deviation. Crucially, there was no significant difference between high and low confidence scores.

Functional imaging results

For the subsequent analysis of the imaging data, I examined whether the hippocampus was involved in the implicit formation of an acoustic sequence. For each participant, I included the respective memory sensitivity value, representing the implicit sequence knowledge, as a covariate within subsequent functional MRI analyses. Testing the main effect of this memory specific covariate would reveal whether there is an individual relation between the BOLD signal changes within the hippocampus and implicit sequence knowledge.

For the first analysis, when all tones were icnluded within analyses, a positive relation between activations in the left hippocampus and the acquired implicit sequence knowledge (i.e. CT score) was found (T(43) = 5.56, p = 0.001, at -38, -22, -12 [x y z]). However, for the additional analysis, i.e. when excluding the salient tone from analyses, I found significant main effects of the covariate within bilateral hippocampus, indicating memory specific effects. To be specific, a positive relation between activations in bilateral hippocampus and the acquired implicit sequence knowledge (i.e. CT score) was found (left hippocampus: MNI: [x=-38, y=-22, z=-14]; T(32) = 3.52, p = 0.001; hippocampus: MNI: [x=24, y=-22, z=-14]; T(32) = 4.03, p = 0.001).

For visualization and a descriptive comparison of the memory specific covariate effects of both analyses (with and without salient tone), the contrast estimates between both analyses in the left and right hippocampus are demonstrated in Figure 4. When comparing both analyses, a similar pattern of the memory specific covariate effects can be observed. Interestingly, when the salient tone had been excluded, the effect of the memory specific covariate was particularly enhanced. As a consequence, I suggested that the salient tone might have evoked different cognitive processes than the other tones, which might thus be reflected in the BOLD signal changes in the hippocampus.

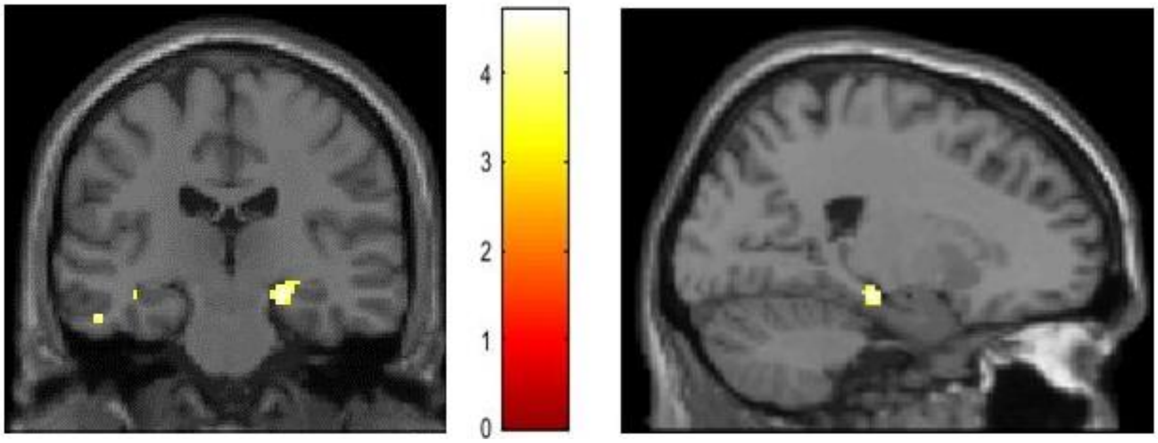

Figure 3. **Main effects of the covariate (CT score) show implicit memory-related specific effects.** Findings reveal a positive relation between the amount of implicitly acquired sequence knowledge (completion task scores) and significant effects within hippocampal regions (p < .05; FWE corrected), i.e. within voxels in the right (-38, -22, -14) and left hippocampus (24, -22, -14). Results based on data of included “implicit” participants. Note: Statistical map thresholded at p<.001.

3.1.5. Conclusion

The present findings of implicit perceptual-based sequence learning are in line with previous important behavioral SRT observations. Among included implicit participants, an above chance performance in the CT was found, suggesting that reliable implicit knowledge about an auditory sequence was acquired.

Furthermore, I observed a positive relation between the BOLD signal changes within the left and right hippocampus and the amount of acquired sequence knowledge without the generation of explicit memory.

Based on these findings, it can be suggested that the hippocampus has a significant functional role in implicit acoustic sequence learning. In particular, in accordance with a previous fMRI study (Rose et al., 2011), presented findings further suggest a general functional role of the hippocampus within MTL structures in implicit sequence learning of perceptual associations. Importantly, present behavioral and imaging findings are in line with pervious crucial imaging studies on implicit associative memory using the SRT or other related implicit learning tasks. In fact, fMRI studies on implicit memory about associative semantic stimuli pairs found that unconscious recollection of the stimuli associations was related to hippocampal activation. Thus, these findings also demonstrated that the "sequential material" per se might not be a mandatory factor for the involvement of the hippocampus during implicit memory formation (Degonda et al., 2005; Henke, Mondadori, et al., 2003; Henke, Treyer, et al., 2003). Thus, present and previous related studies on implicit memory revealed that the significant functional role of hippocampal structures can be attributed to explicit as well as to implicit memory formation processes (Duss et al., 2014; Henke, 2010; Rose et al., 2011; Schendan et al., 2003).

Proposing a more general functional role of the hippocampus for implicit learning of pure perceptual (sequential) associations is in accordance with previous published theories on hippocampal contribution to implicit (and explicit) associative learning processes (H. Eichenbaum, 2017; Henke, 2010). Accordingly, memory systems should not be classified by the level of conscious involvement, as proposed in previous theories. In contrast, memory systems should be differentiated on the level of functional contribution. Hence, across the literature, it is now widely assumed that the function of hippocampal structures particularly reflects the rapid encoding of flexible associations, which is independent of the involvement of explicit or implicit memory. Memory systems should be classified by the stimuli modality representing "what had been learned", and not by the involvement of participants' awareness (Henke, 2010; Rose et al., 2011). However, based on presented imaging findings, I also propose that hippocampal structures are involved not only during faster but also during slower implicit memory processes of pure perceptual-based associations. Taken together, the presented findings of this study clearly support the assumption that the properties of the learned material should be used to differentiate or to classify between memory system.

3.2. Study 2 – Incidental associative learning

3.2.1. Participants

Fifty-six healthy individuals volunteered (age: 18-35 years, 35 females, 26 males) to participate in the fMRI experiment. Four participants were excluded due to medical reports or technical difficulties during fMRI measurements. All participants had normal or corrected-to-normal vision.

3.2.2. Study design and paradigms

Experimental set-up and stimuli

Stimuli consisted of 16 different images and 16 different sounds representing neutral object images and real life environmental sounds, respectively. Stimuli were selected from an internal database and had an unambiguous assignment to an animal or non-animal category. Crucially, for each participant, auditory and visual stimuli were randomly assigned into novel bound audiovisual pairs which were not semantically related. For example, a picture of an owl and a sound of a car were simultaneously presented to the participants. Hence, this prevented a congruency effect within each stimulus pair (Parise & Spence, 2012) and ensured that participants acquired novel associations between arbitrary multimodal information during the experiment.

Experimental procedure

The employed experimental design consisted of two phases, the incidental paired-associate learning phase and the explicit recollection phase, as illustrated below (figure 2).

The incidental paired-associative learning task

A traditional methodological approach to investigate associative memory across modalities is the paired-associate learning paradigm (Howard Eichenbaum & Bunsey, 1995). As the focus of the second fMRI study was on the neural processes of multimodal associations, I created an incidental paired-associate learning paradigm with neutral object images and environmental sounds as perceptual stimuli, which reflected an unambiguous assignment to an animal or non-animal category (Figure 2). Across trials, auditory and visual stimuli were simultaneously presented, however, the two unimodal stimuli were not semantically related to each other. Within each trial, an auditory and a visual stimulus were presented simultaneously to the participants and lasted for 2 second. Stimulus presentation was followed by a central fixation point with an inter-trial interval (ITI) randomly varying between 3 and 6 seconds. To illustrate, an image of an owl was presented with a sound of a mobile phone. Importantly, this specific approach ensured not only that *new* associations could be acquired, but also prevented a congruency effect within each stimulus pair (Parise & Spence, 2012).

To ensure that participants actually processed both unimodal stimuli, they were instructed to make a so-called animacy judgment as quickly (within the ITI) and as accurately as possible. To be specific, participants had to decide

a) whether both (unimodal) stimuli were related to a living or non-living stimulus (i.e. an image of an owl and a sound of a dog, or an image of a car and a sound of a mobile phone, respectively), or

b) whether both (unimodal) stimuli represented different categories (i.e. an image of an owl and a sound of a mobile phone).

Noteworthy, unbeknownst to the participants, the aim of the experiment was to investigate whether the audiovisual associations could be learned incidentally. To test this, I arranged the auditory and visual stimuli into two equally distributed categorical conditions: the "consistent" and the "variable" condition. The critical difference between the two conditions was the underlying binding regularity. For the consistent condition, corresponding unimodal stimulus pairs were assigned into "fixed" or "stable" audiovisual pairs. Thus, those stimulus pairs were repeatedly presented together throughout trials (i.e. the image of an owl has always been presented with the sound of a mobile phone). In contrast, unimodal stimulus pairs of the variable condition were continuously recombined into different audiovisual stimulus pairs across learning trials (i.e. the image of a squirrel has been paired with different sounds across trials, see Figure 2). Importantly, participants were informed neither about the underlying binding regularity nor about the categorical conditions. To sum up, within this specific incidental paired-associate learning task, participants could acquire both multimodal knowledge about new ("stable") audiovisual associations (consistent audiovisual pairs) but also the ability to differentiate the newly learned multimodal material (consistent audiovisual pairs) from various different audiovisual stimuli (variable audiovisual pairs).

The recollection task

For the test phase, I applied the logic of a force-choice recollection task in order to identify the amount of explicit (and implicit) knowledge (please see "General Materials and Methods"). A written instruction presented to the participants explicitly stated the presence of two conditions of audiovisual pairings during the learning phase, and that the task was now to decide to which category the presented stimulus pairs belonged. Hence, the aim of the recollection phase was to objectively measure the amount of explicit multimodal knowledge acquired under an incidental condition.

To measure this, I used the same multimodal pairs as in the paired-associate learning task (Figure 2). However, within the recollection task, audiovisual pairs were presented in a sequential order, i.e. as unimodal stimuli. Using successive unimodal stimuli rather than synchronous stimuli allowed to investigate whether the acquired knowledge about the multimodal information and the neural correlates can be transferred to unimodal conditions. To be specific, in each trial, two unimodal stimuli were first presented to the participants with a temporal delay using a jitter of 3 to 6 seconds.

With regard to the two different conditions, the eight multimodal stimulus pairs of the constant condition were identical to those of the learning task. Unimodal stimuli of the variable condition, however, were now randomly assigned into eight "fixed" multimodal pairs. To be specific, the variable condition contained now eight "fixed" multimodal pairs, which remained constant within the recollection task. To illustrate, two unimodal stimuli of the variable condition, referred to as image A and sound B, were now presented always together. This was done to assess participant's ability to discriminate between the two multimodal conditions, the constant and variable condition. After two unimodal stimuli had been sequentially presented to the participants, they were first explicitly instructed to identify whether those two unimodal stimuli had been consistently paired in the previous learning task. To illustrate, if the two stimuli represented one specific audiovisual pair of the constant condition, or not, i.e. represented two unimodal stimuli of the variable condition. Then, each response was followed by a confidence rating. Participants had to evaluate whether they were (a) "sure - high confidence", or (b) "unsure - low confidence" about their response. Each audiovisual pair was presented four times, with the auditory and visual stimulus in first position twice, respectively. The recollection phase consisted of 64 completion task trials (32 for each condition: constant vs. variable) and 64 confidence rating trials (sure vs. unsure), a total of 128 trials.

Taken together, this approach allowed us to address the questions of whether the two different parietal networks were also involved during explicit recollection under successive presentation of unimodal stimuli. Further, I tested whether the involvement of the two parietal networks were already required during the presentation of the first or second stimulus. I assumed that activations in the two parietal networks are particularly active during the point in time when a memory decision was required. In other words, I assumed that the regions of interest were most dominant at the presentation of the second stimulus.

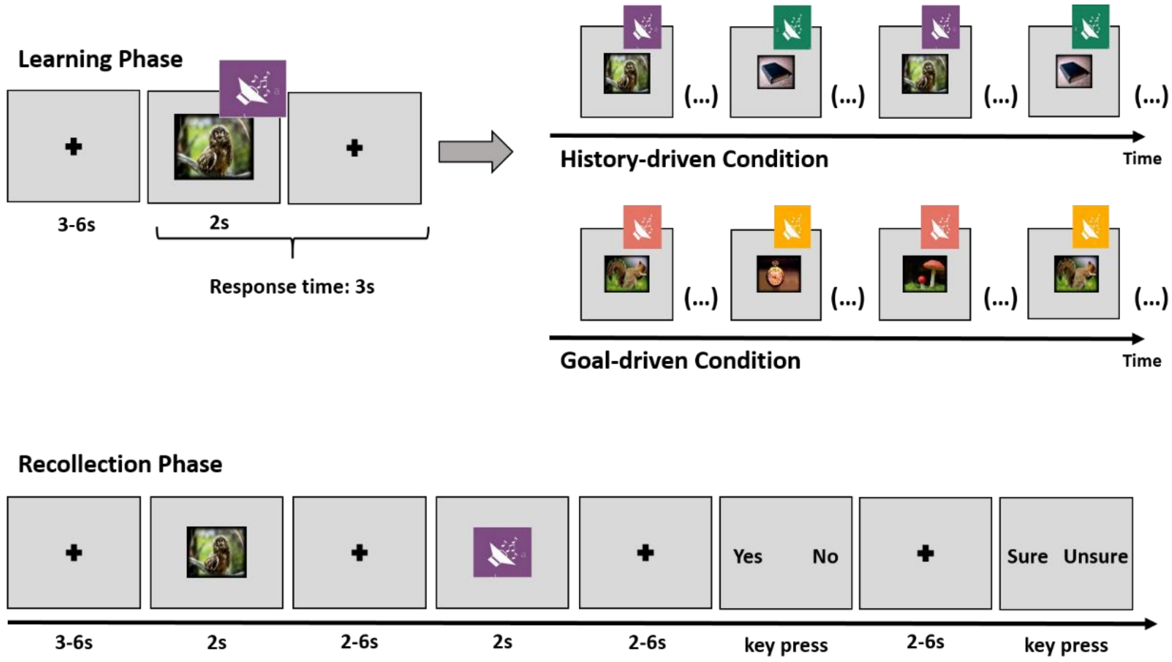

Figure 4: **Schematic illustration of the learning and recollection task of study 2.** (A) The incidental paired-associate learning task is used to investigate associative memory across modalities using auditory stimuli. (B) The recollection task is used to assess the acquired multimodal knowledge and the conscious state of the learner. Note: Within this illustration, the colored sound icons were only used to indicate the different auditory stimuli, however they were not shown as visual icons to the participants.

3.2.3. Analyses

Statistical analyses of behavioral data

For both, the learning and the recollection phase, I only included correct responses in the subsequent fMRI analyses. The recollection phase was used to assess the amount and the status of multimodal knowledge by two criteria: the completion task performance in combination with the confidence ratings and the verbal report (please see “General Materials and Methods”).

First, I only included participants who performed above chance level on their correct responses. The confidence rating was used to identify whether participant’s knowledge was explicit (Z. Dienes, 2007; Z. Dienes & Perner, 1999). Participant’s knowledge was characterized as explicit if both performance scores were above 50% (at least 33 correct responses among the 64 recollection task trials) and accompanied by high confidence rating. Finally, participants were instructed to verbally describe the hidden binding regularity (constant vs variable) of the audiovisual pairs in post-experimental interviews. Within the post-experimental interviews, participants were explicitly instructed to describe what they have noticed within the learning phase by writing all the distinctive features they have noticed on a post-experimental questionnaire. Participants were classified as “not explicit” if they have noticed anything or were not able to give any (correct) examples for each condition (constant vs variable). Only if these two criteria were met, participants were included within subsequent analyses.

To identify whether there is a relation between memory performance and individual event-related blood oxygen level-dependent (BOLD) activations in the region of interest, I assessed participants’ memory sensitivity (please see “General Materials and Methods”). To assess this, I calculated the statistic *d’* for each participant. The *d’* represents the standardized difference between participant’s hit rate and false alarm rate. The sensitivity value of each participant was then used within subsequent fMRI analyses.

