Précis of

# Temporal dynamics and mechanisms of oscillatory pattern reinstatement in human episodic memory

A thesis presented to the University of Birmingham for the degree of DOCTOR OF PHILOSOPHY

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Life unfolds over time and we naturally perceive its temporal dynamic and rhythmicity. Such rhythmic information remains accessible afterwards in our memory system: We might hum a melody that we heard on the radio and we can reproduce the steps of a dance accurately. In other words, we can reinstate temporally accurate and vivid memories in our mind's eye (and ear), even though we certainly do not recall all of our memories with such exact recapitulation. Importantly, rhythmicity and temporal structure are a key property of our nervous system (Buzsáki, 2006). Just like our hearts beat rhythmically, our brains oscillate at inherent frequencies that can be measured via time-resolved electrophysiological recordings (Nunez & Srinivasan, 2006). The role of these so-called neural oscillations in the processing of information is a topic of active investigation.

This thesis links the modulation of oscillations that are marked by a decrease in amplitude to the representation of content-specific information that unfolds in memory over time. A new method is introduced that can track oscillatory patterns that are specific to previously perceived content, when memories of that content are brought to mind. Eventually this method is leveraged to track the replay of continuous video material that spans several sub-events (scenes). Corroborated by behavioral evidence that establishes memory replay as proceeding in a forward direction and at a faster speed than perception, the neural tracking of patterns unveils an intricate dynamic: Neural pattern reinstatement proceeds in a forward direction, but it can operate at different speeds. Specifically, it is shown that estimating the speed of replay within sub-events underestimates its overall speed. Analogous to the skipping between different tracks on a CD player, these data suggest that replay of continuous episodes in memory that entails the reinstatement of temporal patterns, can be sped up by skipping between sub-events.

#### Background

#### **Episodic Memory**

Episodic memory is the memory for our personal experiences and their temporal relationship; it can loosely be described as mental time travel (Tulving, 1972, 1993). In practice, our episodic memory allows us to access information that is no longer present in the world around us. The related term "memory reinstatement", describes the evocation of information from the past and is also referred to as recollection (Yonelinas, 2002). This reinstatement of information can be investigated with a cued-recall paradigm (e.g. Fisher & Craik, 1977), whereby a cue is associated with a target during learning (memory encoding) and the memory of the target must be reinstated upon a later presentation of the cue (memory retrieval).

#### **Neural Oscillations**

Neural oscillations are rhythmic fluctuations in the ongoing local field potential which can be measured with electroencephalography (EEG) and magnetencephalography (MEG) (e.g. Long et al., 2014; Staudigl & Hanslmayr, 2013; Zhang et al., 2015). Neural oscillations have been linked to cognitive functions in numerous ways (Buzsáki, 2006). Importantly, decreases in the amplitude of oscillations in the alpha and beta (8-30 Hz) frequency bands are robustly associated with successful episodic memory formation and retrieval (Hanslmayr & Staudigl, 2014; Long et al., 2014; Zion-Golumbic et al., 2010).

#### Information in oscillatory power decreases

Recently a link between power decreases in the alpha and beta band and the representation of information-rich content in memory has been suggested (HansImayr et al., 2012). The 'information via desynchronization' framework observes that a reduction in synchronous firing of cell assemblies results in a decrease of oscillatory power; this allows for complex information to emerge, because neural assemblies can perform more separate actions. Thus, the theory postulates that power decreases in alpha and beta oscillations mark the representation of information-rich memory content.

#### Alpha frequency in perception

Desynchronization, which is marked by power decreases, is also relevant for perception (Harris & Thiele, 2011; Jensen & Mazaheri, 2010; Marshall et al., 2015). Specifically, there is evidence that fluctuations at 7/8 Hz rhythmically sample a continuous input stream during perception (HansImayr et al., 2013; Jensen et al., 2012; Landau & Fries, 2012; VanRullen et al., 2011, 2007). It is therefore possible that similar oscillatory mechanisms that guide perception also guide "re-perception"—that is, memory reinstatement—of sensory events.

