SPATIO-TEMPORAL FEATURE REPRESENTATIONS OF REACTIVATED MEMORIES

BY

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Abstract

How does the human brain recover memories of past events? The neural processes of memory retrieval are still not fully uncovered. This doctoral thesis is concerned with the spatio-temporal feature representations of reactivated episodic memories. Classical theories and empirical evidence suggest that the revival of memory representations in the brain is initiated in the hippocampus, before activity patterns in cortical regions reactivate to represent previously experienced events. The current doctoral project tests the assumption that the neural processing cascade during retrieval is reversed with respect to perception. This general framework predicts that semantic concepts and modality-independent information is reconstructed before modality-specific sensory details. This backward information flow is also assumed to affect the neural representations when memories are recalled repeatedly, enhancing the integration of new information into existing conceptual networks. The first two studies investigate the neural information flow during retrieval with respect to the reactivated mnemonic representations. First, simultaneous EEG-fMRI is used to track the presumed reversed reconstruction from abstract modality-independent to sensory-specific visual and auditory memory representations. The second EEG-fMRI project then zooms in on the recall of visual memories, testing whether the visual retrieval process propagates backwards along the ventral visual stream transferring from abstract conceptual to detailed perceptual representations. The reverse reconstruction framework predicts that conceptual information, due to its prioritisation, should benefit more from repeated recall than perceptual information. Hence, the last, behavioural study investigated whether retrieval strengthens conceptual representations over perceptual ones and thus promotes the semanticisation of episodic memories. Altogether, the findings offer novel insights into retrieval-related processing cascades, in terms of their temporal and spatial dynamics and the nature of the reactivated representations. The results also provide an understanding of memory transformations during the consolidation processes that are amplified through repeated retrieval.

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Publications and presentations

At the time of this thesis submission, the following publications and conference contributions were derived from this doctoral research. For the thesis, published articles and conference abstracts or summaries have been adjusted to match the format of the rest of this thesis.

Publications

Lifanov, J., Linde-Domingo, J. & Wimber, M. (2020). Feature-specific reaction times reveal a semanticisation of memories over time and with repeated remembering. 10.1101/2020.09.11.292813.

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Conference contributions

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Abbreviations

Abbreviation	**Definition**
A1	primary auditory cortex
A2	secondary auditory cortex
A3	tertiary auditory cortex
AAL	automated anatomical labelling
ANOVA	analysis of variance
BA	brodmann area
BCG	ballistocardiogram
BOLD	blood-oxygen-level-dependent
BUIC	Birmingham University Imaging Centre
CA	cornu ammonis
CI	confidence interval
DG	dentate gyrus
EEG	electroencephalogram
EPI	echo-planar imaging
ERC	european research council
FIR	finite impulse response
FMRI	functional magnetic resonance imaging
FOV	field of view
FWE	family wise error
GLM	general linear model

HERA	hemispheric encoding retrieval assymmetries
hIT	human inferior temporal cortex
ICA	independent component analysis
LDA	linear discriminant analysis
MEG	magnetic encephalogram
MNI	Montreal Neurological Institute
MP	magnetization prepared
MRI	magnetic resonance imaging
MTL	medial temporal lobe
MVPA	multivariate pattern analysis
PET	positron emission tomography
RAGE	rapid gradient echo
RDM	representational dissimilarity matrix
RM	repeated measures
ROI	region of interest
RSA	representational similarity analysis
RT	reaction times
SAR	specific absorbtion rate
SD	standard deviation
SENSE	SENSitivity Encoding
SNR	signal to noise ratio
SPM	statistical parametric mapping
STEM	science, technologiy, engineering, and mathematics

TE	echo time
TFCE	threshold-free cluster enhancement
TOI	time of interest
TR	repetition time
V1	primary visual cortex
V2	secondsary visual cortex

Chapter 1 - General introduction

Our environment consists of an overwhelming amount of dynamic, multidimensional and multisensory stimuli and offers us unique experiences on a daily basis. The only way to make sense of events as they unfold and to maintain a coherent narrative of our experiences is by being able to transform, maintain and recall inner representations of our sensations. The memory network plays a central role in these functions (e.g. Allen & Fortin, 2013; Dere et al., 2008). It helps to transform novel experiences into memories, and to use previously stored memories to interpret novel experiences. However, little is still known about what information is recovered during memory retrieval, when and where in the brain. The work in this doctoral thesis investigates the spatio-temporal neural mechanisms of episodic memory retrieval, and the transformation of the related memory representations.

When encoding a novel event, sensory information is initially processed in a feedforward sweep. It is assumed that this process follows a hierarchical perceptual-to-conceptual processing gradient as the information travels along the sensory pathways (T. Carlson et al., 2013; Cichy et al., 2014; Linde-Domingo et al., 2019; Martin et al., 2018). In contrast, it is still unclear if retrieval follows a hierarchical cascade, and what memory representations are reactivated at the various stages of this process. In this thesis, I will present an accumulation of findings showing that the retrieval process follows a hierarchically and spatially reversed stream from modality-generic (instead of modality-independent as hypothesized) and highly abstract to sensory-specific and perceptually detailed representations. The first two experiments are EEG-fMRI studies, aiming to unravel the retrieval processing cascades and to deconstruct the retrieval process into its representational components. Multivariate analysis methods, including linear classification and representational dissimilarity

analyses, are used to isolate and then compare the representations that are reactivated at a given time (EEG) in a given brain region (fMRI) within a data fusion. This makes it possible to locate, temporally and spatially, the dominant modality and feature representations that are active at different hierarchical processing stages during retrieval. In contrast to the initial modality-independent to sensory-specific stream hypothesis, the first simultaneous EEG-fMRI study shows that when retrieving auditory or visual memories, general modality information is simultaneously activated in cross-modal as well as sensory-specific areas early in time. Then, stimulus-specific representations are reconstructed in sensory-specific areas at a comparatively later time point. A second EEG-fMRI study then zooms in on the visual domain to show that the sensory-specific visual reconstruction process is reversed in retrieval with respect to encoding. In particular, the findings reveal that late ventral visual areas are reactivated before early visual areas and reflect a conceptual-to-perceptual processing stream. After establishing the evidence for a mainly feedback, conceptual-to-perceptual retrieval stream that propagates from hippocampal to neocortical structures, the final experiment is a reaction time (RT) study, demonstrating that the prioritised access to conceptual item features during retrieval promotes a semanticisation of memory representations in the longer-term, which exceeds the naturally occurring effects of consolidation over time.

Episodic memory

Overview

To provide the necessary background information, I will here introduce the concept of episodic memory. While following memory transformation processes sequentially from perception over memory formation to retrieval, I will describe the major characteristics of episodic memories. Together, I will show that episodic memories are multisensory, multi layered, multi-dimensional and malleable. Finally, I will introduce current knowledge gaps and evolving research questions.

Episodic memories are multisensory

What is episodic memory? To understand what makes episodic memories unique, I will first introduce a number of theoretical concepts that concern memory in general here. Defining memory cannot be done with a few words only. In layman’s terms, memory includes any influence that the past has on present information processing. In scientific terms, memory is therefore often characterised as an information processing system that transforms, stores and retrieves input data (Sherwood, 2015). Both descriptions reveal that memory is not one operation unit with a single function, but rather a broad system that contains many operations with individual functions (Squire, 2004). The first evidence for distinct and possibly independent memory functions has been shown in a case description of the amnesic patient H.M. (Scoville & Milner, 1957), who showed severe forgetfulness of newly and pre-surgery acquired memories but preserved the ability to learn new motor coordination skills after hippocampal resections. Researchers have spent decades trying to explain this dichotomy and to facilitate the understanding of the memory system with its underlying brain processes (Squire, 2004). Attempting to categorize different memory processes according to their operations, the division between declarative and non-declarative memories has been proposed (Squire, 2004; Squire & Zola-Morgan, 1988).