Functional MRI acquisition and data preprocessing

Functional MRI data were collected on a Siemens 3 Tesla Prisma MR system with a 32-channel head coil. A standard gradient echo-planar imaging (EPI) T2*-sensitive sequence was used with parallel imaging (GRAPPA; in-plane acceleration factor = 2) and simultaneous multi-slice acquisitions (slice acceleration factor 2). Each functional volume contained of 54 continuous axial slices obtained with a 0.5 mm interslice gap (TR = 1636 ms, TE=29 ms, flip angle=70°, voxel size= 2 x 2 x 2). Finally, after functional imaging, I acquired a structural high-resolution T1-weighted image for each participant using a magnetization prepared rapid gradient echo (MPRAGE) sequence (voxel size= 1x1x1 mm).

For pre-processing and statistical analyses of the functional MRI data, I used the statistical parametric mapping (SPM12; http://www.fil.ion.ucl.ac.uk/spm/; Welcome Department of Imaging Neuroscience, London, UK). Using field maps, functional Images were realigned and unwarped to the first volume. Then, the T1 weighted structural scans were coregistered with the functional images and segmented into the different tissue classes (grey matter, white matter, and cerebrospinal fluid). Using the DARTEL toolbox (Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra), the resulting individual subjects’ tissue class images (grey matter, white matter) were applied to the structural images to create a structural group template, and to the functional images for spatial normalization. Finally, functional Images were smoothed with a 6mm full width at half maximum (FWHM) isotropic Gaussian kernel.

Statistical analysis of functional data

Learning phase

The fMRI data consisted of two different experimental conditions, the constant vs variable condition, subdivided into three different sessions. To allow a better time resolution of the two conditions across learning, I divided each learning session into two equally large intervals, resulting in 6 learning sub-sessions. The fMRI data was analyzed by an estimation of the BOLD signal for each condition (stimulus condition: constant vs variable) and session (sub-session: 1-6) and errors (incorrect responses) modeled as a hemodynamic response function. Using a general linear model, regression coefficients were obtained for each regressor (condition in session). Expect for the error regression coefficients, beta weights for each regression coefficients (of only included onsets of correct responses) were entered into a group analysis using a flexible factorial design.

The outcome of learning was assessed by comparing the two conditions within the final session of learning and using the memory sensitivity value (d’) as a covariate. For a visualization of the relation between the parietal BOLD signal responses and the d’ of each participant, I used the toolbox rfxplot for SPM12 (Gläscher, 2009; http://rfxplot.sourceforge.net) to retrieve first level data of each participant. For each participant, I extracted the maximal signal intensity of the beta values within a sphere of 4mm around the group peak voxel, and then fitted a linear regression between the signal intensity and the behavioral measures.

Assuming that multimodal knowledge was acquired gradually over time, I were interested whether there were time course dependent changes in ventral and dorsal activity across sub-sessions (i.e. sub-session 1 – 6) and condition. In particular, I tested whether ventral and dorsal region differed in their functional involvement across time. This was statistically implemented at the level of the group analysis as an interaction contrast of condition x time separately for each assumed functions (i.e. increase in activation for (1) constant vs. variable condition and (2) variable vs. constant condition). This allowed to dissociate the different time courses across the learning phase between conditions. Further, for each conditions separately, I tested for an increase of activity across the 6 sub-sessions. Finally, to directly test for the assumed dissociation related to ventral vs dorsal distinctions in the multimodal learning process, I further performed a repeated-measures ANOVA using the following factors: region (dorsal, ventral), condition (constant, variable) and sub-session (1-6). Data for the repeated-measures ANOVA was retrieved from first level data, using the toolbox rfxplot. For each participant, I extracted the maximal signal intensity of the beta values (for condition and session) within a sphere of 4mm around the group peak voxel.

Finally, I tested for time-dependent changes in activation within hippocampal regions across multimodal learning sessions. I tested for an increase of neural activity in both categorical conditions, respectively, in order to examine whether hippocampal activity were found in both conditions, or whether hippocampal responses were limited to one specific condition.

Recollection phase

As in the learning session, I assumed that activations of the two different parietal networks can also be observed during successful recollection, while relying on experienced-dependent processing (constant condition), or attentional control for task-dependent processing (variable condition) based on the formation of stable multimodal associations.

I analyzed the fMRI data by an estimation of the BOLD signal for each condition (stimulus condition: constant vs. variable), event (stimulus event: first vs. second), type (stimulus type: visual vs. auditory) and errors (incorrect responses) modeled as a hemodynamic response function. Following the same procedures as for the learning trials, contrasts for each regression coefficients (but not the error regression coefficient) were built and transmitted into a flexible-factorial design including the inter-subject variability as random effects, while using stimulus event, stimulus type and stimulus condition as repeated factors.

For both events, the first and second stimulus event, I examined recollection-related effects when comparing between conditions (constant vs. variable), regardless of stimulus modality (visual or auditory). This contrast allowed examining whether the same parietal networks were involved during explicit recollection of the new acquired multimodal knowledge under successive presentation of unimodal stimuli.

Region-of-interest

For both the learning and the recollection phase, I reported significant fMRI effects at a threshold of p<.05, corrected for familywise error (FWE) using whole brain analysis. Region-of-interest (ROI) analysis was used to examine learning-related activation in bilateral parietal cortex, with particular interest in the difference in neural response between ventral and dorsal regions of the bilateral parietal cortex. To address this, I first defined a 20mm ROI sphere based on the peak activation coordinates from a large-scale, multi-domain meta-analysis of Humphreys and Ralph (2014), which investigated the functional role of the posterior parietal cortex in several different cognitive domains (Humphreys & Ralph, 2015). Accordingly, for the left hemisphere [-48 -64 34] and its corresponding location in the right hemisphere [48 -64 34] were used in subsequent functional analyses. Furthermore, I extended our ROI analysis by including a ROI for the posterior medial cluster of the “dorsal default mode network” that was taken from an atlas defined from resting-state connectivity (Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2012). Hence, the subsequent

ROI analysis covered lateral and midline parts of the PPC, which have been frequently reported to play critical functional roles for specifically complex, higher order, multimodal associations (Baldassano et al., 2017; Janice Chen et al., 2017). Finally, I expected hippocampal involvement during both the flexible acquisition and organization of abstract multimodal information and the retrieval of the new acquired memory. In the subsequent analyses, I applied a ROI from the Harvard-Oxford structural atlas comprising the left and the right hippocampus. All significant fMRI results were reported at a voxel-level threshold of $p < .05$ FWE small volume corrected (SVC).

3.2.4. Results

Behavioral results

Learning phase

The aim of this study was to test whether audiovisual associations can be learned under incidental learning conditions, and to examine then the related underlying neural correlates.

With regard to the behavioral performances of the paired-associate learning task, it was found that participants' mean overall error rates were very low across sessions (mean: 1.08%, SD: 0.6%). With respect to the participants' reaction times, I calculated the mean response times (RTs) with regard to the onset of the stimulus for each single input and for each condition separately (see Figure 5). A repeated-measure ANOVA [factors session and condition (constant/variable)] revealed a general decrease of RTs across sessions ($F(5, 255) = 7.,6$, $p < 0.001$) and a difference between conditions ($F(1,51) = 79.8$, $p < 0.001$). Crucially, the interaction between session and condition ($F(5, 255) = 34.63$, $p < 0.001$) demonstrated that the constant condition was processed faster than the variable condition across learning sessions. As previously assumed, RT analysis indicated a benefit in processing stable constant multimodal associations. Behavioral findings indicated that participants paid attention to the multimodal learning task. Importantly, only participants who showed above chance performance and acquired memory that was of explicit character were included within subsequent fMRI analyses.

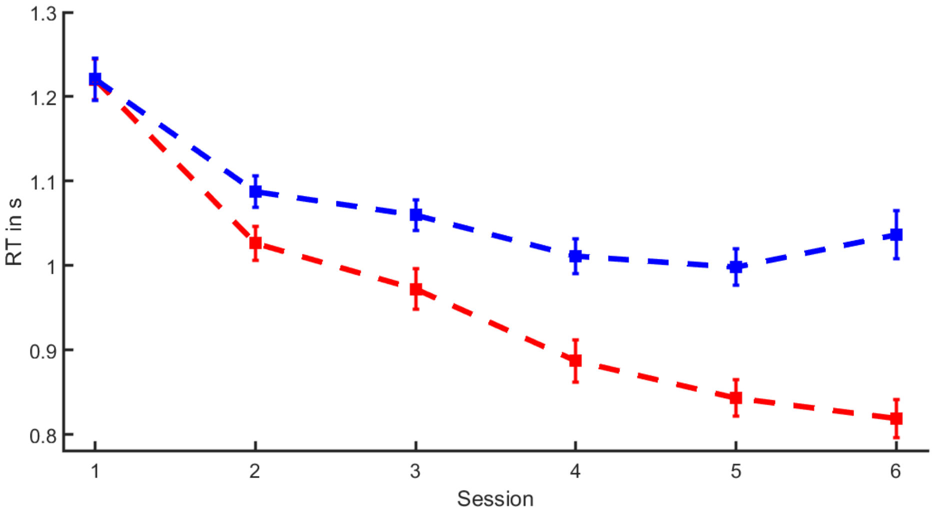

***Figure 5.* Behavioral results.** The more pronounced decrease in reaction times (RTs) across learning sessions for the constant (red) condition compared to the variable (blue) condition demonstrates fast processing of incoming information based on stable multimodal associations. Error bars indicate standard deviations.

Test phase

For the test phase, I had to exclude two participants which did not met the criteria to assure explicit multimodal knowledge, one participant with a high rate of "no responses" (>50%), and one participant due to technical failure during the fMRI measurements. All included participants reported the existence of two different conditions with different binding regularities in post-experimental interviews. Among included volunteers, no individual participant was below chance level in correct answers. The group mean score of the completion task performance (score: 74%) was above the chance level of 50%, in which 76% of the correct answers were accompanied with high confidence ratings (total score of correct and high confidence answers: 58%). Furthermore, I used a one sample t-test to tested whether correct responses (in percentage) were statistically significant above the chance level of 50%, supporting that a reliable multimodal knowledge was acquired ($T(51)=13.32$, $p < .001$). Among correct answers of the constant condition, 94% were given with high confidence indicating a great amount of explicit awareness on the newly learned information, i.e. the novel acquired knowledge of the fixed multimodal associations. Thus, recollection behavioral data revealed that the constant audiovisual stimulus pairs were successfully learned throughout sessions. Based on participants' recollection performances, I calculated participants' performance sensitivity, *d'*, in order to assess participant's ability to discriminate between constant and variable multimodal pairs. For the constant condition, I calculated a mean *d'* score of 1.94, while participants' performance sensitivity varied from zero to 4.31.

fMRI results

Learning phase

Imaging results indicated a clear functional differentiation of PPC recruitment regarding both conditions. For the constant condition, increased activations in the left vPPC, including the left AnG were found (MNI coordinates: x=-48, y=-70, z=38; T=5.31; FWE $p < .05$ whole brain corrected; MNI coordinates: x=-52, y=-60, z=42; T=5.01; FWE $p < .05$ whole brain corrected) when comparing both conditions within the final learning session. Additionally, effects in the right AnG (MNI coordinates: x=56, y=-60, z=38; T=3.9; SVC FWE $p < .05$), left posterior cingulate gyrus (MNI: x=-4, y=-42, z=34; T=3.24; SVC FWE $p < .05$), and right hippocampus (MNI: x=32, y=-24, z=-14; T=3.39; SVC FWE $p < .05$) were specific for constant multimodal pairs. On the other hand, effects for the variable condition could be related to more dorsal regions of the PPC (MNI coordinates: x=26, y=-66, z=-46; T=7.19; FWE $p < .05$), including the bilateral SPL (MNI coordinates: x=-30, y=-58, z=40; T=5.27; MNI coordinates: x=32, y=-58, z=44; T=4.99; SVC FWE $p < .05$). Furthermore, for whole brain analysis, I found activations in the occipital cortex, middle frontal gyrus, bilateral insula, cerebellum, and motor related regions (see Appendix A – study 2 for full whole-brain corrected results).

A positive relation between the memory sensitivity values (d') and activation within the left (MNI coordinates: x=-52, y=-68, z=30; T=4.17; SVC FWE $p < .05$) and right AnG (MNI coordinates: x=46, y=-54, z=46; T=3.65; SVC FWE $p < .05$) was found. This significant relation reveals that the AnG activity was sensitive to the amount of the acquired multimodal memory (see Figure 6).

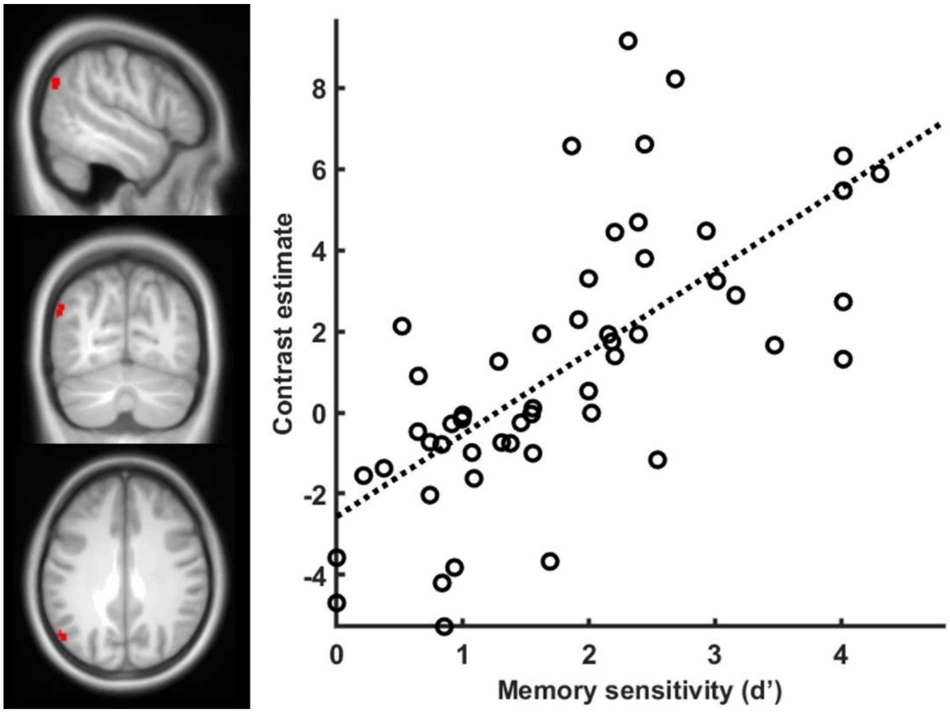

***Figure 6*. Activation in the left angular gyrus and recollection strength of multimodal information.** The correlation between the maximal signal intensity within the left AnG and the behavioral measure (d') of each participant is plotted. It revealed a positive correlation between memory sensitivity and increased activations in the left AnG (Pearson correlation; r ~= 0.73 and p< 0.001). Note: Dots are single-subject values. The dotted line represents the linear regression line, indicating the extent of correlation between the two variables on the vertical and horizontal axes.

By comparing the time course of ventral and dorsal activity across learning sessions, the emergence of the functional dissociation of PPC recruitment was analyzed (interaction effects of time x condition). Across learning sessions, increased activation of constant multimodal stimulus pairs compared to variable multimodal stimulus pairs was found in the left AnG (MNI: x=-48, y=-70, z=32; T=4.07; SVC FWE p < .05; see Figure 7).

The reversed contrast (i.e. time-dependent increase in activation for variable > constant condition) revealed significant activation within a more dorsal region of the parietal cortex, the left (MNI coordinates: x=-32, y=-54, z=36; T= 4.65; SVC FWE p < .05; see also Figure 7) and the right superior parietal cortex (MNI coordinates: x=34, y=-56, z=44; T= 4.09; SVC FWE p < .05). Furthermore, I found significant activation within the right precuneus (MNI coordinates: x=10, y=-62, z=22; T= 3.22; SVC FWE p < .05).

The subsequent repeated-measures ANOVA across regions revealed a significant interaction effect (region x condition x and sub-session; F(5,255)=45.78; p < .05), confirming the dissociation between ventral vs dorsal regions in the multimodal learning process and showed that this functional dissociation emerged with learning.