#### Contribution of the thesis

This thesis links the reinstatement of memory content to the electrophysiological phenomenon of decreases in the amplitude of oscillations. Specifically, reinstating information-rich content from memory yields decreases in the amplitude of an oscillation that contains a content-specific oscillatory pattern. This new approach is then used to track content in memory over time. For the first time, the unfolding of a continuous memory representation is observed in oscillatory neural activity. Behavioral experiments corroborate the finding that memory reinstatement proceeds in a forward direction. The dynamics of neural replay suggest that forward replay is more than the exact recapitulation of the original experience; skipping between sub-events appears to speed up memory replay.

#### The temporal signature of memories

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#### A paradigm to elicit memory reinstatement

The first study was designed to test the prediction that decreases in oscillatory power contain information about memory content. It was hypothesized that signatures of perceptual content would be detectable in desynchronizing frequency bands when humans recall information-rich stimuli from memory. In two experiments, video and sound clips were associated with words, while neural activity was recorded via electroencephalography (EEG).



Figure 1: Cued-recall paradigm. (a) In the visual experiment, participants associated short video clips with unique word-cues. In each trial, one out of four videos played for 3 seconds and was immediately followed by a unique word-cue. Later during retrieval, the unique words or new words (that served as baseline items) were shown. Participants were asked to retrieve the associated video from memory. (b) In the auditory experiment, the same paradigm was used, except that instead of videos, short sound clips played for 3 seconds. (c) During cued-recall, participants answered after being given the depicted response options. They would either select the corresponding video, identify a word as new, or convey that they remembered the word but not the associate ('old' option). (d) In the auditory condition options were represented by pictograms of characteristic instruments from the sound clips.

In order to elicit the reinstatement of the video/sound clips from memory, a cued-recall paradigm was used. In the visual experiment, participants repeatedly saw one out of four short video clips that was immediately followed by a unique word-cue (Figure 1a). The task was to associate the word-cue with the video. Later, during retrieval, participants were presented with the unique word-cues and were asked to retrieve the exact video that it was associated with. In the auditory experiment, participants listened to one out of four short sound clips, followed by a unique word (Figure 1b). Later they retrieved the sound clip upon presentation of the word-cues. It was hypothesized that during retrieval, power in the

alpha/beta frequency band would decrease upon the presentation of the word, whenever the correct video/sound was remembered. Furthermore, this decrease in power was hypothesized to reflect the reinstatement of content-specific information.

#### Oscillatory power decreases mark the successful reinstatement of content from memory

To test whether successful memory retrieval was associated with decreases in alpha/beta power, power was contrasted in different time and frequency bins between those trials in which the correct association was remembered and those trials in which the association was forgotten. In another contrast, remembered trials were compared with baseline trials (new words during retrieval). Successful memory retrieval was associated with strong power decreases in the visual (Figure 2a) and auditory (Figure 2b) condition. Power decreases were strongest in the lower alpha frequency band (peaking at 8Hz). Reconstructing sources of these power decreases implicated parietal, temporal and frontal areas in the visual (Figure 2c) and auditory (Figure 2d) condition.



Figure 2: Memory-related power decreases during retrieval. (a) Successful memory reinstatement was associated with a cluster of strong power decreases in the lower frequencies (<40 Hz) in the visual condition, and (b) in the auditory condition. (c) Sources of power decreases in the lower alpha band (~8Hz) were reconstructed for the visual and (d) auditory condition. In both conditions, these power decreases spanned broad areas in parietal, temporal, and frontal regions.

#### Oscillatory patterns from perception re-emerge when content is reinstated from memory

Because the information-rich stimulus was presented many times (i.e. the same video/sound slip was associated with many unique word-cues), temporal patterns of activity from the perception of the clips could be identified via representational similarity analysis (Kriegeskorte, 2008). Specifically, if retrieved patterns reflect perceptual content, the similarity between perception and retrieval of the same content (e.g. watching movie A, recalling movie A) should be higher than the similarity between perception and retrieval of different content (e.g. watching movie A, recalling movie A).