While non-declarative memory includes a collection of systems that are responsible for unconscious performance, including procedural skills, associative and non-associative learning, priming and perceptual learning, the umbrella term has been created to make a clear distinction from declarative memory (Squire, 2004). Declarative memory in contrast involves the conscious recollection of knowledge and experience representations (Squire & Wixted, 2011). To be more precise, declarative memory on the one hand comprises semantic memory, which includes the knowledge about facts and meaningful concepts. Semantic memories are often recollected in a stand-alone fashion, without any associated perceptual recollection or detailed descriptions of how that memory was formed. An example of a semantic memory could be remembering one's own date and place of birth. On the other hand, declarative memory also includes episodic memories, which as indicated by the name, represent in-person experienced episodes with all their multisensory conceptual, spatio-temporal and sometimes emotional recollections (Tulving, 1972).This could for example be a memory of the last birthday including time and place of the birthday dinner, the smell of the food, the colour and taste of the cake and the music playing in the car on the way home. Thus, in contrast to the abstract but compact semantic memories, episodic memories represent a whole repertoire of multisensory, multidimensional attributes that were initially perceived in an event. Importantly, they include perceptions from all our senses, i.e. visual, auditory, tactile, olfactory and gustatory experiences. Episodic memories thus enable us to consciously re-experience the past, which is particularly distinctive from the other types of memories, and why it has been referred to as mental time travelling (Tulving, 1972, 1985).

Episodic memories are multi-layered

As this thesis is mainly concerned with episodic memories of auditory and visual stimuli, I will now give some background information on the formation of episodic memories of these two modalities in particular. Before episodic memories can be formed, initial sensory processing transforms our sensory input into a form that the brain can represent and prepare for long-term storage. Important integrative processes happen along those sensory processing pathways, such that we are able to make sense of our experiences. When we perceive auditory or visual stimuli, low-level perceptual features are encoded in primary sensory areas, as they enter the brain. As such, neurons in the primary visual cortex respond differentially to features as colour, orientation, spatial frequency (Tootell et al., 1998; Henriksson et al., 2008; Henriksen et al., 2016) and neurons in the primary auditory cortex have a similarly specific tuning for different auditory frequencies (Humphries et al., 2010). At this stage, experiences are coded as concrete sensory-specific brain representations that yet lack information about meaning. As the modality-specific perceptual information progresses further along its respective sensory “what” stream of the brain (which is further described in more details in Chapters 1 and 2), its representation becomes more abstract, meaningful and gets integrated into pre-existing semantic networks (Binder & Desai, 2011; Borowsky et al., 2007; Devereux et al., 2013; DeWitt & Rauschecker, 2012; Gow, 2012; Hickok & Poeppel, 2007; Valyear et al., 2006). For example, representational brain activity patterns initially coding for a yellow curved object would start to represent a banana, or representations of an intermittent high frequency sound would further evolve into the representation of a ringing bell. The sensory-specific and perceptual to modality-independent conceptual processing are involved in everyday activities, such as object recognition, or social interaction. But the different stages of sensory processing are not only important, as they are fundamental neural correlates of the conscious experience of an event. The experience of both perceptual details and a conceptual understanding of our experiences are also a prerequisite for the storage of the multi-layered episodic memories. Once the input information has been processed on several levels of abstraction, perceptual and conceptual information is converged in the medial temporal lobe (MTL) ready for storage in the longer term (Staresina et al., 2011; Suzuki & Amaral, 1994). In fact, David Marr summarises accordingly, that it is actually the interpretation of a perception that is saved within a memory (Marr, 1971).

Episodic memories are multidimensional

The transfer from sensory input to memory formation is called memory encoding (Rugg et al., 2015). The MTL, including hippocampus and its surrounding cortical structures, is known to play an important role during memory encoding. It is the central brain network, where all sensory information coincides from neocortical associations areas. While information about the content of sensory input is transmitted to the perirhinal cortex, spatial information arrives in parahippocampal cortex, before being projected to the lateral and medial portions of the entorhinal cortex respectively (Knierim, 2015; Staresina et al., 2011). Additionally, amygdala and orbitofrontal cortex provide information about emotional context to the entorhinal cortex (Rolls, 2016). From here, information is relayed to and finally combined within the hippocampus, a structure responsible for the multi-dimensional, contextual, emotional and spatio-temporal association of events into coherent entities (Knierim, 2015; Suzuki & Amaral, 1994). To understand the associative integration of multi-dimensional characteristics of episodic memories within the hippocampus, the following section discusses the anatomy and underlying functions of the hippocampus in more detail.

Both the medial and lateral parts of the entorhinal cortex transmit information to overlapping cells of the dentate gyrus (DG) and cornu ammonis (CA)3, allowing the combination of multi-dimensional information (Knierim, 2015). While sparse projections from dentate gyrus to the CA3 via the mossy fiber pathway are responsible for the pattern separation, reducing representational overlap across events, recurrent collateral projections within the CA3 enable auto-associative memory processes and ultimately bind related information of various sources together (Treves & Rolls, 1992). The established associations within the CA3 also reactivate, whenever part of an event representation is missing, completing the pattern of a previously encoded event (Rolls, 2010). Finally, separately activated representations of episodic memories can be conjoined via the Schaeffer collateral synapses to CA1 which then projects back to entorhinal cortex directly as well as indirectly via the subiculum (Treves, 1995; Rolls, 2010). The special attributes of hippocampal circuits thus do not only enable the segregation of different unique events while binding together related information of the same event (Danker et al., 2017; Horner et al., 2015). They also help to complete a representation of an event when only partial information is given, for example by a memory cue (for example see Horner et al., 2015). The operations above, and the plasticity induced in these hippocampal circuits (Lømo, 2003), ultimately conclude the initial memory encoding process which result in enduring changes in the brain, referred to as memory engram (Schacter et al., 1978), and set the stage for the retrieval process.

Episodic memories are malleable

Neuroscientific research has been very successful in unravelling the neural representations underlying the initial sensory processing that result in memory encoding. But what exactly happens when we recall an event from memory and how do mental representations unfold during the retrieval process? Early work described that the recall of episodic memories starts with an ecphoric process, in which a cue that has partial overlap with the information of a previously encoded event, reactivates the engram, or associative patterns, and initiates a search for the remaining information of the memory trace (Schacter et al., 1978; Tulving, 1976; Tulving et al., 1983). Many early theories but also later neuroscientific findings (such as described in the previous section) have suggested that this ecphoric process starts with pattern completion in the hippocampus and propagates from there to cortical structures. More specifically, the hippocampus is believed to provide an index to the previously encoded memory traces in neocortex, such that cortical encoding patterns can be reconstructed (Damasio, 1989; Teyler & DiScenna, 1985; Teyler & Rudy, 2007). Assuming that the engagement of higher-level sensory and association cortices provides the fundament for mental representations of sensory events (Damasio, 1989), it is then plausible to infer that similar cortical engagement is needed to re-establish a mental representation when recalling an experience from memory in absence of the sensory event. In fact Tulving and Thompson pointed out the overlap between perception and retrieval with regard to the subjective experience (Tulving & Thomson, 1973). Correspondingly, early theories already suggested that the reactivation dictated by high-order “convergence zones” reaches up to early sensory cortices (Damasio, 1989), while state-of-the-art neuroscientific research has provided evidence of cortical re-engagement in mental representations of episodic memories (for a review see Danker & Anderson, 2010; McClelland et al., 1995).