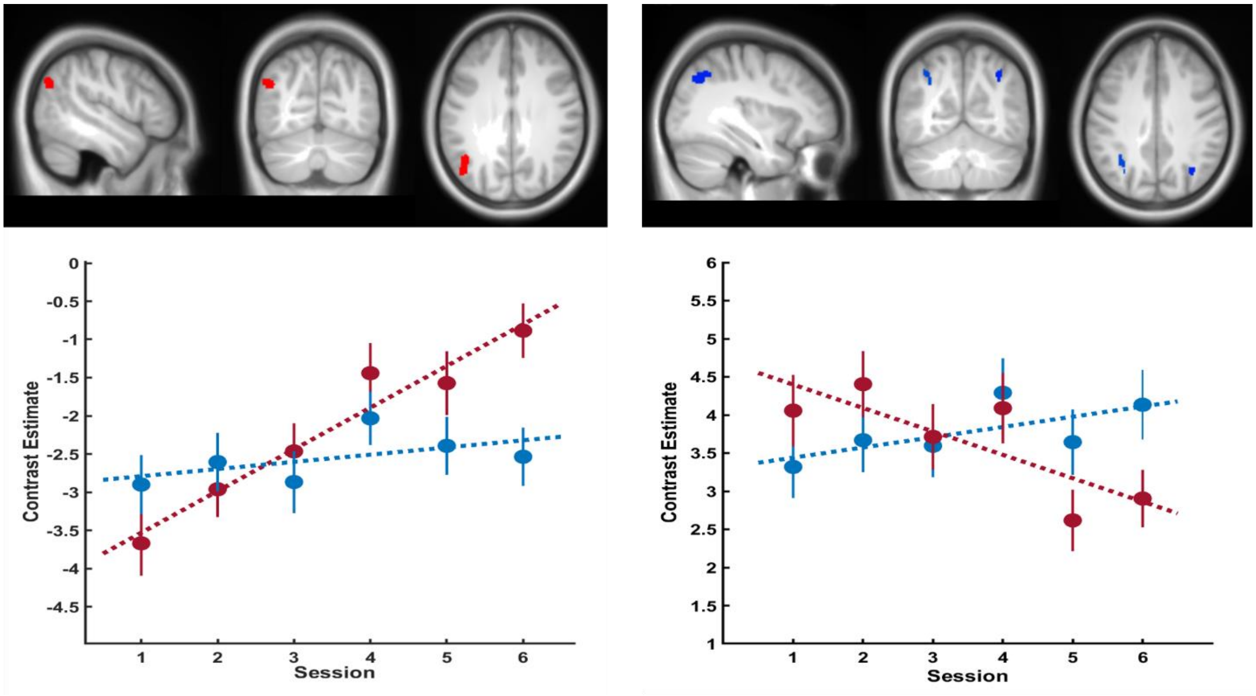

***Figure 7.* Different functional roles for the ventral and dorsal posterior parietal cortex during the acquisition of multimodal knowledge.** I found increased activation in the left AnG for the contrast constant > variable (upper left panel, activation in red), and increased activation in the left SPL for the contrast variable > constant (upper right panel, activation in blue). For visualization, I extracted the mean contrast estimates at the peak coordinate in the left AnG (x=-48, y=-70, z=32) and left SPL (x=-32, y=-54, z=36) across session and each condition, respectively. A linear function (regression) was fitted to the extracted data to reveal the neural effects of multimodal learning across session and condition. Line graphs represent the multimodal learning-related effects between the factors condition (red: constant condition, blue: variable condition) and session. Lower left panel: For the constant condition, AnG activity increased during learning of constant multimodal material in comparison to the variable material. Lower right panel: In contrast, fMRI signal increased within the left SPL during learning of variable multimodal associations but decreased for constant associations. Note: Error bars indicate SEM.

Estimating the main effects of learning, I investigated the increase and decrease across sessions and condition separately. For both conditions, for the increase-across-session analysis, activations within regions of the bilateral insula, the medial segment of the superior frontal gyrus, the bilateral MTL, the left posterior cingulate cortex, transverse temporal gyrus, and the left supramarginal gyrus increased over trials (see appendix A – study 2 for full whole-brain corrected results). Interestingly, only the constant condition was associated with a hemodynamic increase in the left AnG. For both conditions, for the decrease-across-session analysis, activations within bilateral precentral and postcentral gyrus, bilateral occipital and inferior frontal regions decreased over trials (see appendix A – study 2 for full whole-brain corrected results). Interestingly, only the constant condition was associated with hemodynamic decreases in the bilateral anterior insula, bilateral superior frontal gyrus, and the SPL.

Finally, for the additional ROI analysis, I found significant effects in bilateral hippocampus (MNI coordinates: Left hippocampus, constant condition: x=-26, y=-12, z=-14, T=4.76; variable condition: x=-28, y=-12, z=-14, T=4.85; Right hippocampus, constant condition: x=30, y=-22, z=-14, T=4.46; variable condition: x=28, y=-22, z=-14, T=4.37, SVC FWE p < .05, see Figure 8).

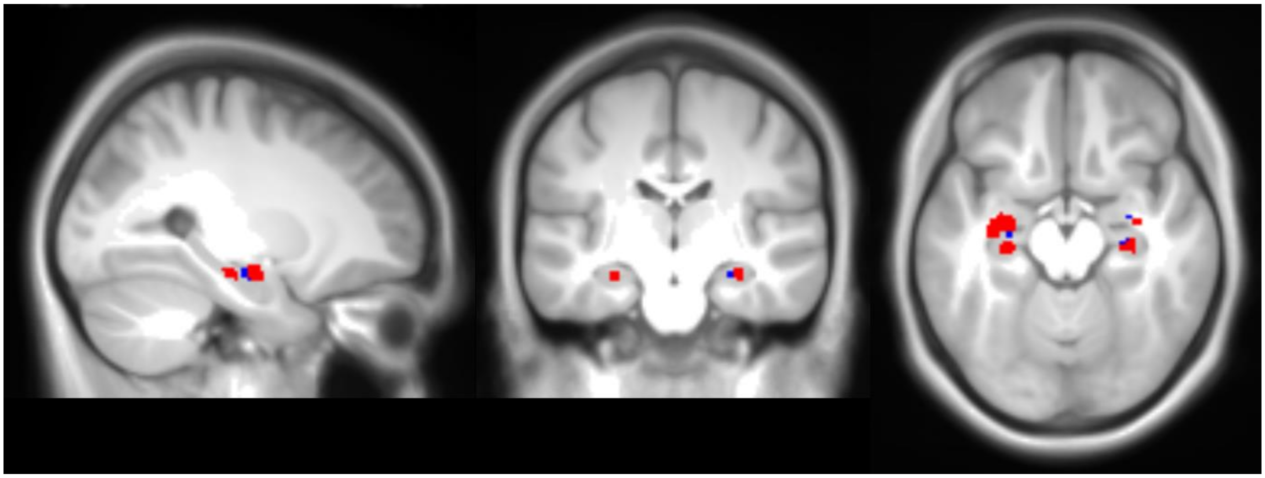

Figure 8. **Increased activity within bilateral hippocampus during multimodal learning.** For both multimodal conditions, history-driven (red) and goal-driven (blue), neural activity increased in right and left hippocampal structures (Left hippocampus: history-driven: x=-26, y=-12, z=-14; goal-driven: x=-28, y=-12, z=-14; Right hippocampus: history-driven: x=30, y=-22, z=-14; goal-driven: x=28, y=-22, z=-14), revealing its involvement in the flexible acquisition and organization of multimodal relational information.

Test phase

During the presentation of the first stimulus, comparing the constant with the variable multimodal condition, I found increased activity within bilateral hippocampus (MNI coordinates: left: x=-18, y=-28, z=-8; T=3.98; right: x=18, y=-30, z=-4; T=4.28; SVC FWE $p < .05$). For activations within the PPC, I found increased activity within the right precuneus (MNI coordinates: x=8, y=-62, z=20; T=3.96; SVC FWE $p < .05$), and the left posterior cingulate (MNI coordinates: x=0, y=-42, z=22; T=3.43; SVC FWE $p < .05$). Furthermore, several regions within occipital, parietal and frontal cortices revealed a reliable differentiation when comparing stimulus conditions (see Appendix A – study 2 for full whole-brain corrected results). However, no activation within regions of interest were found within the reverse contrast (i.e. variable > constant).

Interestingly, ventral and dorsal PPC activations were particularly found after the presentation of the second stimulus, regardless of stimulus modality and demonstrated a comparable dissociation as in the learning phase. The constant condition showed significant effects within the ventral PPC, including the bilateral AnG (MNI coordinates: left: x=-40, y=-74, z=32; T=4.66; right: x=52, y=-58, z=16; T=7.32; SVC FWE $p < .05$; see Figure 9, top panel). Furthermore, increased activations were found within the hippocampus (MNI coordinates: left: x=-32, y=-24, z=12; T=4.80; right: x=40, y=-20, z=-16; T=4.97; SVC FWE $p < .05$), bilateral precuneus (MNI coordinates: left: x=-4, y=-62, z=16; T=4.33; right: x=10, y=-60, z=18; T=4.25; SVC FWE $p < .05$), and the right posterior cingulate (MNI coordinates: x=2, y=-48, z=34; T=4.3; SVC FWE $p < .05$). For the variable condition, increased activation within dPPC was detected. This contrast revealed increased activation in bilateral superior parietal regions (MNI coordinates: left: x=-28, y=-52, z=40; T=6.57; FWE $p < .05$ whole brain; right: x=48, y=-62, z=44; T=4.93; SVC FWE $p < .05$; see Figure 9 (bottom panel).

Notably, for both contrasts (second stimulus event: constant > variable, variable > constant), whole brain analysis demonstrated increased activations within several different regions across the brain which are commonly associated with episodic memory formation (see appendix – study 2 for full whole-brain corrected results).

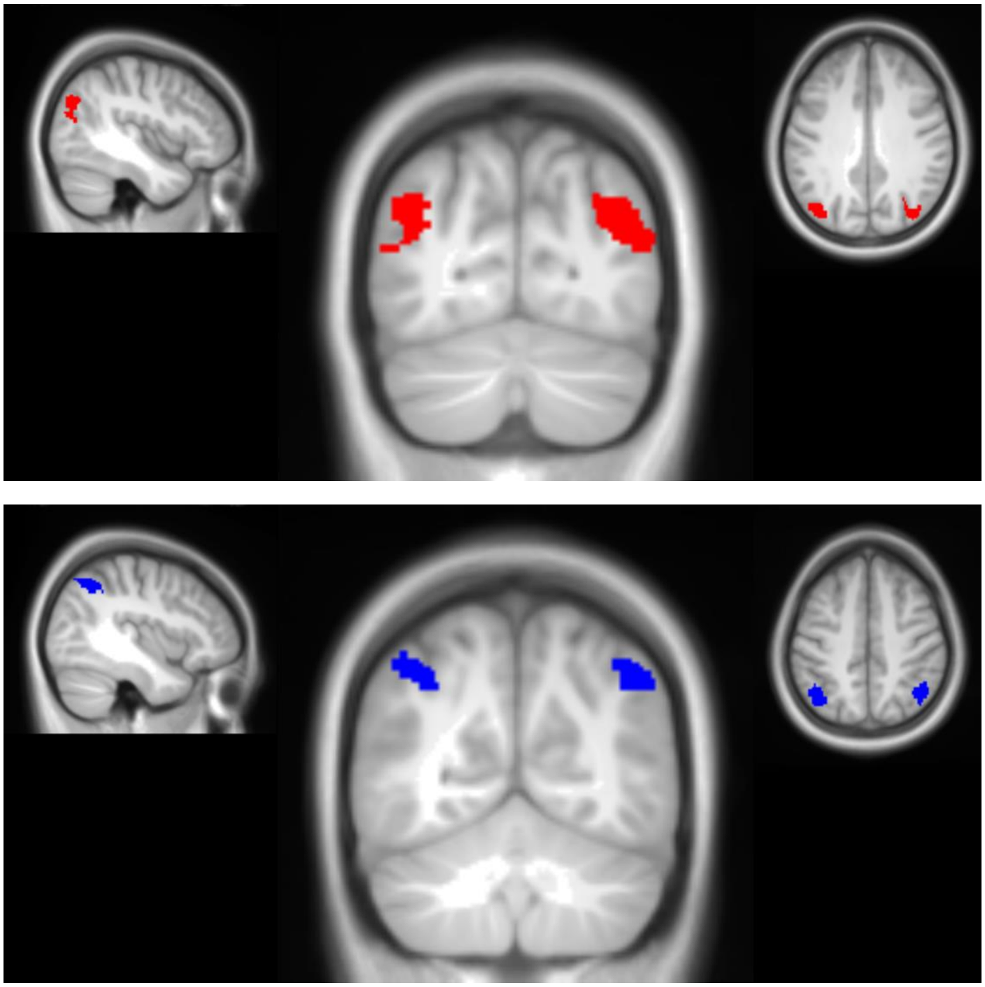

Figure 9. Recollection-related effects in ventral and dorsal regions of the parietal cortex. Upper panel (activation in red): The retrieval of constant multimodal associations was related to increased activity within ventral regions of the parietal cortex, in bilateral AnG (MNI coordinates: left: x=-40, y=-74, z=32; right: x=-52, y=-58, z=16). Lower panel (activation in blue): Increased activity within dorsal regions of the parietal cortex, in bilateral SPL (MNI coordinates: left: x=-28, y=-52, z=40; T=6.57; right: x=48, y=-62, z=44), was associated with the recollection of variable multimodal associations.

3.2.5. Conclusion

Within one multimodal paradigm, I observed a clear functional dissociation of the vPPC and dPPC during memory acquisition of multimodal associations. I suggest that this functional difference can be attributed to two different processing modes related to the developed memory. On the one hand, learning consistent audio-visual combinations can affect neural processing based on the development of (strong) memory for distinct pairs (i.e. history-dependent memory processing). On the other hand, weaker memory for changing multimodal associations resulted in intentional, goal-directed behavior requiring the serial processing of single stimuli from the different modalities. Examining the functional differentiation of the networks during incidental associative learning, a strong relation between memory and network dynamics was revealed.

The behavioral results demonstrated a more pronounced decrease in RTs across learning sessions for constant compared to variable audiovisual stimulus pairs. The imaging results revealed that increased activity in the vPPC, the left AnG, was not only related to constant processing, i.e. history-dependent multimodal memory, but also scaled with memory sensitivity (d'). The AnG might contribute to the automatic memory acquisition of stable multimodal associations, which rely on the constant condition, i.e. history-dependent factors. In contrast, neural activation of the dPPC, the SPL, decreased in response to consistently paired associations (constant condition), but increased for audiovisual pairs following a variable binding regularity (variable condition). The continuous recombination of unimodal information required a constant demand for attentional mechanisms for successful task-directed behavior, which might rely on the recruitment of the SPL. Interestingly, I observed this difference in PPC activations in both memory stages, learning and recollection. Overall, presented findings suggest that the essential difference between the functional involvement between ventral and dorsal regions do not depend on item memory or the memory stage per se, but on variable or constant factors modulating memory processing of multimodal associations and related internally integrated episodic representations.

With respect to the hippocampus, I found increased activations during learning of both constant and variable condition, while, during recollection, activations were limited constant trials. In line with previous memory accounts (Cohen et al., 1997; Henke, 2010), hippocampal function has been interpreted as being primarily involved in the initial establishment and rapid processing of new and flexible relational representations (Eichenbaum, 2017; Henke, 2010; Ranganath et al., 2005), even under incidental learning conditions (Duss et al., 2014; Henke et al., 2013; Rose et al., 2011). Furthermore, present hippocampal activation has been related to the reactivation of learned associative representations when using associative retrieval cues (Duss et al., 2014), consistent with present recollection data. Considering the rich anatomical connections among PM regions (Rushworth et al., 2006; Seghier, 2013; Uddin et al., 2010; Vincent et al., 2008, 2006; Xu et al., 2016), a functional interaction between the hippocampus and related PPC regions during associative processing has been assumed (Cooper and Ritchey, 2019; Ramanan et al., 2018; Shimamura, 2011). Taken together, a critical functional involvement of ventral and medial PPC regions and the hippocampus in relational memory-dependent processing of episodic information while maintaining constant contextual meaning can be suggested (Ranganath and Ritchey, 2012; Ritchey et al., 2020).