To measure the similarity between patterns of activity from perception and patterns of activity from retrieval, a method was used that is traditionally applied to quantify communication between channels **(Lachaux et al., 2000; Mormann et al., 2000)**. This measure of phase coherence over time quantifies the similarity between temporal activity patterns in a particular frequency band between two different sites. In this thesis, this measure was borrowed in order to quantify similarity between perception and retrieval.



regure 3: Source reconstructions of content-specific pattern reinstatement. In the visual experiment (left) content-specific temporal patterns from the video clips emerged during cued-recall. These patterns were reinstated in the right parietal lobe. In the auditory experiment, content-specific temporal patterns from the sound clips reemerged in the right temporal lobe.

Contrasting the similarity between perception and retrieval of the same content with the similarity between perception and retrieval of different content revealed content-specific pattern reinstatement in both the visual and the auditory experiment: Significant pattern reinstatement was identified in the lower alpha band (~8Hz), the frequency band that showed the strongest memory related power decrease. Control frequencies below and above this band did not express pattern reinstatement. Source reconstruction localized these effects in brain regions that are characteristic for visual and auditory processing in the respective experiments: Peak effects were localized in the superior parietal lobule in the visual and in the right inferior temporal gyrus in the auditory experiment (Figure 3).

#### Power decreases are stronger where content-specific oscillatory patterns emerge



Figure 4: Interaction of power decreases with pattern reinstatement. (a) The areas where contentspecific patterns reemerged during cued-recall are shown. (b) These areas showed stronger power decreases in the respective condition. The association between power decreases and the reinstatement of sensory information also predicts that stronger power decreases should be observed in those regions where replay occurred. To test this prediction, the power of the frequency band where replay occurred was contrasted between the two experiments and between the visual and auditory regions of pattern reinstatement. A significant interaction between the visual and auditory condition was found: power decreases were stronger in areas where content-specific oscillatory patterns were localized in the respective conditions. This provides an additional spatial link between the reinstatement of contentspecific information and power decreases.

#### Replay of content-specific temporal patterns during associative memory formation Published as (Michelmann et al., 2018) in Journal of Cognitive Neuroscience

Linking alpha power decreases to the reinstatement of content-specific temporal patterns confirms the implication of this ubiquitous phenomenon in the representation of perceptual information in memory. Power decreases, however, have also been associated consistently with successful memory formation



Figure 5: Encoding phase of (a) the visual experiment and (b) the auditory experiment. The full experiment is described in Figure 1. In each encoding trial participants saw one out of four videos/sounds that was immediately followed by a unique word-cue. During the presentation of the word-cue, participants had to maintain a representation of the video/sound in order to form the association. (e.g. Long et al., 2014). Consequently, this raises the question of whether power decreases that mark the successful formation of memories also reflect the representation of perceptual content. Critically, the above study separates the perception of video/sound clips during encoding from the formation of memories (Figure 5): the word-cue is presented after the video/sound, such that in order to associate the word-cue with this stimulus, a representation of the video/sound content needs to be maintained. It was therefore hypothesized that content-specific sensory information would be present in this interval when associations were formed successfully. Accordingly, power decreases in the alpha/beta frequency band should indicate the successful formation of associative memories and harbor content-specific patterns.

#### Oscillatory power decreases mark the successful formation of episodic memories

In a first analysis, those encoding trials in which memory associations were formed successfully (i.e. the association was later retrieved correctly), were contrasted with those encoding trials in which memory associations were not formed successfully. This contrast revealed that strong and sustained power decreases marked the successful formation of associations. Power decreases also marked the perception of video/sound clips that were successfully associated; critically however, power decreases were strong during the association interval (Figure 6). Because of the reduced amount of data in these analyses, source modeling was not conducted. The topography of power decreases on the scalp is displayed in Figure 6 c-d.



Figure 6: Power decreases are associated with successful memory encoding. (a) When videos are associated with word-cues in the visual condition, power decreases in the lower frequencies (<30 Hz) mark the perception of the video (between 0 and 3 seconds) and the interval of association (between 3 and 7 seconds after video onset). (b) In the auditory condition, power decreases in the lower frequencies (<30 Hz) mark the perception of the sound and the interval of association. (c) The topography of the sustained power decrease in the lower alpha band (~8Hz) displayed a broad topography with a parietal maximum over the left hemisphere. (d) Decreases in 8Hz power were also distributed broadly in the auditory condition, with maxima over left parietal and right frontal regions.