These previously described theories and findings suggest that memory recall is underpinned by processes that restore the neural and in turn mental state of our initial sensory experience. Everyday life, however, shows us that episodic memories are not exactly copies of our experiences. Apart from the extreme situations when we retell stories in a way they did not actually happen (Brewin & Andrews, 2017) or when some memories get forgotten completely (Joensen et al., 2018), the most common phenomenon is when we remember the gist but forget specific details of an event (Ahmad et al., 2019; Brady et al., 2013; Hauer & Wessel, 2006; Winocur & Moscovitch, 2011). These observations imply that memory retrieval does not produce perfectly matching photocopies of an event but, at least to some degree, a partly reconstructive process. Similarly, Schacter relates seven observed memory flaws (Schacter, 2002) to the (re)constructive nature of memory, and argues that as beneficial the memory reconstruction can be, it is also subject to malfunction (Schacter, 2021), or incompleteness (Ahmad et al., 2019; Brady et al., 2013; Hauer & Wessel, 2006).

Concerning neural processes of this (re)construction, some parallels have been drawn between retrieval and sleep (further discussed in Chapter 3). During sleep, hippocampal-cortical communication is believed to reactivate memories, strengthen the intermediate connections and relay episodic memory traces from the hippocampus to neocortex, which has been strongly related to memory consolidation (Dudai et al., 2015). Importantly, within this process, episodic memories have been shown to lose some of the detailed episodic characteristics, while maintaining the conceptual gist of an event (Ahmad et al., 2019; Lutz et al., 2017). While this representational transformation has been believed to mainly happen during sleep, more recent work has proposed that active remembering can enhance this transformation (Dudai et al., 2015; Ferreira et al., 2019; Winocur & Moscovitch, 2011). As the retrieval related hippocampal-neocortical dialogue provides an opportunity to strengthen the intermediate connections and integrate them in reciprocal semantic networks, it is assumed that we simultaneously forget specific details on the way (Ahmad et al., 2019; Brady et al., 2013; Dudai et al., 2015; Hauer & Wessel, 2006; Káli & Dayan, 2004; McClelland et al., 1995; Winocur & Moscovitch, 2011). The reactivation of memories both during sleep and wake may thus transform the initially encoded memory, showing how plastic and malleable our memories are.

Research aims

I hope to have shown that episodic memories are not only multifaceted and multidimensional but also highly dynamic and subject to representational transformations. To summarise, I have pointed out that episodic memories are formed by the encoding of sensory input into so-called engrams (Josselyn & Tonegawa, 2020). The initial sensory representations provide the scaffold for later to-be-remembered memories. As sensory input propagates from cortical structures to the hippocampus, the encoding process follows a detailed, multi-sensory to modality-independent, conceptual gradient. When episodes are recalled from memory, that memory trace within the hippocampus gets reactivated and the re-experience of episodic memories requires reinstatement of initial sensory patterns. Finally, I have shown that cortical memory representations undergo changes during retrieval and memory consolidation. From the introduction, it can be seen that the perception processes within episodic memory encoding are relatively very well studied. The aim of this doctorate thesis is to extend our understanding of the reconstructive processes underpinning episodic memory retrieval. In particular, this project aims at exploring how episodic events are represented in the brain while reconstructed from memory, and how these representations change with repeated retrieval. The following three main hypotheses guide the work in this thesis.

1) The first hypothesis states that during retrieval, modality-independent representations are reactivated in cross-modal brain regions before sensory-specific representations are reconstructed. Evidence for this assumption comes from the work suggesting that the retrieval process starts off in the hippocampus before it propagates to neocortical structures (Staresina & Wimber, 2019). Additional evidence discussed in the second chapter has given reason to assume a reverse reconstruction in comparison to the initial perception of an event. Since the initial steps of encoding show a sensory-specific to modality-independent representation transformation, it was tested whether this information stream is reversed during retrieval. The hypothesis was tested in a simultaneous EEG-fMRI study, in which participants encoded and subsequently recalled paired associates each consisting of a word and a dynamic video or audio clip. First, classification analyses were used to determine when in time

and where in the brain individual video and audio clips can be decoded. Then, representational similarity analyses were used to trace the representational information processing in the brain during the retrieval process within individual participants.

2) The second hypothesis states that during the recall of visual information specifically, the retrieval process propagates backwards along the ventral visual stream following a conceptual-to-perceptual gradient. This hypothesis goes hand in hand with the first hypothesis and similarly assumes a reversed reconstruction stream in comparison to perception/encoding. The hypothesis was tested by a consecutively acquired EEG-fMRI study, in which participants perform a verb-object association task and subsequently had to recall the object upon presentation of the cue. Like in the first project, multivariate analyses were used to trace information processing during retrieval and test for a backwards stream. Importantly, the stimulus material was designed to include a conceptual dimension (animate versus inanimate objects) that was orthogonally represented to a second, perceptual dimension (images presented as drawings and photographs). This manipulation was used to specifically test if the reversed stream followed a conceptual-to-perceptual gradient.
3) The last hypothesis states that the repeated recall of an event facilitates access to conceptual features over perceptual details, and strengthens such semantic features in the long-term beyond sleep-dependent consolidation effects. Under the assumption of a backwards progressing retrieval stream (as described in the first two hypotheses and empirical chapters), the hippocampus dictates reactivation of neocortical representations. As the hippocampus is spatially

closer to brain regions representing conceptual features than those representing perceptual details, it can be assumed that communication is enhanced between the former regions, which could ultimately lead to stronger semanticisation. This hypothesis was tested by a simple reaction time task, staged across multiple days, which measured how fast participants could recall perceptual and conceptual features of a visual memory. Participants of a repeated retrieval group learned verb-object associates and then repeatedly recalled the object upon the presentation of a cue, each time answering either a perceptual or conceptual question about the object as rapidly as possible. To test if episodic memories semanticise over time, we compared their performance on day one to a delayed memory test 48 h later. Then, to test if the retrieval-induced semanticisation effects extend beyond natural consolidation effects of sleep, we compared the performance on day 2 with a group who repeatedly studied the materials on day 1.

Chapter 2 - Reconstructing Visual and Auditory Trajectories of Episodic Memories in the Human Brain

At the time of thesis submission, this chapter represents preliminary analyses (Julia Lifanov, Ben Griffiths, Simon Hanslmayr, Ian Charest and Maria Wimber).

Abstract

In contrast to the information transformation processes occurring during sensory perception, the neural processing hierarchies supporting memory recall are still poorly understood. In this simultaneous EEG-fMRI study, we used multivariate analysis methods to explore the processing stream supporting the recall of visual and auditory memories. Participants were asked to associate a dynamic video or audio clip to an unrelated word in an encoding phase, and then recall the dynamic clip upon presentation of a word cue during a subsequent retrieval phase. Using classifiers, we decoded visual and auditory processing from spatially distinct fMRI and temporally resolved EEG patterns. By means of representational similarity analyses, we were then able to map the representational geometries of visual and auditory voxel patterns onto the time course of event related potentials. Successful memory recall was accompanied by early hippocampal, cross-modal, and sensory-specific activations around 550-600 ms, followed by a feedback reinstatement along sensory visual and auditory pathways. The processing of generic modality could be traced back to cross-modal and sensory activations early in time, whereas the processing of clip-specific elements was reflected in temporally later sensory-specific reinstatement. Finally, our results descriptively show the retrieval-induced information processing cascade starting from the medial temporal lobe to the reinstatement of sensory areas.