Assuming that memory is an integral component of information processing, I suggest that memory-dependent processing of multimodal associations are modulated by different factors (such as constant regularities or variable structures) underlying functional different processing networks (Hasson et al., 2015; Theeuwes, 2019). Examining the functional differentiation of the networks during incidental associative learning, a strong relation between memory and network dynamics was revealed. The pronounced engagement of the AnG during constant processing of multimodal associations support previous accounts, classifying it as a heteromodal associative region that contributes to the global integration and access of acquired associative information (Bonner et al., 2012; Ramanan and Bellana, 2019; Ritchey et al., 2015; Rugg and King, 2018; Shimamura, 2011). In contrast, the functional role of dorsal PPC regions, including the SPL, were attributed to task-directed attentional processes required for controlled informational processing and related goal-directed behavior, i.e. the variable condition. Presented results suggest that the essential difference between the functional involvement between the vPPC and dPPC do not depend on item memory or the memory stage per se, but on goal-driven or history-driven factors modulating associative memory processing.

3.3. Additional behavioral study 3 – implicit sequence learning of crossmodal associations

As the presented dissertation is on the neural correlates associated with associative memory processing, this additional behavioral study will only be described briefly. However, I highlighted the main significant finding within the following passages on incidental crossmodal learning on a pure perceptual level independent from motor learning.

3.3.1. Participants

Forty healthy individuals volunteered to participate in this behavioral experiment. Thirteen participants were excluded due to dropouts, technical difficulties during measurements, or data quality. The final sample included twenty-seven participants (age: 19-32 years, 13 females). All participants had normal or corrected-to-normal vision.

3.3.2. Study design and paradigms

Stimuli

Within this behavioral study on crossmodal memory, eight different stimulus types were used (four visual and four auditory stimuli). Stimuli were chosen arbitrary from a stimuli pool database of well distinguishable colors and tones. The general stimuli set-up was almost identical to the classical SRT paradigm (please see "Introduction"). Thus, for the visual and auditory stimulus presentation, I used an almost identical visual layout, as described in the following.

The visual stimuli were presented as rectangular patches of color (80 pixels side length, 28mm, 72 dpi) on a 23-inch screen (SyncMaster P2370; Samsung), which was positioned 1.1m in front of the participant. I used four different colors (V1: yellow, V2: magenta, V3: blue, V4: black). The colored rectangular patches were displayed in a semi-circle on the screen. The location of the rectangular patches was assigned to the corresponding response keys. For the visual trials, a single (colored) target square was displayed in the middle of the screen, as illustrated in Figure 3.

The auditory stimuli consisted of four different tones, i.e. sine wave samples (A1: 120Hz, A2: 286Hz, A3: 389Hz and A4: 527Hz), which were chosen according to (Conway & Christiansen, 2006). As in the presented fMRI studies, the auditory stimuli were presented via headphones at individually adjusted volumes. Black circles with different diameters were displayed in a semi-circle on the screen, as illustrated in Figure 3. Those black circles were used to "visually" represent the different tones, i.e. different sine wave samples and to indicate the current response mapping. Thus, as for the visual domain, the location of the black circles was assigned to the corresponding response keys. To illustrate, the biggest circle represented the lowest frequency (120Hz), while the smallest circle represented the highest frequency (527Hz).

The cross-modal audio-visual serial reaction time task

Within this additional behavioral study, I examined whether a pure-perceptual crossmodal sequence could be learned implicitly. To be specific, I tested whether the cross-modal, sequential presentation of visual and auditory stimuli would also result in implicit (sequence) learning. As in the classical SRT paradigms (Nissen & Bullemer, 1987), a target stimulus appeared in the center of the screen. The task was to press the keys, which correspond to the identity of the target stimulus as fast as possible.

As in the classical SRT paradigm, visual rectangles were displayed in a semicircle on the top of the screen to reflect the corresponding response options. The positions of the rectangles in this circle directly corresponded to the position of the response buttons. To test then for crossmodal sequence learning, I presented auditory and visual stimuli in a successive order. Hence, using a modified version of the classical SRT, the to-be-learned perceptual sequence contained eight difference stimulus types from two different modalities (visual: four different colors, auditory: four different sinusoidal tones). Furthermore, the modality in which a stimuli was presented alternated across learning trials (sequence: "auditory stimulus A" follows "visual stimulus A" follows "auditory stimulus B" follows "visual stimulus B" etc.).

Importantly, to observe "pure perceptual" sequence learning, audio-visual sequence had to be experimentally isolated from motor response learning (see "Introduction"). As in study 1, the motor response sequence was decoupled from the cross-modal perceptual sequence by randomizing the response key mapping (Rose et al., 2011). This modified approach allowed to examine pure perceptual implicit sequence learning, however, it also has a disadvantage. Due to the continuous trial-by-trial remapping of response buttons (Rose et al., 2011), participants are forced to search for the current "correct" response button. Thus, the learner was not able to prepare motor responses in advance, which resulted in a high variance in reaction times (Rose et al., 2011). In other words, it might be more difficult to detect a significant decrease in response speed for the perceptual sequence compared to a determined motor sequence (Rose et al., 2011). Based on previous studies, I therefore implemented a probabilistic regularity within this audio-visual sequence in order to detect changes in reaction time across learning trials (Cleeremans & McClelland, 1991). This probabilistic series allowed to detect any changes in reaction time between stimuli which were highly predictable (regular stimulus) and those which appeared unpredictably (deviant). In particular, faster reaction times would strongly indicate that the target stimulus processing benefit from the implicitly acquired knowledge about the regular, highly predictable crossmodal sequence. The probabilities for all perceptual stimulus transitions were included in a transition matrix. For example, a probability of "1" means that a visual stimulus (e.g. V1) would be always followed by an auditory stimulus (e.g. A1), or vice versa. For the presented task, each transition of the regular stimulus sequence (for example: A1-V1-A2-V2-…) was presented with a probability of 0.85. The specific order in which the auditory and visual stimuli were presented was determined by this matrix. For an overview of the specific transition matrix, please see the respective paper (Taesler, Jablonowski, Fu, Rose, & Taesler, P., Jablonowski, J., Fu, Q., & Rose, 2019). To sum up, while previous paradigms focused only on one modality when examining the implicit learning effect in an SRT, this specific task was used to test whether the implicit sequence learning effect can also be found when using pure perceptual stimuli from two different modalities.

The total experiment consisted of 1500 trials which were presented sequentially, while auditory and visual stimuli were alternated each trial. The task was to respond as fast and correctly as possible. The experiment was subdivided into 5 session with 300 trials each and a short (~1 minute) break in between.

For the post-experimental mapping of implicit and possible explicit knowledge, participants were first asked whether they have noticed any kind of regular structure or pattern in the stimulus material. However, to ensure that no explicit knowledge was acquired, participants were instructed to select possible stimulus pairs from the presented stimulus pool that they thought might have appeared regularly successively, i.e. as transitions (almost identical to test phase of fMRI study 1). Noteworthy, participants were also told to guess if they were unsure about their response. To assess whether the knowledge was of implicit or explicit character, participants were instructed to rate their confidence about their response. This free recall task was open ended, i.e. participants had the possibility to enter as many stimulus combinations as they liked. Taken together, as in the fMRI study 1, I applied the logic of a generation task for the test phase of the third behavioral study. This approach allowed to identify the amount of implicit and possible explicit crossmodal sequence knowledge.

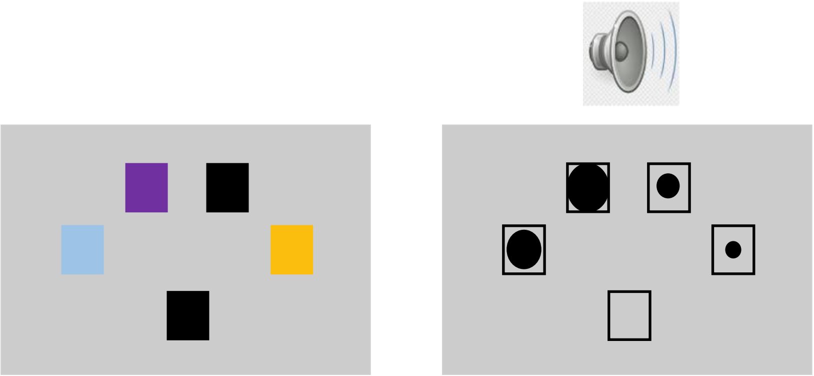

Figure 10: **The experimental design of the crossmodal learning task.** (Left panel) For the visual modality, the target visual stimulus was displayed in the middle represents and had to be matched as fast as possible. (Right panel) For the auditory modality, the back circles were used to represent the four different sine wave frequencies and the location of the corresponding response keys. However, no visual target reference was presented in the center of the screen, as the auditory stimuli was presented via headphones.

3.3.3. Analyses

As in fMRI study 1, the free recall performance in combination with the confidence ratings were used to assess the amount of implicit and explicit knowledge of the stochastic crossmodal sequence. To do so, I calculated the percentage of correct response as well as high and low confidence ratings across correct responses. The number of high confidence correct stimulus pairs (or transitions) was then divided by the total number of response inputs during the free recall task, indicating the final performance score.

3.3.4. Results

In total, almost half of the participants (48%, 13 participants) reported noticing a regularity or a sequence within the stimulus material. However, most of those participants just reported in the periodical transition between auditory and visual stimuli, thus it remained unclear whether they noticed any specific regular transaction, which occur constant throughout the experiment. Interestingly, the free recall performance however demonstrated that only four participants among those 13 participants were able to reproduce any correct stimulus pairs. Further, those participants differed in their proportions of correct to incorrect reproductions of stimulus pairs (stimulus transitions) with 33%, 28%, 14% and 11% correctly reported stimulus transitions. All the other participants reporting any regular structures did not managed to reproduce any correct stimulus transition, even with unlimited attempts. Based on the logic of a classical generation task, this ratio of incorrect free recalls as well as low-confidence responses reported in the post- experimental test clearly demonstrated that the acquired crossmodal knowledge was of implicit nature, even for those participants that claimed to have noticed a regular structure.

Crucially, results indicated a different discriminability for visual and auditory stimulus types. Even though the participants reliably distinguished all stimuli, the mean reaction times and error rates differed across the eight stimulus types. On the one hand, the response to visual stimuli was in general faster than towards auditory stimuli. On the other hand, error rates were higher for auditory stimuli than for visual stimuli. Interestingly, within the auditory modality, the responses to the two middle tones (A2 and A3) was faster as the other two tones (A1 and A4), even though those tones were generally more difficult to discriminate. However, error rates were also higher for the two middle tones (A2 and A3). Taken all these points into consideration, the learning rates across trials differed not only for modality but also for stimuli within the corresponding modalities. However, I did not found any correlation to global error rates or reaction time differences between stimuli within or across modality.

3.3.5. Conclusion

Within this additional behavioral study, I investigated the incidental learning process in a crossmodal learning condition. As previous SRT only used unimodal stimuli, within this modified crossmodal version of the SRT I presented different visual and auditory stimuli in an alternating fashion. Importantly, to exclude motor learning, motor responses were mapped randomly across trials, which ensured that the pure perceptual learning was taken place independently from motor learning. Results demonstrated the successful crossmodal implicit learning effect of a pure perceptual sequence. This finding is of great interest as it extends our understanding of the implicit learning system and suggest the possibility that crossmodal information can be learned implicitly. In contrast to a recent theory, the dual system account, Keele and colleagues (2003) stated multiple unimodal learning systems are only able to work in parallel when no guided attention or explicit awareness is involved (Keele et al., 2003). Hence, it is assumed that multimodal learning occurs in a different system which requires the involvement of consciousness. Accordingly, consciousness is needed to integrate the unimodal information into a single unified representation or associations. However, present and more recent studies revealed that crossmodal representations can be even processed without the involvement of consciousness (Conway & Christiansen, 2006; Haider et al., 2020). Taken together, the presented study reveals that crossmodal perceptual representation including different stimulus modalities can be learned implicitly.

4. Discussion

The aim of the studies included in this dissertation project was to examine incidental associative learning within and across different perceptual modalities and the underlying neural correlates. In particular, I investigated the neural correlates underlying the incidental acquisition of relational (episodic) representations using unimodal (study 1) and multimodal perceptual stimuli (study 2). Furthermore, on the behavioral level, I aimed to examine whether incidental associative learning across modalities is actually possible (study 2 and 3), and whether this acquired knowledge requires the involvement explicit guided attention, or whether this knowledge could also be acquired implicitly (study 3). Based on the characteristics of episodic events, within these current incidental learning paradigms, the included pure perceptual stimuli followed a specific temporal regularity or arrangement. The presented results do support recent accounts on associative learning processes and extend prior knowledge on the convergence of relational information during episodic memory formation. Furthermore, the findings not only support but also negate some hypotheses of this dissertation.

As mentioned in the introduction, the implicit learning effect has already been well examined across different behavioral and imaging studies while mostly using different types of visual stimuli. Thus, within presented studies I used auditory as well as visual stimuli. I revealed that pure perceptual implicit learning does not only occur within the auditory modality, but also across different modalities - or at least the visual and auditory modality. My findings are of particular importance as they reveal that the implicit learning effect is not limited to visual dependencies or a single modality (study 1 and 3). In addition to that, presented results further support the assumption that multimodal representations can be learned implicitly without the involvement of explicit guided attention (study 3).

More importantly, since perception is actually multimodal, presented studies (could) thus serve as a starting point for future fMRI studies on incidental sequence learning and implicit memory formation across the auditory and visual modality. Furthermore, as reported in the beginning of this dissertation, the hippocampus, the ventral posterior parietal lobe (in particular, the angular gyrus) and the anterior temporal cortex have been frequently related to processes of declarative memory. In fact, those critical regions have been frequently classified as convergence zones for multimodal processing. Within the presented fMRI studies, I provided evidence for a significant involvement of the hippocampus (study 1 and 2) and the angular gyrus (study 2) when participants' incidentally acquired novel and relational knowledge about semantically incongruent – and thus previously unrelated - pure-perceptual episodic events. In particular, within both fMRI studies, I was able to support the modern theory on memory systems that hippocampal involvement is not limited to explicit memory, but also involved in implicit episodic memory formation. With respect to the second fMRI study, so far no one appears to have revealed the difference in the functional contribution to multimodal processing of the ventral and dorsal regions of the parietal cortex within one paradigm. However, I was able to show that both the hippocampus and the angular gyrus were significantly involved in processing different perceptual stimuli into a conjunctive memory representation. Interestingly, not only the AnG, but also the precuneus and the posterior cingulate cortex were activated during memory processing of contextual information. All these regions appeared to be critically involved during the associative memory formation of mental contextual representations supporting the multimodal nature of episodic memory. Finally, presented findings concerning the activation of the dorsal parietal cortex was rather related to attentional control processes. In contrast to other studies on multimodal processing, I did not find any activation within regions of the anterior temporal cortex (see "Introduction").

In the following, these findings are discussed in more detail and integrated within the current state of research on associative memory processing of perceptual associations. Within this section, I further discuss how the presented findings are important for future directions in this field and address remaining open questions.

4.1. The hippocampus and its functional role in processing new and flexible relational representations

The overall direction of the presented results did not only reveal hippocampal involvement in the systematic formation of relational memories within (study 1) and across modalities (study 2), but also demonstrated that hippocampus-dependent processes were independent of the involvement of awareness about the acquired memory. In line with the specific characteristics of the episodic human memory system, the presented findings support the assumption of a hippocampal recruitment in both implicit and explicit episodic memory formation.

Challenging the traditional memory framework

Based on neurobehavioral studies of amnestic patients and imaging SRT studies with healthy participants, the functional role of MTL structures, including the hippocampus, were soon exclusively related to explicit memory (Squire & Zola, 1996). Forms of implicit memory were assumed to rely on different cortical regions, such as basal ganglia or motor cortices (for more details, please see: “Scientific background and research question”). The traditional memory framework has been challenged by several imaging studies using the SRT or other paradigms on implicit memory. These studies demonstrated that person’s level of awareness is not a mandatory factor for hippocampal involvement during associative learning (Chun & Phelps, 1999; Henke, Treyer, et al., 2003; Preston & Gabrieli, 2008; T. P. Reber, Luechinger, Boesiger, & Henke, 2012; Rose et al., 2011). As the traditional SRT task employed a fixed stimulus-response mapping, it can be assumed that different associations from different modalities (motor vs perceptual associations) are acquired, which are governed by different learning systems. Based on the study by Rose et al. (Rose et al., 2011), in my second study, I was able to disentangle the motor and perceptual learning system within one SRT task. This specific approach allowed addressing the question of whether the functional role of the hippocampus is specific for visual but not auditory associations or whether its engagement can be generalized to other pure-perceptual sequential associations - or at least generalized to the auditory and visual modality. Using auditory associations, study 1 provided additional evidence for bilateral hippocampal activation during implicit learning of perceptual dependencies. To be specific, bilateral hippocampus activations were positively related to implicit knowledge of auditory associations. Hence, this study and a previous study within our group (Rose et al., 2011) were able to relate hippocampal recruitment to pure-perceptual associations, suggesting a general function role of the hippocampus in pure-perceptual associative learning. Importantly, these findings are consistent with other SRT studies indicating hippocampal engagement in implicit memory processes (Gheysen et al., 2011, 2009; Grafton et al., 1995; Ling et al., 2015).