Content-specific temporal patterns are maintained during associative memory formation

# a)150ggb)ggg

the auditory condition, one cluster of content-specific

patterns was located over right frontal areas.

In order to test whether power decreases in the lower alpha band harbored content-specific patters from the video/sound clips, pattern similarity was assessed between the perception of the stimulus material and the intervals in which associations were formed. Comparing similarity between instances of same memory content (e.g. watching movie A, maintenance and association of movie A) with similarity between instances of different memory content (e.g. watching movie A, maintenance and association of movie B), revealed that content-specific temporal patterns were present during the formation of associative memories (Figure 7).

## Speed of time-compressed forward replay flexibly changes in human episodic memory

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The previous studies demonstrate that temporal patterns of activity reappear in a frequency band that is marked by power decreases when we reinstate information from memory and when we form associations with previously perceived content. The ability to track these temporal patterns engenders the question of how information is structured in memory when we replay long episodes that have an inherent structure.

In a new paradigm, participants learned to associate word-cues with scenes within structured videos (Figure 8). These videos (henceforth referred to as video-episodes) were six seconds long and consisted of three distinct two-second-long scenes. In learning blocks, participants saw one out of four video-episodes superimposed by a transparent text box. In one of the scenes, a unique word-cue appeared. Later during retrieval blocks, a unique word-cue was presented. Participants were first asked in which exact scene they had seen the word-cue (selecting from the options 1, 2, and 3). Only after that participants were asked to select the correct video episode, confirming successful retrieval. The crucial assumption is that, in order to select the correct scene, participants evoke a representation of the video-episode in their head.



Figure 8: Paradigm to assess the speed and direction of memory replay. During encoding participants saw one of four video-episodes, i.e. short videos that consisted of three distinct scenes. Critically, in each trial a unique word-cue appeared in one of the scenes. Later during retrieval, the word-cue was presented again and participants were asked to recall in which exact scene they had seen the word. Upon selecting the correct scene number (1, 2 or 3) the exact video-episode was prompted with screenshots from the scenes, to confirm that the response was based on a correct memory. Critically, participants must evoke a vivid representation of the video-episode to recall the correct scene number.

#### Compressed replay in behavior with cued-recall

In a first series of behavioral experiments, the temporal dynamics of memory replay were addressed by



Figure 9: Compressed forward replay in response time (RT). In a behavioral version of the paradigm, participants were asked to select the correct scene number (1,2, or 3) as quickly as possible (left). Response times were faster for the first, compared to the second and third position (y-axis shows difference from each participants average RT), indexing that replay proceeded in a forward direction. In a control experiment (right) participants were asked to decide as quickly as possible, whether a displayed screenshot-word combination was intact (i.e. displayed scene is where the word was learned at encoding) or rearranged (i.e. different scene from the same video-episode). Importantly, the modulation of response time with position vanished in this condition, suggesting that replay in the forward direction hinges on the active reinstatement of the memory content.

leveraging response times. The prediction was that retrieving the exact association between word and scene via cued-recall would require scanning through memory in a forward direction. It should therefore take longer to arrive at a later scene in memory. This prediction was confirmed: Compared to association that were learned in the first scene, participants were on average 116ms slower for the second scene and an additional 176ms slower for the third scene (Figure 9, left). This means that forward replay was also compressed, because the duration of the videoepisode was much longer than the duration of memory replay (6 seconds with 2 seconds per scene). Critically, if these response times reflect the duration of scanning through memory traces, this modulation should hinge on the requirement to reinstate sensory information. A control retrieval task therefore replaced

the cued-recall with associative recognition, which requires memory-based judgments (Figure 9, right). In this retrieval task, word-cues were superimposed on screenshots from the scenes; this association could either be intact or rearranged. Critically, deciding whether the association was intact or rearranged required memory of the exact word-scene association from encoding. Arguably, this judgement did not require the reinstatement of sensory information in an ordered way. No modulation of response times was observed in the associative recognition task, supporting the hypothesis that the response time modulation with position reflects the forward scanning through memory traces.