Introduction

Memories can bring back detailed and near realistic impressions of past experiences to the extent that they can even affect us emotionally. What makes episodic memories so similar to real experiences are the rich multimodal representations of our different senses, such as vision and audition, which can be part of the subjective recollection. As such, we can not only visualize the facial features of the people we have only met once, but also recognize the sound of their voice. We know that these visual and auditory features are represented in the brain when people recall past experiences (Nyberg et al., 2000; Slotnick & Schacter, 2006; Wheeler et al., 2000). It is yet unclear, however, how these memory representations of different modalities unfold in the brain over time once a reminder is given. Using an EEG-fMRI fusion, we explore the spatio-temporal activity cascades when visual and auditory memories of dynamic clips are being recalled, with a focus on the reactivation of generic modality information as compared to sensory-, or in this case clip-specific processes.

Neuroscientific research has extensively explored how new experiences are represented in the brain while they are perceived aurally or visually, and how the underlying information processing evolves. Information from both modalities is assumed to progress along two separate information processing streams with different functions: the dorsal and ventral pathways. Concerning vision, the dorsal “where” pathway represents orientation- or location- and motion- specific visual information, stretching from early visual areas over medial temporal to the parietal lobe regions, once it exits the lateral geniculate nucleus (Hebart & Hesselmann, 2012; Valyear et al., 2006). Representations along this stream proceed from spatial and temporal frequency via motion and rotation to self-motion and multimodal integration (Perry & Fallah, 2014). Roughly corresponding to this visual-dorsal stream, the auditory dorsal pathway starts at the primary auditory cortex and progresses via the posterior superior temporal gyrus to parietal areas, and is supposed to serve the transformation of auditory to articulatory and motor representations (Hickok, 2012). As such, the dorsal stream for both modalities supports processes that put information into spatial and motor context and are subject to increasing abstractness.

While the dorsal pathway generally deals with spatial interpretation of incoming information, the more content-oriented ventral “what” pathway on the other hand prioritises identity-specific processing and integration. In the visual domain, activation spreads from occipital via the inferior temporal to the medial temporal lobe (Borowsky et al., 2007; Valyear et al., 2006). Along this path, visual information progresses hierarchically from low-level perceptual to high-level conceptual information within the first 300 ms after stimulus onset (T. Carlson et al., 2013; Cichy et al., 2014, 2016; Martin et al., 2018). Hence, representations of visual characteristics are thought to transform into meaningful object information. The corresponding ventral pathway in the auditory modality in contrast follows a stream along the middle and superior temporal areas to the temporal pole before converging with the visual stream (DeWitt & Rauschecker, 2012; Gow, 2012; Hickok & Poeppel, 2007). Similarly to vision, the auditory processing stream along the superior temporal gyrus also holds a hierarchical processing structure from early acoustic to more semantic features within the first 300 ms, transforming low-level perceptual to higher-level meaningful information (Lowe et al., 2020; Li et al., 2019).

Following the sensory-specific visual and auditory processing, information of both modalities eventually coincides in cross-modal regions, such as the posterior/inferior parietal and inferior and medial temporal lobe, at a relatively late stage. At this point, the semantic meaning of incoming information is processed and represented in a modality-independent or amodal fashion, before all information from the different sources is finally bound together in the hippocampus for the retention in the longer term (Danker et al., 2017; Horner et al., 2015; Rolls, 2010).

Having established this general perceptual-to-conceptual gradient when processing external information in either of the two modalities, the question arises how this information is represented when recalling experiences from memory. Classical literature suggests that the memory recall process starts within the hippocampus, which is supposed to then dictate further reactivation of other cortical regions (Quiroga, 2012; Teyler & DiScenna, 1985). During this reactivation, activity patterns observed during the perceptual experience of an event are supposed to be re-established, recreating the mental representations of the past experience (Damasio, 1989). Indeed, it has been demonstrated that such a cortical reinstatement during the recall of multimodal memories is a prerequisite of successful remembering (Huijbers et al., 2011; Staresina et al., 2012; Thakral et al., 2015). Univariate analyses in neuroimaging studies have found reactivation in sensory-specific cortical areas that were previously involved in the encoding of an event: retrieval-related reactivation included regions in the occipital cortex for visual memories (Johnson & Rugg, 2007) and superior temporal cortex for auditory memories (Nyberg et al., 2000; Wheeler et al., 2000). More recent findings provide evidence for cortical reinstatement by using multivariate methods that can match the encoding and retrieval fMRI activity patterns at a much more fine-grained, voxel-specific scale (Polyn et al., 2005; Ritchey et al., 2013; Wing et al., 2014). While occipito-temporal regions are reinstated during visual retrieval (Bosch et al., 2014; Gordon et al., 2014; Griffiths, Mayhew, et al., 2019), regions including inferior frontal gyrus, postcentral gyrus, cingulate cortex and insula have shown high encoding-retrieval similarity for auditory stimuli (Danker & Anderson, 2010; Griffiths, Mayhew, et al., 2019).

Apart from these examples of sensory-specific reinstatement, more cross-modal parietal and late temporal areas have been found to be involved both in auditory and visual recall (Buckner et al., 1996; Huijbers et al., 2011; Tulving et al., 1994; Waldron et al., 2014), and often been related to semantic or episodic representations (Favila et al., 2018, 2020; Ferreira et al., 2019; Jeong & Xu, 2016). Interestingly, it has been shown that cross-modal areas are associated with successful access during cued-recall, whereas sensory-specific regions held information that was not sufficient to support cued recall, but could support successful recognition via a familiarity signal (Salami et al., 2010). These findings indicate a possible dependency between cross-modal and sensory-specific reactivation: Even if sensory-specific representations are available, they can only be accessed by involvement of higher-order, cross-modal regions. Thus, the literature so far suggests that retrieval relies on sensory-specific reinstatement presumably mediated by cross-modal activation.

While the studies above point to the spatial location of sensory-specific and cross-modal representations during the retrieval of auditory and visual information, the exact spatio-temporal hierarchy along which these different memory elements are reactivated has not been uncovered yet. Recent literature suggests that superordinate semantic categories are represented before perceptual details when recalling an object from memory (Linde-Domingo et al., 2019; Lifanov et al., 2021). When subjects recalled the perceptual or conceptual details of an object, reaction times and accuracies demonstrated that access to conceptual features is prioritised over perceptual features. Similarly, decoding feature patterns from EEG while participants recalled an object, conceptual features were decoded before perceptual ones (Linde-Domingo et al., 2019). Given the temporal prioritisation of conceptual features during retrieval and the dependence of sensory-specific perceptual reinstatement on cross-modal activation, we investigate the possibility that spatial brain representations first get activated in cross-modal regions of the brain before information recovery progresses to perceptual and more sensory-specific regions.