Furthermore, both fMRI studies included in this dissertation provided reliable evidence for the assumed functional role of the hippocampus during both forms of memory acquisitions, intentional and incidental. Using incidental learning paradigms, I did not only demonstrate a positive relation between bilateral hippocampal activation and implicit memory of perceptual associations (study 1), but also revealed significant hippocampal involvement during both incidental acquisition of (non-sequential) relational material and intentional retrieval of the new acquired relational memory (study 2). Hence, it can be further suggested that hippocampal structures operate independently of both the involvement of awareness and of whether the learned material was sequential. Consistent with previous studies using different paradigms on implicit memory, it was shown that hippocampal engagement did not depend on whether the incidentally acquired material was sequential, but rather relied on the relational binding of perceptual episodic events in general (Duss et al., 2014; Gheysen et al., 2011; Henke, 2010; Henson, 2005; Rose et al., 2011; Wang & Giovanello, 2016). To illustrate, using non-sequential perceptual material, studies on implicit memory revealed hippocampal activation during the incidental acquisition of relational associations, such as face-name or face-scene associations (Degonda et al., 2005; Hannula & Ranganath, 2009; Henke, Mondadori, et al., 2003; Henke, Treyer, et al., 2003). Accordingly, hippocampal involvement in relational memory processes was suggested. This assumption was further supported on the level of single neuron recordings, revealing hippocampal involvement in the binding of both spatial and non-spatial perceptual information in both rats (Terada et al., 2017) and human beings (Quiroga et al., 2005).

A growing body of evidence is inconsistent with the traditional memory framework in which human memory systems are classified by the involvement of awareness. As discussed throughout this thesis, neither (explicit) awareness nor intentional retrieval might be a mandatory factor for the involvement of hippocampal structures in episodic memory (Duss et al., 2014; Henke, 2010; Henke et al., 2013; Konkel & Cohen, 2009; Konkel, Warren, Duff, Tranel, & Cohen, 2008). A recent fMRI study directly addressed this issue and demonstrated that neither intentional nor incidental retrieval processes had an effect on the functional involvement of MTL structures, including the hippocampus (Wang & Giovanello, 2016). Independent of retrieval intention, hippocampal structures were proposed to be differentially recruited during retrieval of item and relational information (Henke, 2010; Henson, 2005; Ranganath & Ritchey, 2012; Wang & Giovanello, 2016). So far, the presented imaging results are consistent with the view that hippocampal involvement are critically involved in relational memory formation. Within both fMRI studies, I have shown that hippocampal activations were related to the flexible binding of temporally structured information into relational (episodic) representations. Using relational material within both studies, the presented findings also indicate that hippocampal structures did not only mediate the formation of associations within modality (study 1) but also across modalities (study 2). The presented results of both fMRI studies are also consistent with the assumption that the hippocampus is crucially engaged in associating item and context information, and organizing complex episodic memories (H. Eichenbaum, 2017). Interestingly, the assumed functional role of the hippocampus in relational memory processes is also supported by its rich anatomical connections with several different sensory cortical pathways (Dickerson & Eichenbaum, 2010; H. Eichenbaum, 2017; Quiroga et al., 2005; Suzuki & Amaral, 1994). Connectivity analysis on neuroimaging data further showed that the hippocampus is functionally highly correlated with a network of several regions involved in episodic memory, such as the posterior parietal cortex, the anterior temporal cortex, the precuneus and the frontal cortex (Buckner et al., 2008; Eichenbaum, 2017; Moscovitch, 2008; Ranganath, 2010; Vincent et al., 2008, 2006). Hence, while receiving input from different cortical areas, hippocampal structures appear to be optimally suited to form unimodal and multimodal relational representation between different perceptual stimuli within or across modalities.

The results presented here not only provide additional evidence for a functional involvement of the hippocampus in the organization of relational (episodic) memory. In fact, my findings also clearly support the assumption that memory systems should not be specified in terms of consciousness, but by the characteristics of the learned material (Duss et al., 2014; Goschke & Bolte, 2012; Henke, 2010; Rose et al., 2011). Thus, within this dissertation, a more general functional role of the hippocampus in relational memory is proposed. In fact, this assumption is consistent with previous frameworks on the functional specification of the hippocampus in associative learning processes (N. J. Cohen et al., 1997; H. Eichenbaum, 2004; Henke, 2010). Accordingly, the key functions of hippocampal structures should not be specified in terms of awareness but should be differentiated by relational processing operations (N. J. Cohen et al., 1997; Henke, 2010; Wang & Giovanello, 2016). With regard to a prominent model by Henke (Henke, 2010), hippocampal involvement is specifically related to the rapid encoding of flexible relations between perceptual associations regardless of the explicit character of the acquired memory. However, considering the presented functional imaging findings, this proposal has to be extended by a more precise functional specification. Within study 1, I have shown that the hippocampus is also involved in slower incidental learning processes of pure-perceptual associations, which involves a large number of learning trials. To be specific, I assumed that the functional role of the hippocampus is not limited to fast perceptual associative learning, but is also involved in slower incidental learning processes of perceptual associations.

Taken together, the assumed function of the hippocampus reflects key features of the human declarative (episodic) memory system, such as the encoding of sequences and the integration of spatiotemporal information within and across perceptual modalities. Consistent with previous findings, the presented findings support the assumption that these core functional processes can occur independently of the involvement of awareness (Hannula & Duff, 2017; Henke, 2010).

4.2. The explicit and implicit episodic memory-related network

Within present studies, activations in the bilateral hippocampus were related to the implicit encoding of an auditory sequence (study 1), the incidental integration of different multimodal information into a coherent relational representation and the explicit recollection of the acquired knowledge (study 2). Across the literature, it has been frequently suggested that the hippocampus acts as a linking hub or convergence zone (Marr, 1971) which is required for the processing of both implicit and explicit relational memories (Henke, 2010; Henke et al., 2013; Konkel et al., 2008; Paul J. Reber, 2013; Reder, Park, & Kieffaber, 2009; Rose et al., 2011). Thus, the presented findings of this dissertation project are in line with several related functional studies.

Interestingly, the presented results are further consistent with a recent meta-analytic comparison of fMRI experiments that investigated whether the implicit and explicit memory system can be associated with similar or different neural correlates (Kim, 2019). Consistent with the multiple learning system view reviewed in the introduction (P. A. Frensch & Rünger, 2003; Haider & Frensch, 2005), this meta-analysis revealed that the implicit and explicit memory system do not operate independently. In fact, these two memory system continuously interact during encoding and retrieval. Within this framework, it was highlighted that explicit and implicit memory-related activations can be characterized by common-encoding networks. However, explicit and implicit memory-related activations are assumed to rely on separate-retrieval networks. With regard to the encoding network, they revealed that activations within the hippocampus, the ventrolateral prefrontal cortex and the ventral temporal cortex were not only involved in perceptual, semantic and relational processing but also overlapped in explicit and implicit memory processing (H. Eichenbaum, 2017; Hannula & Duff, 2017; Henke, 2010; Kim, 2019). The findings of this meta-analysis regarding the general functional role of the hippocampus in relational memory are consistent with the results presented in my thesis, as hippocampal activation was found during implicit sequence learning, as well as during incidental learning and explicit retrieval of multimodal associations. Taken together, the presented results provided additional support for the assumption that the hippocampus is an essential component of the episodic memory network.

As already mentioned in the introduction, during episodic memory-related processes, the hippocampus functionally interacts with a network of several cortical regions which are modulated by different cognitive functions (H. Eichenbaum, 2017; Ranganath, 2010; Maureen Ritchey, Libby, & Ranganath, 2015; Voss et al., 2012). Importantly, within my second study, not only activations within the hippocampus, but also within the AnG were related to relational processing of perceptual associations. To be specific, AnG activation scaled with the amount of the acquired explicit multimodal knowledge acquired under an incidental learning condition. Furthermore, a significant increase in the AnG was only found for the constant audiovisual stimulus pairs but not for stimulus pairs of the variable condition. In contrast, increased activity in the SPL was only found for the stimulus pairs of the variable condition. Importantly, these findings were found in both memory stages, learning and retrieval. Thus, it can be assumed that the ventral and the dorsal posterior parietal cortex differ in their functional contribution during contextual-related processes.

Interestingly, these findings are also in line with the meta-analytic comparison of fMRI experiments by Kim, mentioned above (Kim, 2019). Accordingly, activations across retrieval-related cortical regions only modestly overlapped during explicit and implicit memory processing (Kim, 2019). To illustrate, explicit retrieval processes were related to regions of the default more network (DMN), including the ventral parietal cortex. To be specific, this meta-analysis and other related studies revealed that regions of the DMN were specifically related to explicit retrieval success of episodic memories (Binder et al., 2009; Kim, 2019; Sestieri et al., 2011). As the DMN has been often related to internally directed cognition, such as autobiographical memory retrieval, laboratory-based recollection, and semantic memory retrieval (Binder et al., 2009; Kim, 2011, 2016), it was suggested that regions of the DMN are involved in the conscious processing of internally generated representation. Thus, the DMN has been frequently associated with explicit retrieval of perceptual associations (Kim, 2019). In contrast, implicit retrieval processes were mainly related to the dorsal attention network (DAN), including the SPL (for more details, please see ”Introduction”). These findings are consistent with previous related studies reporting that the DAN is specifically involved in attentional control and external stimulus processing (Cabeza, 2008; Corbetta & Shulman, 2002; Sestieri, Capotosto, Tosoni, Luca Romani, & Corbetta, 2012; Spaniol et al., 2009). Hence, during explicit and implicit memory retrieval, activations within related cortical regions were attributed to segregated neural networks (Kim, 2019). This difference in functional involvement has been explained by the assumption that the demand for specific cognitive processes, such attention, representation, evaluation, and the attentional control of retrieved information, differs in explicit and implicit memory processes.

The assumption that segregated neural networks differ regarding their functional contribution during episodic memory processing are consistent with the presented results of study 2. However, the different effects of study 2 might not be explained by an implicit-explicit-memory account, but by a difference in functional involvement during multimodal processing of perceptual associations. This assumption is consistent with studies on episodic memory, as the ventral parietal cortex has not only been related to the default-mode network, but also to critical cognitive functions which are required in episodic memory processing (Humphreys & Ralph, 2015; Seghier, 2013; Shimamura, 2011; Vilberg & Rugg, 2009a; Xu et al., 2016). As noted earlier, explicit memory can incidentally develop due to participants’ voluntary or involuntary awareness about the repeated presentation of stimuli (Butler & Berry, 2001; Haider & Rose, 2007; Rose et al., 2010). Kim and colleagues found that retrieval-related activity in the ventral parietal cortex was not only associated with high confidence responses, but also with repetition enhancement effects (i.e. repeated stimuli > first stimulus) in incidental learning tasks (Kim, 2016, 2019). While the ventral striatum and the ventrolateral prefrontal cortex were found to directly precede the emergence of awareness (Rose et al., 2010), it is not yet clear whether the ventral posterior partial lobe plays also a critical function during the generation of awareness for the learned material. Interestingly, a relation between the functional involvement of ventral parietal lobe and the level of consciousness has already been assumed within recent studies (Kim, 2019; Legostaeva et al., 2019). However, within this experiment, I did not directly address the question of whether AnG activations can be attributed to the memory processing accompanying the process of consciousness. With respect to study 2, it would be of great interest to examine whether there is a relation between participants’ explicit knowledge (i.e. the time point at which explicit memory emerged) and the recruitment of the AnG. From this perspective, the presented findings could serve as a starting point for future studies addressing the question of whether the AnG is relevant for the generation of awareness about the acquired relational knowledge.

Taken together, the presented fMRI findings corroborate meta-analytic findings and related studies regarding the essential role of the hippocampus and the ventral parietal lobe in episodic memory organization during incidental learning situations. On the one hand, the presented findings are in line with the assumed functional role of the hippocampus in both implicit and explicit processes related to episodic memory, in particular during encoding. On the other hand, results of study 2 provided additional support for a significant functional involvement of the ventral posterior parietal cortex during incidental episodic-related processes and explicit recollection. In particular, within study 2, the results clearly showed that there is a functional dissociation between the ventral and the dorsal posterior parietal lobe during multimodal memory processes of perceptual associations - within a single paradigm. With respect to previous theories on the functional role of the posterior parietal cortex in episodic memory, the presented findings of study 2 are discussed in more detail in the following sections.

4.3. Multimodal processing

4.3.1. The posterior parietal lobe

Using an incidental paired-associate learning task (study 2), I was able to relate associative memory-related activations between two multimodal conditions either to the ventral or the dorsal posterior parietal lobe. Within both conditions, attention had to be paid to two unisensory stimuli simultaneously (for more details, please see “General Materials and Methods”). While an equal number of unimodal stimuli was used in both conditions, the only difference was the underlying binding regularity (constant vs variable condition). This approach allowed relating activations of the ventral or the dorsal PPL to either a consistent or a variable appearance of multimodal stimulus pairs within one paradigm. Increased activation of the AnG was related to the binding process of two previously unrelated unimodal stimuli into a common audiovisual representation (constant condition), during both incidental learning and explicit recollection. Interestingly, increased activation of the AnG also scaled with memory sensitivity (d'). In contrast, increased activation within the SPL was specific for the variable condition, in which multimodal pairs were continuously recombined. Importantly, all these effects were found during both memory stages (learning and recollection). Therefore, I suggest that this significant difference in activation is due to a difference in functional involvement when contextually rich information is processed. In particular, I propose that the angular gyrus had a specific functional role in processing episodic, consciously-accessible knowledge that was acquired under an incidental condition.

Consistent with meta-analytic and within-study evidence on episodic memory, presented results indicated a distinctive functional role of the vPPC and the dPPC during incidental learning and explicit retrieval of episodic information (Gilmore et al., 2015; Humphreys et al., 2021; Hutchinson et al., 2014; Kim, 2010, 2019; Rugg & King, 2018; Spaniol et al., 2009; M. Uncapher & Wagner, 2009; Vilberg & Rugg, 2009a). Although several theories on memory proposed that the posterior parietal lobe is recruited in multimodal processing, they often assign different cognitive functions to the same neural areas while parcellating the parietal cortex in different ways (Humphreys & Ralph, 2015; Nelson et al., 2010; Seghier, 2013). As all the accounts on the function of the AnG have experimental support, they can be classified into an “attention-based”, “content-based” or an “integration/history-based” theory of AnG function based on their assumed function of the posterior parietal cortex.

The attentional reorienting account

In line with previous meta-analyses and reviews, the findings presented in this dissertation thus support the suggestion that the functional involvement of the vPPL and dPPL cannot be fully explained by an attentional reorienting account alone (Gilmore et al., 2015; Hutchinson et al., 2014; Rugg et al., 2015; M. R. Uncapher et al., 2006; M. Uncapher & Wagner, 2009). To be specific, I proposed that an attention-reorienting account for the function of the ventral region of the PPL is not a feasible explanation for my findings (Cabeza, Ciaramelli, & Moscovitch, 2012; Ciaramelli et al., 2008). To be specific, studies supporting an attention-based function of the parietal cortex propose that the ventral parietal cortex does not reflect a memory process, but the allocation or reorientation mechanisms of attention to internal sensory representations that is driven by external stimuli or internal content (Cabeza et al., 2012; Ciaramelli et al., 2008; Corbetta & Shulman, 2002). However, the presented results are not consistent with the assumption that the function of the angular gyrus reflects processes of (button up) attentional orienting mechanisms (Cabeza et al., 2008; Ciaramelli et al., 2008). With regard to the present incidental learning task (study 2), the two multimodal condition (constant vs variable condition) contained an equal number of auditory and visual stimuli and thus attracted similar attention. In particular, activations within the AnG were specific for constant audiovisual pairings, whereas activations in the SPL were specifically related to processing variable (i.e. variable) multimodal pairs. In other words, relational, multimodal knowledge which can be "automatically" acquired was related to the ventral region of the left parietal hemisphere (Humphreys & Ralph, 2015; Humphreys et al., 2021). In contrast, memory processes which required an increased demand for executive control and attention, i.e. such as processing multimodal stimulus pairs which were continuously recombined (variable condition), were associated with the dorsal region (Cabeza et al., 2012; Ciaramelli et al., 2008). Taken together, the presented results only partly support the attentional reorienting account.

