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Review

How brain oscillations form memories — A processing based perspective on oscillatory subsequent memory effects

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ABSTRACT

Brain oscillations are increasingly recognized by memory researchers as a useful tool to unravel the neural mechanisms underlying the formation of a memory trace. However, the increasing numbers of published studies paint a rather complex picture of the relation between brain oscillations and memory formation. Concerning oscillatory amplitude, for instance, increases as well as decreases in various frequency bands (theta, alpha, beta and gamma) were associated with memory formation. These results cast doubt on frameworks putting forward the idea of an oscillatory signature that is uniquely related to memory formation. In an attempt to clarify this issue we here provide an alternative perspective, derived from classic cognitive frameworks/principles of memory. On the basis of Craik's levels of processing framework and Tulving's encoding specificity principle we hypothesize that brain oscillations during encoding might primarily reflect the perceptual and cognitive processes engaged by the encoding task. These processes may then lead to later successful retrieval depending on their overlap with the processes engaged by the memory test. As a consequence, brain oscillatory correlates of memory formation could vary dramatically depending on how the memory is encoded, and on how it is being tested later. Focusing on oscillatory amplitude changes and on theta-to-gamma cross-frequency coupling, we here review recent evidence showing how brain oscillatory subsequent memory effects can be modulated, and sometimes even be reversed, by varying encoding tasks, and the contextual overlap between encoding and retrieval.

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Introduction

During the past two decades the interest in the role of brain oscillations for the formation of human memories has grown considerably. Driven by the obvious links between synchrony and synaptic plasticity (Buzsaki and Draguhn, 2004; Düzel et al., 2010; Fell and Axmacher, 2011) an increasing number of researchers have begun to investigate brain oscillations in memory experiments, measuring oscillations either non-invasively with EEG/MEG or invasively with intracranial EEG during

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encoding of memories in humans (Axmacher et al., 2006; Hanslmayr et al., 2012; Nyhus and Curran, 2010). In the early days, most studies focused on specific frequency bands (e.g. theta) and simple parameters (e.g. power or coherence), however, with increasing computational power later studies investigated several frequency bands and more complex parameters (e.g. phase–amplitude coupling), thus broadening the empirical database of brain oscillatory correlates of memory formation. These new data, however, have also drawn a rather complicated and heterogeneous picture in showing that oscillatory dynamics in various frequency bands are related to memory formation in various different ways. Although most theoretical concepts in this field focused on theta and gamma oscillations (e.g. Düzel et al., 2010; Fell and Axmacher, 2011), alpha and beta oscillations may be equally important for memory formation (Hanslmayr et al., 2012). Additionally, increases as well as decreases in activity in any of these frequencies have been related to memory formation. Table 1 demonstrates this by showing a selective overview of studies investigating brain oscillatory correlates of memory formation. Although the studies reported in Table 1 differed considerably in whether they focus on pre-stimulus activity (e.g. Guderian et al., 2009), inter-areal or inter-trial phase-synchronization (Burke et al., 2013; Fell et al., 2001, 2008), or the interplay between short-term and long-term memory (Khader et al., 2010; Meeuwissen et al., 2011), discrepant findings have been obtained with regard to stimulus induced amplitude changes and memory formation. In an attempt to clarify this complex picture we here provide a new, processing based view, inspired by classic cognitive memory concepts, within which brain oscillatory correlates of memory formation can be interpreted.

A naïve researcher interested in how brain oscillations contribute to the formation of memories might ask whether memory formation is accompanied (i) by a specific brain oscillation, or (ii) by a specific type of oscillatory behavior (e.g. increases or decreases in amplitude). Based on the current empirical evidence (see Table 1), the answer to the first question would be that all frequency bands, from 3 up to 100 Hz, are associated with the formation of a memory trace (see Düzel et al., 2010; Hanslmayr et al., 2012; Nyhus and Curran, 2010; for reviews). Similarly, the answer to the second question would be that several, partly opposing types of oscillatory behaviors, e.g. increases and decreases in amplitude, correlate with memory formation. This is even true for single frequency bands where both power increases and power decreases have been associated with successful encoding of a memory (see Table 1). Importantly, increases and decreases in oscillatory amplitudes have been observed in similar task active brain regions (e.g. hippocampus, left inferior frontal gyrus) and therefore, none of these two questions can be answered satisfactorily. In this review we try to provide a new, processing based perspective on the brain oscillatory correlates of memory formation to clarify this complicated picture.