In theory, direct and indirect anatomical connections from medial temporal structures to the parietal lobe, as found in the macaque brain, would enable such an initially cross-modal reactivation (Insausti & Muñoz, 2001; Kobayashi & Amaral, 2003; Lavenex et al., 2002; Muñoz & Insausti, 2005). From the parietal lobe, efferent pathways to the occipital and superior temporal cortex, as found in the macaque (Selemon & Goldman-Rakic, 1988), could then enable more detailed sensory-specific processing. Similarly, medial temporal structures can access superior and inferior temporal cortices via direct efferents, entering the auditory and visual ventral stream retroactively (Insausti & Muñoz, 2001; Muñoz & Insausti, 2005). The evidence that the retrieval process starts off in and is guided by the hippocampus (Bosch et al., 2014; Staresina & Wimber, 2019), progressing from abstract to detailed information processing (Linde-Domingo et al., 2019), and the indications of a possible dependency between modality-independent and sensory specific processing (Salami et al., 2010) lead us to our research question. We tested if during retrieval, cross-modal parietal and temporal regions representing abstract modality-independent information become activated before visual and auditory areas reinstate more detailed sensory-specific information.

To test our research hypothesis, we examined the spatio-temporal neural processing stream during the recall of visual and auditory memories, using a simultaneously acquired EEG-fMRI dataset of 21 participants, who performed a simple memory task (data from Griffiths, Mayhew, et al., 2019). The participants of the described dataset were asked to associate short (3 sec) visual movie clips or auditory sound clips with a random word each in an encoding phase, and to subsequently retrieve the associated clip upon presentation of the related word cue during recall. Using multivariate classifiers, we first mapped the spatial representations during encoding and retrieval on the brain, and then tracked how they evolve over the time course of a trial in the EEG. Then, by means of representational similarity analyses (RSAs), we fused the EEG and fMRI data and mapped the temporal processing cascades on the brain. Together, this research uncovers visual and auditory representations during recall in time and space.

Methods

Participants

The current study describes a dataset that has been acquired and published by Griffiths and colleagues (Griffiths, Mayhew, et al., 2019). For clarification, the methods and preprocessing steps will be summarized here, but for further information on the sample, paradigm, data acquisition or preprocessing please refer to the related previous publication (Griffiths, Mayhew, et al., 2019). The dataset includes data of twenty-one native English participants from the local student population at the University of Birmingham with normal vision (with or without correction). The number of participants resembled the one of a previously published study that used the same study design (Michelmann et al., 2016). The study had been ethically approved by the Research Ethics Committee at the University of Birmingham, complying with the Declaration of Helsinki.

Material

The stimulus materials included 192 words from the MRC Psycholinguistic Database (Coltheart, 1981), four video and four audio clips, all being emotionally neutral. The video clips all included silent recordings picturing one of the dynamic sceneries including: a bike, a farm, an underwater scenery or a waterfall; whereas audio clips included melodies played by one of the following four different instruments: an accordion, a guitar, a piano or a trumpet (Fig. 1.1).

Procedure

Participants performed a memory task (Michelmann et al., 2016; Griffiths, Parish, et al., 2019; Griffiths, Mayhew, et al., 2019), in which they were asked to associate dynamic video or audio clips with pseudo-randomly allocated words (Fig. 1.1). Each participant went through four task runs with alternating clip modalities (two video and two audio task runs in alternating order). A task block included 48 encoding trials, a distractor task and 48 retrieval trials with clips of only one modality, i.e. either only video or only audio clips. The order of modality blocks – whether a subject started with an audio or video block - was counterbalanced between participants. A total of 192 unique words and eight clips (four video and four audio clips) were used for the association task. This way, each dynamic clip was first paired with 24 unique words in total during encoding and then cued by each unique word once during recall, so 24 times in total. As there were two task runs for each modality, the clip-word pairs were equally distributed among the two. This means that each clip was used 12 times for both encoding blocks of the respective run and 12 times for both retrieval blocks of the respective run each. The presentation order of the individual dynamic clips within a block was randomized. The task was performed inside the fMRI scanner during simultaneous fMRI and EEG recordings.

Encoding

Encoding trials started with a fixation cross that was jittered around 2 s with a maximum deviation of 250 ms. Next, a video or audio clip appeared on the screen with a duration of 3 s, followed by the allocated word for another 3s. Participants were instructed to learn the word-clip pairings by creating a vivid link between the two. Before participants could proceed to the next trial, they were asked to rate the plausibility of their associative link within a maximum time of 4 s. Decisions were made by button press.

Distractor

After the encoding phase, participants performed a numerical distractor task for 2 min, in which they were asked to indicate as fast as possible whether each of the consecutively presented numbers, ranging between 0 and 99 was odd or even, with feedback being provided for each response.

Retrieval

After the distractor task, participants progressed to the retrieval phase. Retrieval trials started with a fixation cross jittered around 2 s with a maximum deviation of 250 ms. The participants were cued with a previously learned word that appeared on the screen for 3 s. During this period, participants were expected to mentally retrieve and replay the video/audio clip previously associated with the word, before they were then presented with a choice of all four different videos/audio clips, from which they had to select the clip they had in mind. Last, participants were asked to rate their confidence about their decision within a maximum time of 4 s before proceeding to the next trial. The order of retrieval trials was randomised such that it did not match the order of encoding in order to avoid confounds by sequence memory.

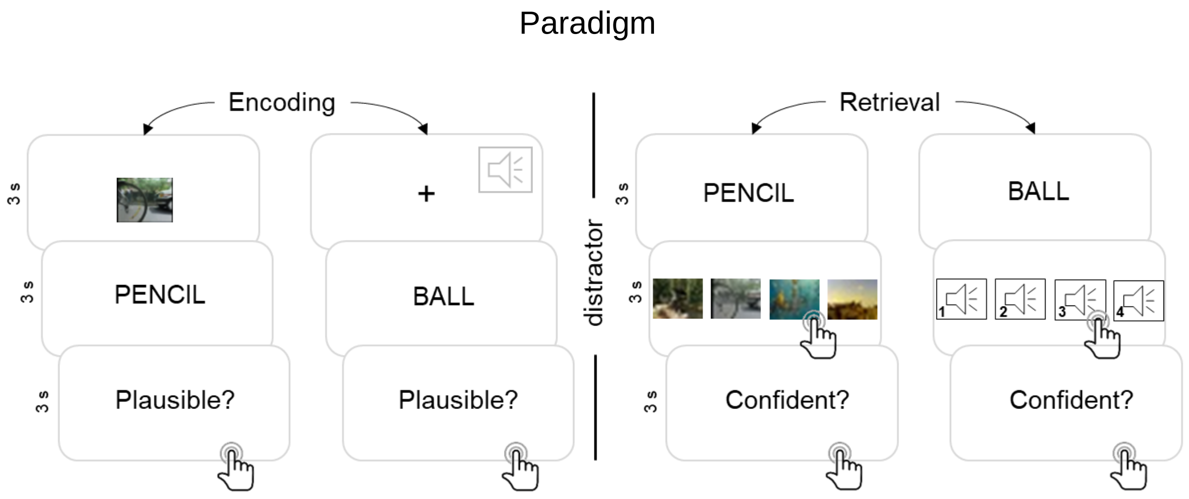

Figure 1. 1

Prototypical task block of the paradigm. Participants either went through a visual or an auditory block at a time. At encoding, participants were asked to associate a dynamic clip (one out of four possible video clips or one out of four possible audio clips, depending on the modality of the task block) to an unrelated individual word, and rate the plausibility of the newly formed association. At retrieval, participants first recalled the previously associated dynamic clip upon presentation of a word cue and then indicated by button press which of the four possible clips they recalled. They then also indicated the confidence in their response. Participants performed four encoding (two of each modality) and four retrieval blocks (also two of each modality). Within each block, each dynamic stimulus of the respective modality was paired or recalled twelve times each, each time with a new unique word. The analyses were mainly addressed at the period of the clip presentation during encoding, and the cue presentation during retrieval. Stimuli depicted are chosen from the MRC Psycholinguistic Database (Coltheart, 1981)*. Figure adapted* from *(Griffiths, Mayhew, et al., 2019).*