On the one hand, the presented results agree with the assumption that the dorsal region mainly reflects top-down attention processes. As for the variable condition of study 2, it was suggested that when memories are weak and relevant information are not readily accessible, executive control processes are particularly engaged (Kim, 2010; Spaniol et al., 2009). Within study 2, the variable multimodal pairs were continuously recombined, thus no stable association between auditory and visual stimuli could be acquired. This might result in an increased demand for top-down attentional control processes, such as interference resolution, working memory, and response selection, in order to perform accurately throughout the experiment (Corbetta & Shulman, 2002; Hutchinson et al., 2009; Kim, 2010; Spaniol et al., 2009). In fact, the presented results revealed that activations in the SPL were mainly related to the variable condition, the condition which particularly required cognitive mechanisms of attentional and executive control (Corbetta & Shulman, 2002; Hutchinson et al., 2009; Kim, 2010; Spaniol et al., 2009). Thus, the presented results support the assumption of a functional role of SPL in top-down attentional control processes and in the detection of behaviorally relevant information (Corbetta and Shulman, 2002; Kim, 2010; Uncapher and Wagner, 2009). On the other hand, the presented results are inconsistent with the suggestion that the activation of the AnG reflects button-up attentional processes. In particular, the attentional reorienting account does not provide a clear explanation for the observed findings that AnG activation increased across learning trials only for the constant condition, but not for the variable condition, and scaled with memory sensitivity. With respect to the presented results, it can rather be assumed that the AnG involvement was specific for multimodal binding-related process of constant stimulus pairs. The specificity of the constant condition involved not only the binding of two previously unrelated unimodal stimuli into a common audiovisual representation. In fact, subsequent reactivation of the acquired memory representation was also required during recollection, particularly when only unimodal information was presented. As already mentioned, activations in the AnG have been related to multiple different functions other than attention (Binder et al., 2009; Humphreys & Ralph, 2015; Seghier, 2013; Vilberg & Rugg, 2012). Thus, consistent with previous suggestions, the presented findings support the interpretation that the involvement of SPL can be explained by an attentional-orienting mechanism. However, I assume that the AnG plays an essential functional role in the formation of relational representations (Bellana et al., 2019; Ramanan & Bellana, 2019; Shimamura, 2011). Taken together, the presented results are in line with previous scientific evidence, suggesting that the involvement of AnG activation cannot be explained by an attentional-orienting mechanism, but can be related to a memory-related mechanism.

The content-based account

Within present study, increased AnG activation was not only associated with consistent multimodal stimulus pairs, but also scaled with memory sensitivity. These findings are in line with previous related studies revealing that in particular the activity in the AnG scaled with memory performance (Humphreys and Ralph, 2014; Van Opstal et al., 2008; Vilberg and Rugg, 2009b). Hence, the presented findings are consistent with the mnemonic accumulator hypothesis by Wagner (A. D. Wagner et al., 2005) which suggested that AnG activity reflected the accumulation of acquired memory content during recognition. With regard to this account and related "content-based theories", the presented results are only partly explained. Proponents of the content-based theory generally assume that AnG activations are related to both the mnemonic content of encoding and the related strength of the new acquired knowledge (Janice Chen et al., 2017; Kuhl & Chun, 2014; Kuhl et al., 2013; Lee et al., 2017; Amy R. Price, Bonner, Peelle, & Grossman, 2015; Van Opstal et al., 2008; Vilberg & Rugg, 2009b). This view has been further extended by assuming that AnG activation particularly reflect the subjective quality of the memory content and a sense of confidence when recollecting memory details (Kuhl & Chun, 2014; Kuhl et al., 2013; Simons & Mayes, 2008; Tibon et al., 2019; Yazar et al., 2017). Although within study 2, I could not examine whether the activation within the AnG was specific for high confidence compared to low confidence responses, the presented findings appear to be consistent with a content-based theory, as AnG activation scaled with memory sensitivity. Nevertheless, neither the attention- nor the content-based explanatory account explains the observed time course dependent changes in ventral PPC activity across learning trails and condition.

In fact, a range of different memory performances recruits the AnG, in particular the left AnG (Humphreys et al., 2021; Seghier, 2013). To illustrate, activations in the left AnG have been frequently related to automatic rather than controlled processing (Humphreys & Ralph, 2015), thematic/conceptual rather than semantic representation (Binder et al., 2009; Bonnici et al., 2018; Davey et al., 2015; Schwartz et al., 2011), autobiographical recall > word pairs recall (Bonnici et al., 2018), semantic judgement > phonologic judgement (Binder et al., 2009), multimodal rather than unimodal (Ben-Zvi, Soroker, & Levy, 2015; Bonnici et al., 2016), high > low meaningfulness (Bonnici et al., 2016; Gilboa & Marlatte, 2017; Amy Rose Price, Peelle, Bonner, Grossman, & Hamilton, 2016). Thus, both the attention-based and content-based theory lack a feasible explanation for the variety of these findings and the presented results. With regard to study 2, AnG activity was only found for the constant multimodal pairs but not for the variable multimodal pairs. In particular, only for constant multimodal trials strong association could be incidentally acquired, which might contribute to contextualize incoming external information easily into already existing internal representation. As this process can improve memory performances (Kim, 2019; Moscovitch, Cabeza, Winocur, & Nadel, 2016), I therefore suggest that this "integration" process of information with context meaning (acquired from previously learned experience) specifically requires the engagement of AnG activation (Hasson et al., 2015; Humphreys et al., 2021; Kim, 2019; Ramanan et al., 2018; Maureen Ritchey & Cooper, 2020).

The integration/history-based account

According to a more history-based view, processing relevant information is not only driven by physical salience or by intentional, top-down goals, but can also rely on the experience or history of a particular stimulus or event (Theeuwes, 2019, 2018). The repeated exposure to constantly paired stimuli can result in a shift of the processing mode from goal-oriented processing towards history-driven processing based on the formation of stable associations (Hasson et al., 2015; Li and Theeuwes, 2020; Theeuwes, 2019). History-driven processing is fast, automatic and flexible, allowing incoming information to be dynamically integrated into meaningful associative representations without much effort (Chang et al., 2020; Hasson et al., 2015; Theeuwes, 2019, 2018). In contrast, when memory is weak, there remains a demand for intentional, goal-driven attentional control for incoming information since each single stimulus is processed in detail. This process is relatively slow and requires more effort (Hasson et al., 2015; Theeuwes, 2018, 2019). In particular, for multimodal stimuli, strong associative memory resulted in a more holistic processing for the different audio-visual combinations and the flexible establishment of memory schemata (Tse et al., 2007).

From this perspective, present results are most consistent with proponents of an integration/ or history-based account. From a history-based explanatory approach, the AnG has been frequently described as an essential associations region, or so called multimodal convergence zone, which is anatomically and functionally well suited to support integrative recollection (Binder et al., 2009; Humphreys et al., 2021; Ramanan & Bellana, 2019; Seghier, 2013; Shimamura, 2011; Xu et al., 2016). Further studies demonstrated that activations within the left AnG revealed to be more sensitive to detailed material and contextually-rich information rather than homogenous material, i.e. containing less contextual-rich and complex features (Bellana, 2018; Bellana et al., 2019; Johnson, Suzuki, & Rugg, 2013; Ramanan & Bellana, 2019). As already mentioned in the introduction, the functional role of the ventral posterior parietal cortex has been clearly differentiated from the ATL in conceptual relational memory processing (Clarke & Tyler, 2015; Davis & Yee, 2019; Kalénine et al., 2009; A. G. Lewis et al., 2015; Schwartz et al., 2011). While the ATL has been generally related to the generation of taxonomic knowledge including the formation of taxonomic relations and categorization, the AnG has been frequently related to formation of thematic relationships (Binder et al., 2009; Davis & Yee, 2019; Schwartz et al., 2011). In particular, activations within the AnG were reported to be sensitive to event-based information, such as such as temporal and spatial coincidences of objects in an (episodic) event ("what objects belong together"). Thus, consistent with an integration-based explanatory approach, the presented results suggest that the AnG reflects multimodal integrative functions which specifically operated on internally generated memory representations of highly relational, multimodal content (Bonnici et al., 2018; Davis & Yee, 2019; G. A. Lewis, Poeppel, & Murphy, 2019; Ramanan & Bellana, 2019; Rugg & King, 2018; Shimamura, 2011; van der Linden et al., 2017).

In additional to that, recent imaging studies demonstrated a relation between the reinstatement of prior knowledge and AnG activation when being incidental to recognition decisions (Bellana, 2018; Bellana et al., 2019; Moscovitch et al., 2016; Ramanan et al., 2018). In study 2, AnG activity was found not only during incidental multimodal learning but also during the successive presentation of unimodal stimuli during explicit recollection. To illustrate, when being confronted with slightly different incoming information (multimodal vs unimodal), it is required to integrate recent experience and prior knowledge. Hence, the presented findings also add to the assumption that the AnG is a significant component of a content-insensitive core recollection network (Hayama, Vilberg, & Rugg, 2012), which is assumed to be functionally involved regardless of the how the acquired memory is tested or the qualitative information associated with the memory content. Interestingly, several regions, including the ventromedial prefrontal cortex, the hippocampus and the AnG, were characterized to be sensitive to past experience relative to other regions of the neocortex (Bellana, 2018; Bellana et al., 2019; J. Chen et al., 2016). Consistent with previous studies, the second study provided additional support for a specific function of AnG in integration processes of contextually-rich information, which includes the binding of multimodal stimulus pairs or the integration of new incoming experience and prior knowledge as found in study 2.

Importantly, within this dissertation, it is not argued that AnG involvement is limited to multimodal information. However, I assume that the AnG is more sensitive to processing multimodal compared to unimodal relational representations (Bonnici et al., 2016; Richter et al., 2016; Sestieri et al., 2012; Tibon et al., 2019). Obviously, multimodal representations are more complex and contextually-rich compared to unimodal representations and thus requires the processing of context meaning (Bellana et al., 2019; Branzi et al., 2020, 2019). That is why a multimodal setting has been used, as it is more sensitive for the examination of this network differentiation. However, future studies should examine whether the same network differentiation will be found when comparing multimodal with unimodal learning.

Negative vs positive subsequent memory

Importantly, although negative subsequent memory effects has been more often found in the ventral region of the PPL (Hutchinson et al., 2009; Lee et al., 2017; M. Uncapher & Wagner, 2009), positive subsequent memory effects are not uncommon and were mostly found when the retrieval time was short (<45min) (Uncapher and Wagner, 2009). This finding is indeed consistent with these and other related findings (Tibon et al., 2019). Crucially, positive memory effects have been frequently examined when the broader context of the learned information had to be considered during encoding and recollection. In fact, these account are consistent with the presented findings. From this perspective, the presented findings are in favor of a more histoy-based interpretation for the function of the AnG (Bonner et al., 2012; Elman and Shimamura, 2011; Humphreys et al., 2020; Ramanan et al., 2018; Ramanan and Bellana, 2019; Rugg and King, 2018; Shimamura, 2011; Vilberg and Rugg, 2014).

Neuropsychological data

Furthermore, additional interesting findings on associative memory processing were provided by neuropsychological data from patients with lesions in the PPC (PPC patients), including the AnG. Compared to healthy controls, PPC patients were not severely restricted when retrieving acquired memory contents, but revealed stronger restrictions when recalling the subjective experience of the learned content (Berryhill et al., 2009; Russell et al., 2019; Simons et al., 2008; Simons and Mayes, 2008). Another study on multimodal cued recall demonstrated that PPC patients were significantly impaired during recollection, particularly when contextually rich episodic memories had to be retrieved (Ben-Zvi et al., 2015). Furthermore, a more recent investigation into associative processing found that PPC patients were impaired in both the integration of multimodal context and subjective evaluation during memory recollection (Ciaramelli et al., 2017). According to their interpretation, only controls, but not PPC patients, were able to use the richness of the learned experience allowing them the reinstatement of related features. This ability represented the critical basis for judging an item as “remembered”. Further studies on verbal and nonverbal memory performance showed that neurodegenerative disease patients with early PPC dysfunction were related to significant episodic amnesia (Ramanan et al., 2020b). Hence, across several studies with PPC patients, it has been pointed out that episodic memory performance relies on the structural integrity of AG-hippocampal connections (Ramanan et al., 2020b), specifically when retrieving personally-relevant episodic details from past experiences (Ramanan et al., 2020a). Interestingly, these findings are consistent with studies using neurostimulation reporting impaired recollection of episodic details and contextual integration after AnG stimulation (Branzi et al., 2021, 2019; Davey et al., 2015). However, there are some studies that attributed AnG effects to the reduced subjective experience of episodic memories during recollection (Koen et al., 2018; Richter et al., 2016; Sestieri et al., 2012; Thakral et al., 2017; Tibon et al., 2019; Yazar et al., 2014). Nevertheless, previous findings accounted for this finding by suggesting that AnG contribution to associative memory processing also requires the conscious access to the quality of the acquired memory, which is the basis for such “subjective” judgements (Rugg and King, 2018).

Preliminary conclusion

Within this dissertation a more general functional role of the AnG in episodic, consciously-accessible memory processing has been suggested. In line with previous studies, the AnG contributes to the process of giving meaning or phenomenological quality to an acquired memory representation within a contextual environment towards intended actions (Moscovitch et al., 2016; Seghier, 2013; I. C. Wagner et al., 2015). Accordingly, the AnG is particularly involved in the generation of internal “situation models” (Ranganath & Ritchey, 2012) “schemas” (Bonnici et al., 2018; Davey et al., 2015; Gilboa & Marlatte, 2017; Schwartz et al., 2011; I. C. Wagner et al., 2015), or “event concepts” (Binder et al., 2009) which allows “vivid” recollection of contextually-rich information and successful goal-directed behavior. Hence, a history-based explanatory account is a feasible explanation for the AnG being sensitive to both the associative binding of multimodal information and the presentation of unimodal information during recollection observed in study 2. Taken together, the present study provided critical evidence for the engagement of the AnG in episodic memory processing and related consciously-accessible conceptual knowledge of contextual information.

4.3.2. The angular gyrus and the hippocampus

From the acquired results and previous related studies, it can be inferred that the angular gyrus and the hippocampus functionally interact during episodic memory processing. Considering that the hippocampus is a critical cortical region for switching between present and past episodes or even future simulations

(Moscovitch et al., 2016), how does the hippocampus functionally interact with the AnG in order to support the memory retrieval of internally generated contextually-rich representations?

Across the literature, it has been frequently shown that both the hippocampus and the angular gyrus were engaged in associating item and context information in order to organize complex episodic memories (H. Eichenbaum, 2017; Humphreys et al., 2021; Maureen Ritchey, Cooper, Ave, & Ma, 2020). Importantly, the presented findings are in line with memory frameworks proposing a functional relationship between the vPPC and the MTL (Ranganath and Ritchey, 2012; Shimamura, 2011; Van Opstal et al., 2009, 2008; Vilberg and Rugg, 2014, 2012). According to these memory frameworks, it has been proposed that the hippocampus was primarily involved in the binding process of the core information of an episodic event (including as the who, what, when, and where) and thus particularly recruited in the initial establishment of relational representations (Ramanan et al., 2018; Ranganath, Cohen, & Brozinsky, 2005; Maureen Ritchey et al., 2015). The angular gyrus, in contrast, is specific for the integration and maintenance of relational, contextually-rich details which allows a perceptually rich recollection (Ramanan et al., 2018; Shimamura, 2011; Vilberg & Rugg, 2012). Our results are consistent with this assumption, as both regions were related to information integration and successful recollection of relational information (Ramanan et al., 2018; Ranganath and Ritchey, 2012; Shimamura, 2011). This functional relation is also supported by structural connectivity studies revealing dense multisensory connections between the AnG both modality specific and modality general cortical regions, such as the hippocampus (Rushworth et al., 2006; Seghier, 2013; Uddin et al., 2010; Vincent et al., 2008, 2006; Xu et al., 2016). With respect to this dissertation, the assumed functional role of the AnG is in line with these frameworks suggesting that the AnG operates as an associative region which interacts with several different temporofrontal subsystems in order to support global integration of the acquired contextual memory (Bonner, Peelle, Cook, & Grossman, 2012; Ramanan & Bellana, 2019; Seghier, 2013; Xu et al., 2017).