We suggest that brain oscillations during encoding primarily index the cognitive and perceptual processes that are carried out during encoding (Encoding strategies modulate brain oscillatory subsequent memory effects section). Further, these processes might or might not be beneficial for memory depending on how later retrieval is carried out (Encoding–retrieval overlap modulates brain oscillatory subsequent memory effects section). Following such a processing based view, different frequency bands can be related to successful memory formation in very different ways. This idea is closely related to two classic and highly influential cognitive concepts of episodic memory, namely the levels of processing (LOP) framework (Craik and Lockhart, 1972) and the encoding specificity principle (Morris et al., 1977; Tulving and Thomson, 1973), which surprisingly have received very little interest from brain oscillatory memory researchers so far. Although these concepts have not gone undisputed (e.g. Tulving, 2001) we will show that these classical frameworks/principles can readily be applied to brain oscillatory correlates of memory formation and might help to understand the relationship between brain oscillations and memory formation. This review is divided into two sections, in the first section (Encoding strategies modulate brain oscillatory subsequent memory effects section) we will consider how brain oscillatory correlates of memory formation vary as a function of different encoding tasks (i.e. levels of processing). In the second section (Encoding–retrieval overlap modulates brain oscillatory subsequent memory effects section), we will then consider how brain oscillatory correlates of memory formation may vary as a function of later retrieval (i.e. encoding specificity principle). Based on theoretical considerations and available empirical data we will focus on two parameters of oscillatory activity: amplitude (Encoding strategies modulate brain oscillatory subsequent memory effects and The role of theta power in encoding–retrieval overlap sections) and theta-phase to gamma-amplitude cross-frequency coupling (The role of theta phase to gamma amplitude coupling in encoding–retrieval overlap section). This is because most data in this field is available for oscillatory amplitude and, because theta to gamma cross-frequency coupling is theoretically strongly implicated in episodic memory formation (Fell and Axmacher, 2011). Due to these reasons the role of other oscillatory measures, e.g. inter-areal synchronization, which, compared to oscillatory amplitude, has only been investigated by a fairly small number of studies, is not considered in this review.

Table 1
A selective overview of studies is provided to illustrate that opposing changes in oscillatory amplitude in different frequency bands have been related to memory formation. Note that although several of these studies also focused on different aspects (e.g. phase-synchronization, pre-stimulus activity) we here just report their findings with regard to stimulus induced power changes (SME = subsequent memory effect; iEEG = intracranial EEG).

Frequency band	SME (amp.)	Authors	Modality
Theta (~7 Hz)	Increases	Hanslmayr et al. (2011a)	EEG–fMRI
		Klimesch et al. (1996a)	EEG
		Lega et al. (2012)	iEEG
		Osipova et al. (2006)	MEG
		Staudigl and Hanslmayr (in press)	MEG
	Decreases	Burke et al. (2013)	iEEG
		Guderian et al. (2009)	MEG
		Lega et al. (2012)	iEEG
		Sederberg et al. (2007)	iEEG
		Staudigl and Hanslmayr (in press)	MEG
Alpha (~10 Hz)	Increases	Khader et al. (2010)	EEG
		Meeuwissen et al. (2011)	MEG
	Decreases	Fell et al. (2008)	iEEG
		Fellner et al. (in press)	EEG
		Hanslmayr et al. (2009)	EEG
		Klimesch et al. (1996b)	EEG
		Sederberg et al. (2007)	iEEG
Beta (~15 Hz)	Decreases	Fell et al. (2008)	iEEG
		Fellner et al. (in press)	EEG
		Hanslmayr et al. (2009)	EEG
		Hanslmayr et al. (2011a)	EEG–fMRI
		Sederberg et al. (2007)	iEEG
Gamma (>30 Hz)	Decreases	Fell et al. (2001)	iEEG
	Increases	Burke et al. (2013)	iEEG
		Gruber et al. (2004)	EEG
		Hanslmayr et al. (2009)	EEG
		Osipova et al. (2006)	MEG
		Sederberg et al. (2007)	iEEG

Encoding strategies modulate brain oscillatory subsequent memory effects

In their seminal paper, Craik and Lockhart (1972) postulated the provocative thesis that a memory trace is just a byproduct of the perceptual and cognitive processes carried out during encoding (see Craik, 2002 for an updated review). Thereby the likelihood of whether information is remembered later is determined by the depth of the perceptual and cognitive analyses carried out during initial processing: The deeper the processing the better the memory, whereby depth refers to the level of semantic, conceptual or cognitive analysis. Meanwhile, a plethora of behavioral studies confirmed this framework in demonstrating that orienting participants towards processing different aspects

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