FMRI data acquisition

The fMRI data was recorded at the Birmingham University Imaging Centre (BUIC, now Centre for Human Brain Health (CHBH)) with a high-field 3T Philips Achieva scanner with a 32-channel SENSE head coil. T2*-weighted functional images were obtained through an echo-planar imaging (EPI) sequence (3 x 3 x 4 mm voxels, 64 x 64 matrix, 32 slices, no inter-slice gap, repetition time (TR) = 2 s, echo time (TE) = 40 ms, full head coverage, field of view (FOV) = 192 x 192 x 128 mm, flip angle (FA) = 80°). Four dummy scans that were later discarded were acquired before each scanning run. The resulting eight runs then each included 255 volumes after subtracting the dummy scans. T1-weighted structural scans (1 mm isotropic voxels, no inter-slice gap, TR = 7.4 ms; TE = 3.5 ms, FOV = 256 x 256 x 176 mm, FA = 7°) were acquired halfway through the experiment. Participants were instructed to lie as still as possible, and foam pads were placed around their heads to additionally prevent motion. The task was presented to participants through a mirror system in the scanner and a JVC SX 21e projector with resolution 1280x1024 at 60 Hz. NATA response boxes were used for behavioural responses (https://natatech.com/).

EEG data acquisition

The EEG data was acquired inside the MRI scanner by using a non-ferromagnetic cap with 64 channels by Brain Products (Munich, Germany). The cap was fixated with tape. The electrode cables, which were bundled and fixated by cable tie were connected to an MR-compatible amplifier outside of the scanner. A synchbox was used to synchronize scanning and EEG clock timings. The EEG data was recorded with a sampling frequency of 5 kHz and the electrode conduction was regulated by adjusting the impedance of the electrodes to a value < 20 kΩ. To correct for motion-induced EEG artifacts within the scanner (Fellner et al., 2016), four electrodes (F5, F6, T7 and T8) were first isolated from the head by placing sticky tape beneath them, and then connected to the reference over externally placed cables (Jorge et al., 2015). This method, previously introduced in simultaneous EEG-fMRI paradigms (Jorge et al.,

2015) enabled the measure of magnetic transmission induced exclusively by head motion, which could later be extracted from other EEG channels.

Analysis

Behaviour

For the inspection of accuracy performance, trials were categorized as ‘recalled’ when subjects linked the correct video/audio clip to the previously associated word, or ‘forgotten’ when they did not. Then, reaction times of all concatenated recalled and forgotten responses were examined. Average values and standard deviations were computed. Since we had no a priori hypotheses about differences in reaction times or accuracies, the reported data were visualised to provide purely descriptive information without making statements on statistical significance.

FMRI data preprocessing

The preprocessing and analysis of the fMRI data was performed in MATLAB 2016a (www.mathworks.com) and SPM 12 (*Statistical Parametric Mapping*, 2007, http://store.elsevier.com/product.jsp?isbn=9780123725608). T2* images were spatially realigned, unwarped and slice time corrected. Anatomical images were segmented and coregistered with the functional images. In contrast to the previous published preprocessing version (Griffiths, Mayhew, et al., 2019), we used the T2* images as stationary images, and the T1 as image that is manipulated for the co-registration, which provided a computing advantage. As preparation for the univariate

GLM, the anatomical and functional images were additionally transformed into MNI coordinates and functional images were smoothed by means of an 8 mm full width at half maximum (FWHM) Gaussian Kernel. However, the functional images used in all multivariate analyses, were analysed in individual native space and without previous smoothing.

ROIs

ROIs were created by means of templates in MNI space created in the WFU PickAtlas (Maldjian et al., 2003, 2004; Tzourio-Mazoyer et al., 2002). These ROIs were then fitted to individual brains by applying inverted normalization parameters, created during segmentation, to the ROI masks. The anatomical masks used for our analyses included: an early visual mask (V1/V2), consisting of Brodmann areas (BA) 17 and 18, an human inferior temporal (hIT) mask, consisting of BA 19 and 37 and inferior temporal gyrus as defined by automated anatomical labelling (AAL, Tzourio-Mazoyer et al., 2002), a primary auditory cortex (A1) mask, consisting of BA 22, another later auditory mask (A2A3), consisting of BA 41 and 42, a temporal pole mask, consisting of BA 38, a superior parietal lobe mask, consisting of BA 7, and an inferior parietal lobe mask, consisting of BA 29 and 30.

EEG data preprocessing

As previously stated, the dataset originated from a previous publication and specifically the EEG data preprocessing was performed according to this publication (Griffiths, Mayhew, et al., 2019). However, the preprocessing steps will be recapped here for clarification. The preprocessing and analysis of the EEG data were performed in MATLAB 2016a (www.mathworks.com) and the Fieldtrip toolbox (Oostenveld et al., 2010; Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, the Netherlands. See http://www.ru.nl/neuroimaging/fieldtrip). Before the conventional EEG analyses, gradient-, heartbeat- and movement-related noise were removed from the data. First, the gradient-related noise was removed. As a preparation for this procedure, the raw data was high-pass filtered with a cut-off frequency of 1 Hz. At each TR, a modelled gradient based on the 60 TRs closest to itself was computed and removed. This computational step was performed by the fmrib toolbox (Iannetti et al., 2005; Niazy et al., 2005). To remove slice acquisition artefacts (32 slices in 2s/16Hz), a bandstop filter (15.5-16.5 Hz) was applied. Next, artefacts induced by heartbeat (ballistocardiogramm (BCG)) were removed. For this step, the data was down-sampled to 500 Hz. Heart beats had previously been acquired during the scan. Using the logged onsets, the BCG artefact was removed from the data by an optimal basis set (fmrib toolbox). Next, extensive head motion indicated by triggers in the logfiles have been deleted before another round of gradient and BCG artefact removal. Finally, rest noise induced by in-scanner motion was removed from the data by a least squares regression using the measurements of the four claw electrodes (Bouchard & Quednau, 2000; Masterton et al., 2007; Daniel et al., 2019; Jorge et al., 2015).

For further conventional analyses, the data was epochs of -2 s to 4 s in relation to the dynamic clip onset at encoding and word onset at retrieval. The data was then further cleaned from eye artefacts, movements and remaining heartbeat artefacts by an independent component analysis. The mean was subtracted from trials, a low-pass filter with a cut-off frequency of 100 Hz was applied and the data was then re-

referenced to the average. After a final manual trial and electrode rejection, demeaning and re-referencing was repeated, cancelling all noise evolving from bad electrodes. Finally, the data was resampled to 128 Hz and a moving average filter with width of 40 ms was applied.

fMRI univariate analysis

After performing an own preprocessing pipeline on the fMRI data, that slightly differed on the previously published procedure (Griffiths, Mayhew, et al., 2019), we first performed some univariate analyses as sanity checks in comparison to the previous findings (Griffiths, Mayhew, et al., 2019).