Presented findings can serve as a starting point for future research while focusing on the assumed dynamic relationship between activations in the left AnG and the hippocampus. As shown in this experimental design, a direct comparison between multimodal memory processing and attentional control within future fMRI or DTI studies would provide a better understanding of how the left AG contributes to episodic memory while functionally interacting with the hippocampus.

4.3.3. Functional involvement of posterior medial parietal regions

Within study 2, significant activations within posterior medial regions, including the precuneus and the posterior cingulate cortex were also found for the constant processing of multimodal associations (constant condition) during both learning and recollection.

The posterior medial system

As already introduced in the beginning, associative memory not only recruits hippocampal structures but also involves connected posterior medial temporal and parietal regions of the posterior medial system (PM system) (Gilmore et al., 2015; Kim, 2018; Ranganath & Ritchey, 2012; M. Ritchey, Yonelinas, & Ranganath, 2014; Maureen Ritchey & Cooper, 2020; Spaniol et al., 2009). Accordingly, the PM system includes the parahippocampus, precuneus, angular gyrus, posterior cingulate, medial prefrontal cortex (MPFC) operating at complementary timescales and are modulated by different memory functions (Aly et al., 2018; Cooper and Ritchey, 2019; Hasson et al., 2015; Ritchey et al., 2020, 2014). While being functionally co-activated with hippocampal structures, PM regions are also anatomically and functionally connected with each other during different memory functions (Ciaramelli et al., 2020; Ritchey et al., 2020). As an integrated hierarchical network, PM regions are involved in processing long-timescale temporal context (Chang et al., 2020; Hasson et al., 2015), carrying information about the spatial and temporal context of events (Ritchey et al., 2020; Schedlbauer et al., 2014). To illustrate, learning a temporal or ordinal structure of an event sequence resulted in an increase in functional connectivity among PM regions (Aly et al., 2018; Arnold et al., 2018; Baldassano et al., 2017; Chen et al., 2017; Cooper and Ritchey, 2019; Schedlbauer et al., 2014). PM regions are critically involved during the online processing of contextual information and the representation of mental contextual models supporting the multimodal nature of episodic memory (Ritchey et al., 2020; Rugg and King, 2018; Tse et al., 2007).

Consistent with presented findings of this dissertation project, not only the AnG, but also the precuneus and the posterior cingulate cortex were reported to be highly sensitive to contextual meaning of a narrative, while other cortical areas are reported to only track the physical properties of a stimulus (Aly et al., 2018; Baldassano et al., 2017; Hasson et al., 2015). In particular, posterior medial regions were found to detect changes in the environment by tracking the history of task outcomes, and thus contribute to the integration of associative information from different modalities (Pearson et al., 2011). A study on explicit associative learning using multiple encoding–recall repetitions found persistent experienced-dependent microstructural changes within medial posterior regions (Brodt et al., 2018). Thus, this region has been associated with new memory traces and related fast-learning processes (Brodt et al., 2018). In line with present findings, the AnG, the precuneus, and the posterior cingulate cortex have been related to associative information processing, while the acquired information/knowledge has contextual meaning in terms of previously acquired knowledge (Baldassano et al., 2017; Branzi et al., 2021, 2020; Brodt et al., 2016; Ritchey et al., 2020). Furth more, this relation was found to be generalized multiple sensory modalities (Baldassano et al., 2017; Bonner et al., 2012; Fernandino et al., 2016).

Critically, studies revealed that the repeated exposure to temporal contextual configurations results in an increased coupling among the precuneus, the posterior cingulate, hippocampus and the AnG (Aly et al., 2018; Baldassano et al., 2017; Brodt et al., 2018; Hasson et al., 2015; Ranganath and Ritchey, 2012). Therefore, not only a relation between associative memory and functional interactions among PM regions has been frequently assumed (Hasson et al., 2015; Ritchey et al., 2020). Indeed, it has been further suggested that PM regions contribute differently to associative memory-dependent processing while operating at complementary timescales (Hasson et al., 2015; Ritchey et al., 2020). Specifically, hippocampal structures are involved during early episodic processing, whereas the AnG, the precuneus and posterior cingulate cortex revealed particularly long processing timescales even over many seconds (Aly, Chen, Turk-Browne, & Hasson, 2018; Baldassano et al., 2017; Hasson et al., 2015). Based on these findings, it has been suggested that the AnG and posterior medial regions can be related to the specific contribution to the sustained recruitment during constant, associative memory processing (Aly et al., 2018; Hasson et al., 2015; Ritchey et al., 2020). Consistent with present results, both the AnG and the precuneus revealed sustained activations when retrieved associative information had to be maintained in memory for a variable delay period (Addis et al., 2007; Thakral et al., 2020, 2017; Vilberg and Rugg, 2014, 2012). In particular, while interacting with the medial PPC regions, the AnG maintains an integrated, multimodal episodic representation in order to support rapid associative processing and related vivid imagination of internal experienced-dependent memory representations (Arnold et al., 2018; Baldassano et al., 2017; Brodt et al., 2018, 2016; Richter et al., 2016; Ritchey et al., 2020). As critical components of the posterior medial network, ventral and medial PPC regions are specific for processing internal situation models accompanied by relevant context cues about the place, time and episodic experiences (Ranganath and Ritchey, 2012; Ritchey et al., 2020). Taken together, present findings provided additional findings for the engagement of ventral and medial PPC regions during associative encoding and retrieval. Based on previous results, present findings emphasized its recruitment during processing history-dependent event sequences and information integration over long timescales (Aly et al., 2018; Hasson et al., 2015; Ranganath and Ritchey, 2012; Ritchey et al., 2020).

4.3.4. Frontal regions

The extraction and integration of contextual details and the formation of stable associations between information from different modalities underlies a complex network of different mechanism requiring constant attentional control. Thus, with respect to study 2, during challenging multimodal learning trials, “variable” trials required, in particular, constant attentional allocation and controlled functional processing. Although I did not explicitly tested for cognitive control within this fMRI study, I so suggest that learning novel and continuously changing (variable) multimodal associations do involve particular controlled processing of the presented information and continuously conflict resolution processes (Dosenbach et al., 2007; Gruber & Goschke, 2004; Kim, 2020). Within present findings of fMRI study 2, activations within superior and middle frontal regions and bilateral anterior insula were particularly found during learning of “variable” associations, which were particularly task-/ or goal-driven as they could not be learned automatically. However, activation were also found during recollection of both conditions, the constant and the variable condition. As critical components of the frontoparietal control network (FCN), these regions are frequently reported to be specific for salience processing and executive control mechanisms (Seeley et al., 2007; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013; Spreng et al., 2010; Vincent et al., 2008). Based on the functional interaction between the FCN and DAN controlling goal-directed planning during incoming information integration between competing internal- and external-directed processes (Long & Kuhl, 2018; Thomas Yeo et al., 2011; Vincent et al., 2008), presented result might be accounted by the constant recruitment of the FCN-related regions.

Critically, increased activation within the precuneus was also found for the present reverse interaction contrast (goal-driven vs. history-driven across session) and the first stimulus event of the recollection task. Based on previous findings, precuneus interaction has not only been observed within the PM network, but also with regions of the FCN, suggesting its functional engagement across various processing states (Kim, 2018; Spreng et al., 2013; Utevsky, Smith, & Huettel, 2014). Accordingly, functional interactions guided by the precuneus were observed to be dependent on task demands (Maureen Ritchey et al., 2020; Spreng et al., 2013; Utevsky et al., 2014). While activations of the precuneus were more pronounced during the constant condition – associative with automatic / history-driven processing - its recruitment during more attentional or control related processing might reflect its flexible connectivity profile based on task demands (Kim, 2018; Spreng et al., 2013). However, this specific assumption remains to be investigated within future imaging studies.

4.4. Limitations and future directions

To reduce the variability in the data and attain more power in the analyses of study 1, it would have been also preferable to investigate a bigger sample size. A bigger sample size would have further increased the probability to have a selected group of participants with explicit memory. This would allow a comparison between participants with implicit memory and participants with explicit memory. In addition to that, this approach would have provided a deeper insight into the difference in neural activation between implicit and explicit memory formation processes. Consequently, this specific experimental approach would have revealed whether previous findings reported within our group could be replicated when using auditory stimuli (Rose et al., 2010, 2011). Taken together, findings within our group could serve as a starting point for future investigations on incidental learning. In particular, future studies should examine whether findings within our group can be generalized to incidental learning of perceptual associations or whether these effects were specific for incidental learning within the visual and auditory modality. Furthermore, within the present study 2, I used a multimodal setting, as it is more sensitive for the examination of the network differentiation underling associative memory-dependent processing. However, future studies should examine whether the same network differentiation could be found when comparing multimodal with unimodal learning.

Although human experience is multisensory in nature, previous research in incidental learning has focused predominantly on learning of unisensory information. However, it is widely known that knowledge acquisition benefits maximally when information is provided by multiple sources compared to a single sensory modality (Shams et al., 2011; Shams and Seitz, 2008). Thus, it remains to be investigated whether implicit memory about multimodal associations can be actually acquired and whether multimodal stimuli can influence the transfer from implicit to explicit knowledge. As almost all participants acquired explicit memory within study 2, I was not able to address the question of whether the involvement of the angular gyrus could be modulated by consciousness. Furthermore, it remains to be investigated how the AnG functionally interact with the hippocampus, and how it supports memory processes of internally generated context. Thus, future investigation should address the question of whether the activation within the angular gyrus can be related to the emergence of awareness about the acquired knowledge and how it functionally interacts with the hippocampus. These approaches would provide additional insight not only into the neural classification of both memory and consciousness but also into the cognitive constraints of nonhuman primates for such processes (Fitch and Hauser 2004; Friederici et al. 2006).

As I have focused on the hippocampus and the angular gyrus, other region in the vicinity of the AnG are also characterized by strong positive responses when episodic memory is retrieved, such as the posterior cingulate cortex, the precuneus or the anterior temporal cortex (Daselaar et al., 2004; Gilmore et al., 2015; Kim, 2010). Like the AnG, activations within these regions scaled with memory sensitivity or were specific for multimodal processing. Future investigation should aim at specifying the difference in functional involvement between the AnG and other regions involved in episodic memory. To illustrate, the ATL and the AnG were particularly associated with multimodal integration processes. Interestingly, within study 2, I did not find any activation within the ATL. As mentioned in the introduction, current theories argue that the AnG and the ATL indeed functionally differ in multimodal memory processes (Davis & Yee, 2019; Patterson et al., 2007; Ramanan & Bellana, 2019). According to these accounts, it has been suggested that the ATL is specific formation of “amodal” taxonomic representations, while the AnG is specific for the formation of “crossmodal”, thematic representation. With respect to study 2, I focused on neural integration processes of semantically-incongruent, novel audiovisual associations. Therefore, the functional difference between these two regions in multimodal integration processes remains to be investigated. To illustrate, future studies could investigate neural integration processes related to the formation of semantically-incongruent compared to semantically-congruent perceptual stimulus pairs within one paradigm. Findings would extend prior theories regarding the functional role of the AnG and the ATL within both encoding and retrieval processes of relational representation.

As memory processing networks are not encapsulated systems (Hasson et al., 2015; Henke, 2010), future studies could investigate whether this dynamic interaction between constant and variable processing networks (i.e. including the engagement of posterior medial and frontal regions) are generally engaged when only implicit memory was acquired. Future investigations could thus reveal the extent to which cortical networks provide both independent and interactive contributions to memory processing during explicit and implicit learning. These findings would provide a better understanding of the related cognitive deficits and underlying associative neural structures as well as conceptual therapeutic approaches. From this perspective, it has to be further acknowledge that episodic memory processes are highly complex and influenced by a variety of modulating factors, such as emotions, outer context variables, stimulus qualities, paradigm specificities and much more. Furthermore, episodic and semantic memory processes are often difficult to differentiate from each other, to identify which cortical regions are specific for multimodal integration, episodic and/or semantic memory formation remains challenging in research. Thus, to address more real-life situations, I repeatedly presented neutral object images and real life environmental sounds within study 2. However, it has to be taken into account that within real-life situation is more likely that many other environmental factors occur separately, simultaneously or even interact with each other. Thus, in order to understand the whole nature of memory formation, future investigations should examine this complex interaction between ongoing neural states and external memory-relevant factors. Ideally, a comprehensive theoretical framework on memory could be proposed in which not only encoding and retrieval processes are clearly differentiates but also essential neural component for memory formation are demonstrated.

5. Conclusion

Taking all the literature and the presented results of this dissertation into deeper consideration, this dissertation extended prior knowledge regarding the functional specification of the hippocampus and the angular gyrus in episodic memory processes. For the hippocampus, I provided additional evidence for both a functional role in the formation of implicit knowledge and the organization of relational (episodic) memory within and across modalities. The presented findings support the assumption that the hippocampus reflects key features of the human declarative memory system, which are recruited independently from the involvement of awareness. Thus, within this dissertation, a more general functional role of the hippocampus in relational memory has been shown.

From an integration-based account, it is further suggested that the angular gyrus acts as a so called multimodal association area or a convergence zone. In line with previous studies, the presented findings revealed AnG involvement in multimodal integration processes which are required for the acquisition and retrieval of highly-relational memories. To be specific, I assume that the functional involvement of the angular gyrus should not be differentiated by whether it is involved during encoding or recollection, or during unimodal or multimodal stimuli presentation. As assumed for the hippocampus, the specific functional role of the angular gyrus has been related to constant, contextual related processes of perceptual associations required to form relevant episodic representations. Within this dissertation, I therefore suggest a more general role for the AnG in the generation and the explicit retrieval of internally generated relational representations. Importantly, the presented findings can serve as a starting point for future research on how the left AG contributes to episodic memory while functionally interacting with the hippocampus.

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A Appendix – Study 1

A.1. The modified SRT using auditory stimuli

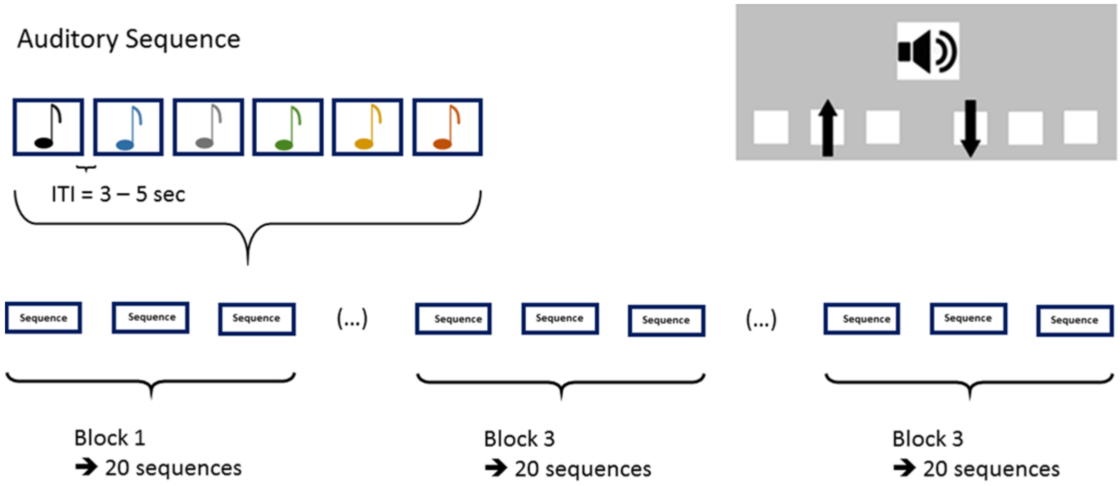

Fig A.1. **The modified SRT.** A more detailed illustration of the experimental set-up, using a modified SRT with auditory stimuli

A.2. Completion task score for each individual tone transition

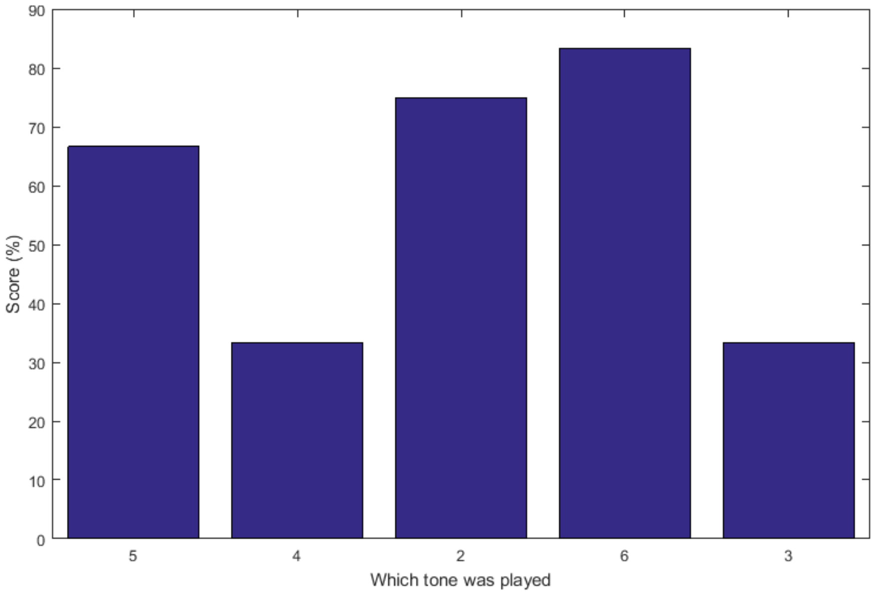

Fig A.2. **Behavioral data of the completion task.** Completion task score for each individual tone transition - labelled as numbers - across included implicit participants. Across included implicit participants, the completion task score for each individual tone transition is revealed.