### Content-specific oscillatory pattern reinstatement is linked to power decreases and to memory performance



Figure 10: Reinstatement of content-specific temporal patterns. When participants recalled the correct word scene association, a cluster of content-specific temporal patterns reappeared on occipito-parietal virtual sensors that were reconstructed via source modeling. When associations were forgotten, no pattern reinstatement was detected.

The above paradigm prompted participants with a scene number so they would evoke a representation of the video-episode from memory. Consequently, power decreases harboring content-specific patterns from perception should be evident in their neural activity during retrieval. In a separate experiment, the same paradigm was therefore realized, while magnetencephalography was measured (compare Figure 8), except that participants were given a fixed interval to recall the correct wordscene association. Successful memory retrieval was marked again by sustained power decreases in the alpha/beta frequency band; content-

specific patterns from perception of the video-episodes were identified within the lower alpha band that expressed a peak in modulation. Specifically, the contrast of similarity between combinations of same content (e.g. watching video-episode A, recalling video-episode A) and similarity between combinations of different content (e.g. watching video-episode A, recalling video-episode B), revealed significant pattern reinstatement in occipito-parietal areas (Figure 10). Importantly, when associations were forgotten, no content-specific patterns reappeared in memory. These findings replicate and strengthen the link between power decreases, content-specific pattern reinstatement, and memory performance.

#### The speed of replay on a global and local scale

Tracking continuous video-episodes with distinct sub-events (scenes) can answer questions about the direction and speed of neural memory replay. Do earlier moments in the video, for instance, also come back earlier into memory? To answer this question, six non-overlapping time windows from the video-episodes were tracked and the distribution of evidence for each window was compared during retrieval (Figure 11). Evidence for earlier windows from the video-episodes reappeared earlier during retrieval, while evidence for later windows from the video-episodes reappeared later. This was indexed by a significant negative lag across the windows between 135ms and 1919ms (i.e. earlier windows precede later windows during that interval) and confirmed that neural replay proceeded in a forward direction. The disparity between the exact reinstatement of patterns from encoding and overall compression (memory replay was much faster than 6 seconds) suggests that not all information is recapitulated in the exact way that it was perceived. It was hypothesized that during memory replay information can be omitted by skipping ahead to salient events such as to the beginning of a new scene. Analogous to the skipping between tracks on a CD player, boundaries between the scenes could serve as steppingstones to speed up the memory scanning process. This hypothesis makes the prediction that the overall speed of replay should be underestimated if it is only calculated based on the lag between those time windows

that belong to the same scene. This was confirmed by a significantly more negative lag within scenes (i.e. slower forward replay) compared to the overall lag, between 550ms and 2350ms during retrieval. Finally, an estimate of the speed of neural replay was derived via descriptive cross-correlations. Distances within scenes were shorter than distances between scenes. The maximal distance between the first and the last (sixth) second in the video-episode was 141ms in memory.



Figure 11: Direction and speed of replay. a) The distribution of evidence for replay during retrieval was compared between different time windows from encoding. Evidence from earlier windows at encoding reappeared earlier during retrieval, signifying forward replay. This was indexed by a negative lag between the different windows (i.e. evidence for later windows from encoding was lagging behind evidence for earlier windows). b) The hypothesis that skips between segments in the video-episode can speed up replay was tested. If skipping speeds up replay, the average lag between windows from the same scene should underestimate the speed, because boundary skips are ignored. This was confirmed by a lag that was significantly more negative within scenes.

#### Conclusion

Decreases in power of neural oscillations are a well-known correlate of successful memory encoding and retrieval (HansImayr et al., 2012; Long et al., 2014; Zion-Golumbic et al., 2010). This thesis demonstrates their role in the representation of information: A new method made it possible to show that memory related power decreases harbor information about the content of episodic memory during encoding and retrieval. This information in oscillations that are marked by power decreases, was subsequently tracked in long and structured videos. Replay of continuous episodes was forward and its speed was faster in memory than during perception, a result further supported by behavioral data. The tracking of replayed patterns in memory suggests that subjects can omit information and speed up the replay process by skipping ahead to the beginning of a new scene. This renders episodic memory as a dynamic process in which power decreases harbor content-specific oscillatory patterns that are accessed and reinstated in a flexible way.

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