To distinguish video and audio processing during encoding and retrieval, we set up a GLM that modelled video and audio clips as boxcar functions with a duration of 3 s at encoding and at retrieval. This was done separate for remembered and forgotten trials and resulted in eight condition regressors (Video encoding remembered, video encoding forgotten, video retrieval remembered, video retrieval forgotten, audio encoding remembered, audio encoding forgotten, audio retrieval remembered, audio retrieval forgotten). We additionally included regressors for button presses, motion, scanner drift and run constants (one regressor per variable containing all onsets). After performing the GLM on each individual dataset, we performed a second-level ANOVA on the whole subject sample using the above-mentioned conditions as within-subject factors. Subsequent t-tests were performed, contrasting video versus audio processing at encoding and retrieval. At encoding, all trials were included in the t-test, whereas only correct trials were used at retrieval. We then additionally tested memory success versus failure for both videos and audios at retrieval.

fMRI multivariate analyses

As preparation for the subsequent multivariate analyses, we ran a second GLM, modelling individual video- and audio-specific regressors as boxcar functions with a duration of 3 s for each individual trial at encoding and retrieval separately. Again, we added regressors of no interest as button presses and nuisance regressors (see above, one regressor per variable containing all onsets). The resulting beta weights were transformed into t-values for following multivariate analyses (Misaki et al., 2010).

fMRI searchlight LDA

To discover differential spatial video and audio processing during encoding and retrieval at the level of hemodynamic activity patterns, we performed a volumetric LDA searchlight analysis on the functional images in native space, separate for each participant (Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013; https://www.mrc-cbu.cam.ac.uk/methods-and-resources/toolboxes/). For each voxel and its surrounding neighbours within a radius of 12 mm, we extracted trial-specific t-value patterns resulting from the corresponding GLM as preparation for multivariate analyses and arranged these as unidimensional feature vectors. At each voxel, we used these feature vectors to classify the generic modality (video versus audio) or the individual clip within its modality. This classification was performed separately for encoding and retrieval, in each case using a 5-fold LDA with 5 repetitions, preserving class proportions, using the MVPA-Light toolbox (Treder, 2020; https://github.com/treder/MVPA-Light). Modality was classified by the default binary LDA as implemented in the toolbox, individual clips were classified by a multi-class LDA. As modalities were presented in different fMRI blocks, we implemented a baseline correction for classification between blocks. The baseline was computed by averaging the decoding accuracy across voxels within participants. After subtracting this average whole-brain decoding accuracy from all voxels within each individual subject, the new baseline-corrected value for each searchlight radius was assigned to its centre voxel. The resulting searchlight accuracy maps were normalized into MNI space and spatially smoothed with a 10 mm full width at half maximum (FWHM) Gaussian Kernel. Then, second level t-tests were performed to find whether voxel-specific classification accuracies across participants are significantly higher than zero. The voxel-specific results were finally plotted on an MNI surface template brain. As one of the participants had too few correct responses in only one of the audio clip trials, we had to exclude this participant from that particular analysis, as the number of trials did not suffice for the cross-validation.

EEG multivariate analyses

EEG LDA

To inspect the temporal progression of video and audio processing during encoding and retrieval, we also performed a time-resolved LDA on the EEG data using the MVPA-Light toolbox (Treder, 2020; https://github.com/treder/MVPA-Light). Clip-specific amplitudes from each of the 64 electrodes at a given time bin were used as feature vectors in the following decoding analyses. We first classified the generic modality (video vs audio) via the default LDA from the toolbox, and then individual video and audio clips among its modality via a multi-class LDA, at each time bin. Within the LDA, we implemented a 5-fold cross validated LDA with 20 repetitions, preserving class proportions. The resulting time-resolved accuracies were saved for each subject individually. Classification accuracies were then tested against chance accuracy (.5 for the classification of modality, .25 for the classification of individual clip) using a cluster-based permutation one sample t-tests with 1000 permutations and a cluster-definition threshold of p < .05 (as in previous publications (Cichy et al., 2019; Cichy & Pantazis, 2017; Dobs et al., 2019)). All cluster permutation tests were implemented by means of the permutest toolbox (https://www.mathworks.com/matlabcentral/fileexchange/71737-permutest by Gerber, 2021; Maris & Oostenveld, 2007; *Permutest*, n.d.).

EEG-fMRI data fusion

ROI fusion

To prepare the fMRI data for the ROI data fusion, we performed a representational similarity analysis on the unsmoothed fMRI data in native space. Specifically, we computed correlation distances (1-*r*) among all trial-specific t-values extracted from predefined anatomic ROIs at encoding and retrieval separately (Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013; https://www.mrc-cbu.cam.ac.uk/methods-and-resources/toolboxes/).

As preparation of the EEG data for the data fusion, we performed an RSA on the clip induced evoked EEG response at each time bin for encoding and retrieval separately.

Using the time-specific amplitudes across electrodes as feature vector, we calculated the correlation distance (1-r) between each pair of trials for each time bin separately.

To ultimately fuse the EEG and fMRI data, we first Fisher's z-transformed the EEG and fMRI RDMs and then computed a second-order correlation of the representational dissimilarity matrices (RDMs) resulting from the separate imaging modalities. For the ROI fusion (as opposed to the searchlight-based fusion described below), we correlated the fMRI-based RDMs of each ROI with the matrices derived from each time bin of the EEG data. This correlation was done within subjects, and resulted in one correlation time course per ROI, displaying the similarity of this region's representational geometry to the geometries of the EEG patterns at different time points. Note that we performed one fusion over all video and audio trials together, in which we merged V1, V2, and extrastriate regions for a visual mask, and A1, A2, A3 for an auditory mask and additionally looked at our cross-modal regions (anterior temporal pole, inferior and superior parietal lobe). Further, we performed one fusion only including video or audio trials for the not merged ROIs within the respective sensory-specific processing pathway plus cross-modal regions (Fig. 1.2).

A one-sample t-test against zero was performed on the ROI time courses to establish if and when representational geometries of an ROI are significantly reflected in the EEG patterns. Significant temporal clusters were detected using a cluster-based permutation test using 1000 permutations and a cluster-definition threshold of $p < .05$, correcting for multiple comparisons in time as in previous studies (Cichy et al., 2019; Cichy & Pantazis, 2017; Dobs et al., 2019).

We then additionally tested if there were any significant peak time differences between the ROI correlation time courses. To do so, we registered the correlation peak time of the predetermined TOI (0 – 1.5 s for encoding, 500 ms – 3 s for retrieval) for each individual subject. We used a repeated measures ANOVA with ROI as the single factor (https://uk.mathworks.com/matlabcentral/fileexchange/5576-rmaov1 by Trujillo-Ortiz, Hernandez-Walls & Trujillo-Perez, 2004; *RMAOV1*, n.d.) to test if there was any significant difference in peak time between the ROIs. If this test yielded a significant effect of the factor ROI, we subsequently used a post-hoc paired-sample t-test to test if there was there was a difference between the correlation peak times of sensory-specific (auditory or visual) and cross-modal ROIs.