A.3. Effects of the memory specific covariate within ROI

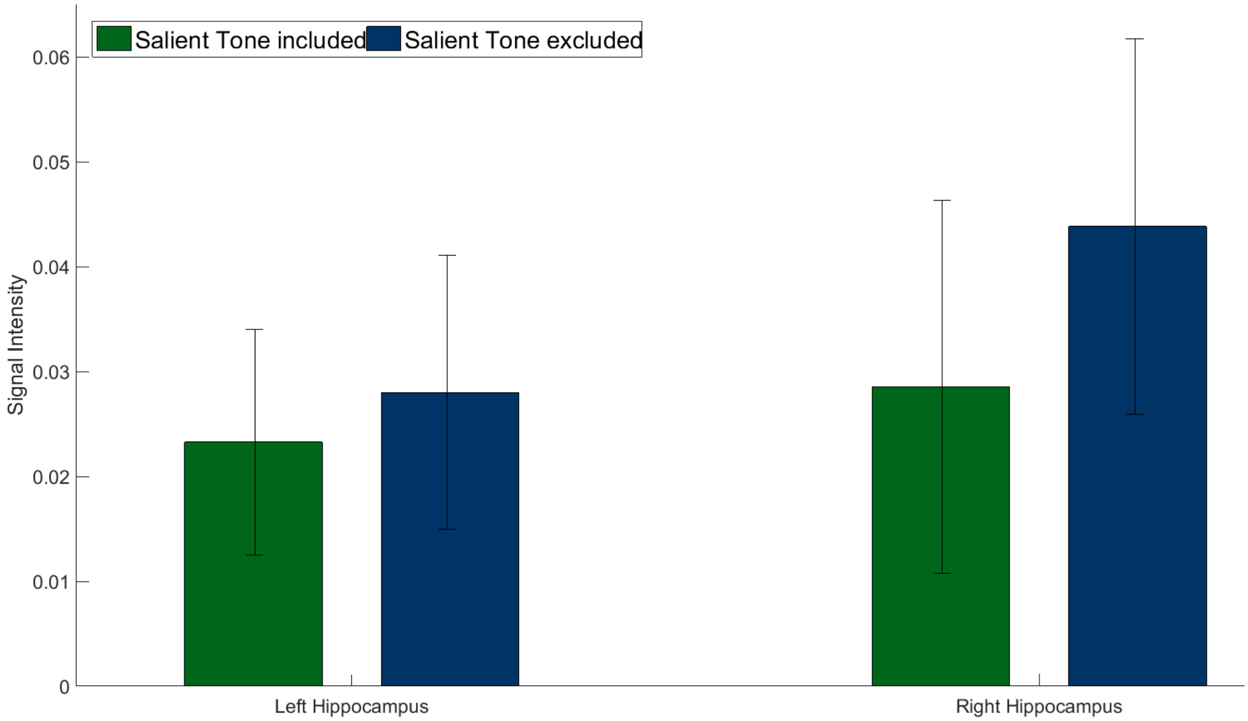

Figure 4. **The effects of the memory specific covariate (CT score) within ROI.** The ROI was centered on coordinates of the right and the left hippocampus. The contrast estimates with a 90% confidence interval are revealed. When the salient tone has been excluded, an enhanced effect of the memory specific covariate can be observed. However**,** a similar pattern of the memory specific covariate has been examined in both analyses: memory related effects in the hippocampus were found when the salient tone was included (green; left: T(43) = 5.56, p = 0.001; right: n.s. after correction for multiple comparison) as well as when excluded (blue; left: T(32) = 3.52, p = 0.001; right: T(32) = 4.03, p < 0.001) from analysis.

B Appendix – Study 2

B.1. Whole-brain corrected imaging results for the last learning session analyses

Last Session: consistent > variable condition

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
L	Angular gyrus	22	5,31	-48	-70	38
			5,01	-52	-60	42

Last Session: variable > consistent condition

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
L	Middle occipital gyrus	371	7,19	-48	-70	38
L	Inferior frontal gyrus	438	6,61	-44	8	28
L	Posterior medial frontal gyrus	51	6,06	-6	8	52
L	Precentral gyrus	52	5,52	-30	-4	54
R	Inferior frontal gyrus	13	5,41	50	18	28
R	Cerebellum (Crus 2)	18	5,26	6	-74	-26
R	Insula	8	5,25	34	26	2
R	Middle cingulate gyrus	5	5,13	6	14	44
L	Insula	5	5,09	-32	22	6

Table B.1. **fMRI effects for the two contrasts of interest during the last session (last learning session).** Note: For whole brain analysis, significant fMRI effects were reported at a threshold of p<.05, corrected for familywise error (FWE).

B.2. Whole-brain corrected imaging results for the Increase/Decrease-across-session analyses

Increase-across-session: constant condition

				MNI Coordinates		
Hem	**Region**	**cluster size**	**t-value**	**x**	**y**	**z**
L	transverse temporal gyrus	108	7,616	-38	-22	6
R	transverse temporal gyrus	114	7,388	42	-20	4
L	Superior medial gyrus medial segment	527	7,228	2	60	2
L	Angular gyrus	235	7,043	-44	-56	26
L	Middle temporal gyrus	70	5,871	-62	-18	-22
L	Posterior cingulate gyrus	80	5,581	-6	-42	36
R	Superior frontal gyrus	12	5,383	16	56	30
R	Medial frontal gyrus	7	5,358	2	58	-20
L	Supramarginal gyrus	15	5,304	-56	-50	34
L	Superior frontal gyrus	5	5,213	-12	54	30
L	Superior medial gyrus medial segment	5	5,134	0	46	-8
R	Middle temporal gyrus	5	5,054	66	-32	-4
L	Superior frontal gyrus	3	4,980	-12	34	54

Increase-across-session: variable condition

				MNI Coordinates		
Hem	**Region**	**cluster size**	**t-value**	**x**	**y**	**z**
L	transverse temporal gyrus	241	8,775	-38	-22	6
R	transverse temporal gyrus	213	8,173	42	-20	4
R	Superior medial gyrus medial segment	146	5,957	6	64	6
R	Middle temporal gyrus	52	5,858	62	-32	-4
L	Posterior cingulate gyrus	2	5,154	-8	-40	36
L	Middle temporal gyrus	4	5,082	-66	-24	-12
L	Supramarginal gyrus	4	5,055	-54	-50	34
L	Precentral gyrus medial segment	3	4,911	-2	-34	72

Decrease-across-session: constant condition

				MNI Coordinates		
Hem	**Region**	**cluster size**	**t-value**	**x**	**y**	**z**
L	Supplementary motor cortex	849	7,577	-24	-12	62
R	Precentral gyru	849	7,320	6	-2	52
L	inferior frontal gyrus	587	7,564	-50	8	26

L	Anterior insula	132	7,018	-32	20	8
R	inferior frontal gyrus	450	7,006	36	8	32
R	Amygdala	29	6,346	24	2	-10
L	Anterior insula	21	6,210	-38	-4	14
L	Postcentral gyrus	79	6,028	-56	-20	38
R	Superior frontal gyrus	105	5,872	24	-4	52
R	Caudate nucleus	30	5,705	12	8	2
R	Anterior insula	24	5,552	32	28	2
R	Fusiform gyrus	10	5,398	28	-48	-10
R	Precentral gyrus	20	5,375	36	-6	54
L	Lingual gyrus	15	5,334	-20	-64	-10
L	Superior parietal lobule	15	5,241	-22	-76	44
R	Lingual gyrus	6	5,206	24	-64	-4
L	inferior occipital gyrus	12	5,143	-34	-72	-16
R	Precentral gyrus	3	5,013	38	-12	52

Decrease-across-session: variable condition

				MNI Coordinates		
Hem	**Region**	**cluster size**	**t-value**	**x**	**y**	**z**
L	Inferior frontal gyrus	143	6,616	58	8	22
R	Amygdala	27	6,575	24	2	-10
L	Postcentral gyrus	35	6,099	-54	-20	38
L	Precentral gyrus	30	5,730	-24	-12	64
L	Inferior frontal gyrus	105	5,645	-56	6	30
L	Supplementary motor cortex	5	5,328	-6	-4	54
R	Supplementary motor cortex	9	5,309	8	-2	54
L	Lingual gyrus	9	5,277	-22	-62	-10

Table B.2. **fMRI effects of the increase-across-session analysis for the two condition respectively (learning).** Note: For whole brain analysis, significant fMRI effects were reported at a threshold of p<.05, corrected for familywise error (FWE).

B.3. Whole-brain corrected imaging results for the recollection analyses (first event)

First stimulus event: Constant > variable condition

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
R	Superior occipital gyrus	5683	8,906	24	-86	30
L	Calcarine gyrus	5683	8,641	0	-94	16
R	Cerebelum (Crus 1)	5683	7,800	46	-64	-22
L	Postcentral gyrus	308	7,206	-44	-18	62
L	Cerebelum (Crus 1)	302	6,236	-48	-64	-26
L	Inferior occipital gyrus	302	6,067	-50	-72	2
R	Precuneus	59	5,980	4	-50	72
R	Posterior medial frontal gyrus	6	5,428	2	-26	76

First stimulus event: constant > variable condition

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
R	Precentral gyrus	383	9,716	38	-16	52
L	Inferior frontal gyrus	79	6,659	-56	6	22
R	Inferior frontal gyrus	132	6,637	56	10	12
L	Insula	46	6,419	-32	12	8
L	Posterior medial frontal gyrus	38	6,318	-6	0	56
R	Insula	50	6,158	40	0	12
R	Posterior medial frontal gyrus	25	5,413	6	2	54
L	Postcentral gyrus	18	5,286	-54	-20	22

Table B.3. **fMRI effects for the two contrasts of interest during the first stimulus event (recollection).** Note: For whole brain analysis, significant fMRI effects were reported at a threshold of p<.05, corrected for familywise error (FWE).

B.4. Whole-brain corrected imaging results for the recollection analyses (second event)

Second stimulus event: constant > variable

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
L	Middle occipital gyrus	11064	10,577	-24	-90	22
R	Precuneus	2018	9,060	8	-52	72
L	Precentral gyrus	59	6,434	-62	-2	10
R	Mid Orbital Gyrus	159	6,315	0	48	-6
R	Putamen	149	6,129	30	-6	-4
L	Superior frontal gyrus medial segment	160	6,310	0	48	-6
R	Putamen	149	6,130	30	-6	-4
L	Superior frontal gyrus medial segment	160	5,790	-2	56	12
R	Transverse temporal gyrus	75	5,790	50	-8	12
R	Precuneus	54	5,620	18	-54	6
R	Posterior cingular gyrus	48	5,540	4	-42	6
L	Inferior temporal gyrus	12	5,360	-44	-16	-22
R	Superior frontal gyrus medial segment	10	5,340	8	62	26
R	Precentral gyrus	18	5,280	32	-22	54
L	Precentral gyrus	14	5,260	-42	-12	36

Second **stimulus event: variable > constant**

				MNI Coordinates		
Hem	**Region**	**Cluster size**	**t-value**	**x**	**y**	**z**
R	Middle cingulate cortex	1027	8,578	6	22	46
R	Anterior insula	365	8,384	34	24	-6
L	Anterior insula	372	8,084	-32	14	8
L	Precentral gyrus	268	8,013	-52	6	20
L	Superior parietal cortex	419	6,896	-28	-52	40
L	Postcentral gyrus	75	6,608	-56	-20	42
L	Inferior frontal gyrus	64	5,984	-48	40	-4
L	Precentral gyrus	46	5,972	-38	-18	54
L	Superior frontal gyrus	22	5,607	-24	-6	50
R	middle frontal gyrus	6	5,315	50	24	28

Table B.4. **fMRI effects for the two contrast of interest during the second stimulus event (recollection).** Note: For whole brain analysis, significant fMRI effects were reported at a threshold of p<.05, corrected for familywise error (FWE).

B.5. Error distribution across learning sessions and participants

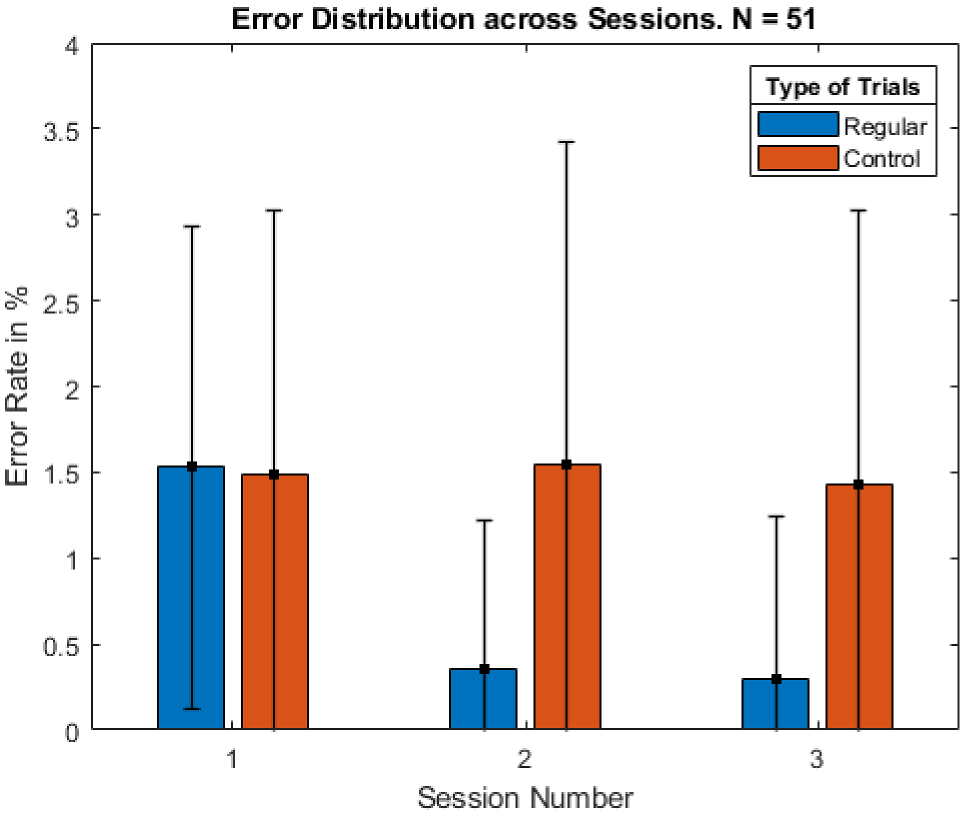

Fig B.1. **Error distribution across learning sessions and participants indicated for each condition separately (regular: consistent condition; control: variable condition).** Error bars indicate standard deviations.

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"Love is what makes you smile when you're tired." [Paulo Coelho]

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Curriculum Vitae

Lebenslauf wurde aus datenschutzrechtlichen Gründen entfernt.

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Ich versichere ausdrücklich, dass ich die Arbeit selbständig und ohne fremde Hilfe verfasst, andere als die von mir angegebenen Quellen und Hilfsmittel nicht benutzt und die aus den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen einzeln nach Ausgabe (Auflage und Jahr des Erscheinens), Band und Seite des benutzten Werkes kenntlich gemacht habe.
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