To test for a sequential information progression from visual and auditory regions towards cross-modal ones, we implemented a linear regression on the cumulative sums of the ROI time courses (based on Michelmann et al., 2019) in the fusion approaches with only video or only audio trials. To do so, we first calculated the cumulative sum of the ROI time courses over the time period from 0 to 1.5 s for encoding, and from 0.5 to 3 s after cue onset for retrieval. For an easier comparison, the cumulative sum of each ROI time course was normalized to an area under the curve that equals 1. For each time point, a linear regression was fitted across the cumulative correlation values of the ROIs within subjects. The resulting slopes of all subjects were then tested against zero in a one-sided cluster-based permutation test (again with 1000 permutations and a cluster-definition threshold of $p < .05$). This method enabled us to test for a forward stream during encoding and a backward stream during retrieval. An example of the rationale is depicted in figure 2.3 of chapter 3. In the case of a forward stream, the ROIs should sequentially activate from sensory-specific towards cross-modal regions. Therefore, the cumulative sums of sensory regions (e.g., V1-V2) should show a higher cumulative sum than cross-modal regions (e.g. temporal pole) already at an early time after stimulus onset. A linear fit across ROIs at a chosen time point should therefore show a significantly negative slope. According to this rationale, a stream from cross-modal to sensory regions would result in a significantly positive slope. Since we expected a sensory-to-cross-modal stream at encoding and cross-modal to sensory stream at retrieval, we used one-sided tests to see if the slope differs from zero (< 0 at encoding, > 0 at retrieval). The sequential ordering of our ROIs was based on a collection of literature on the ventral and dorsal visual and auditory streams from anatomical and neuroimaging studies (Borowsky et al., 2007; Cichy et al., 2016, 2017; Costanzo et al., 2013; DeWitt & Rauschecker, 2012; Felleman & Essen, 1991; Gow, 2012; Hebart & Hesselmann, 2012; Hickok & Poeppel, 2007; Lowe et al., 2020; Valyear et al., 2006).

Searchlight fusion

For a better spatial resolution and a spatially focused perspective on the data fusion, we then performed a volumetric searchlight analysis (Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013). Within each participant, we computed an RDM from the trial-specific t-value patterns at each voxel v, including a surrounding sphere with a radius of 3 voxels (as resulting from the multivariate GLM), and compared them to the time-resolved EEG RDMs in a second order correlation for each time of interest (TOI). Since our main research questions were focused on retrieval, we performed the data fusion using all trials, only video trials, and only audio trials. In contrast, the data fusion for encoding was performed only once, using all trials, mainly as a sanity check. The fused data was Fisher's z-transformed. The searchlight fusion (Fig. 1.2) was performed using pyRSA (https://github.com/Charestlab/pyrsa) which works on Python (van Rossum, 1995), using the sys and os module, SciPy (Virtanen et al., 2020), NumPy (Harris et al., 2020), and nibabel (https://github.com/nipy/nibabel/releases).

To test for significant EEG-fMRI pattern similarity at individual voxels, we normalized the correlation maps into MNI space, smoothed them with 10 mm FWHM Gaussian kernel and then tested them in a one-sample t-test against zero at each single time bin. Within this t-test, we performed a spatial maximal permuted statistic correction, combined with a threshold free cluster enhancement (Nichols & Holmes, 2002; Smith & Nichols, 2009). This cluster-based analysis was performed using the toolbox MatlabTFCE (http://markallenthornton.com/blog/matlab-tfce/) with 1000 permutations, a height exponent of 2, an extent exponent of 0.5, a connectivity parameter of 26 and a step number for cluster formation of .1 as suggested by Smith & Nichols (Smith & Nichols, 2009). The analysis resulted in a "fusion movie", representing time-resolved spatial t-maps, which indicate significant similarity between the representational structure of the EEG time series and individual voxels (or rather, spheres around a voxel).

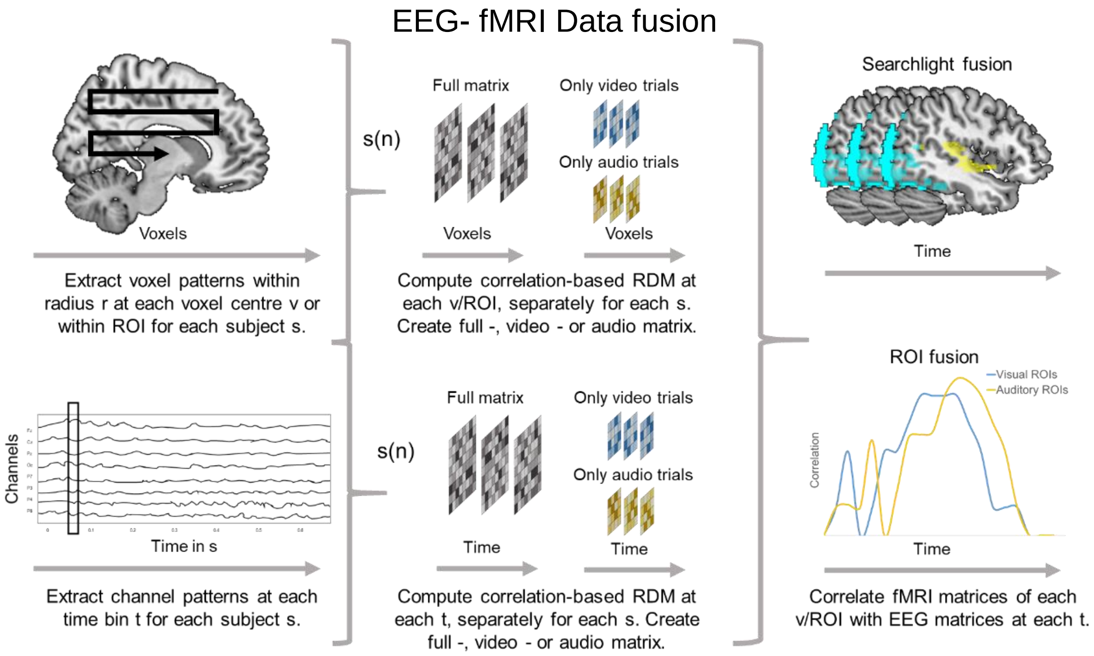

Figure 1. 2

Overview of ROI and searchlight fusion approaches. First, brain activity patterns are extracted from fMRI and EEG to create correlation-based representational dissimilarity matrices (RDMs) in the spatial and temporal domain, respectively. Then, second-order correlations of the RDMs from the two imaging modalities are computed for the data fusion. FMRI RDMs can be performed at each voxel centre including voxels within a specific radius, or for larger regions of interest (ROI). Depending on this choice, the data fusion will be searchlight- or ROI-based. FMRI and EEG RDMs can be created using all trials, only video trials, or only audio trials.

Figures

Figures were created using the raincloud plots Version 1.1, ColorBrewer 2.0 (from www.ColorBrewer.org by Cynthia A. Brewer, Geography, Pennsylvania State University), colorbrewer schemes 2.0 for Matlab (https://www.mathworks.com/matlabcentral/fileexchange/34087-cbrewer-colorbrewer-schemes-for-matlab by Charles, 2021; *Cbrewer*, n.d.), Inkscape 1.0.1

(https://inkscape.org/), WFU PickAtlas v3.0 (Maldjian et al., 2003, 2004), MRIcron (www.mricro.com, Rorden & Brett, 2000) and a colin 27 average brain template (http://www.bic.mni.mcgill.ca/ServicesAtlases/Colin27, Holmes et al., 1998).

Results

Behaviour

Before analysing the neuroimaging data, we explored the behavioural data including reaction times and accuracies (Fig. 1.3). On average, participants were similarly fast at recalling video (*M* = 1.29 s, *SD* = .20 s) and audio clips (*M* = 1.27 s, *SD* = .20 s). In contrast, participants achieved a higher accuracy when recalling videos (*M* = 73.83 %, *SD* = .10 %) than audios (*M* = 52.91 %, *SD* = .10 %) on average. The visualised data are for purely descriptive purposes (Fig. 1.3).

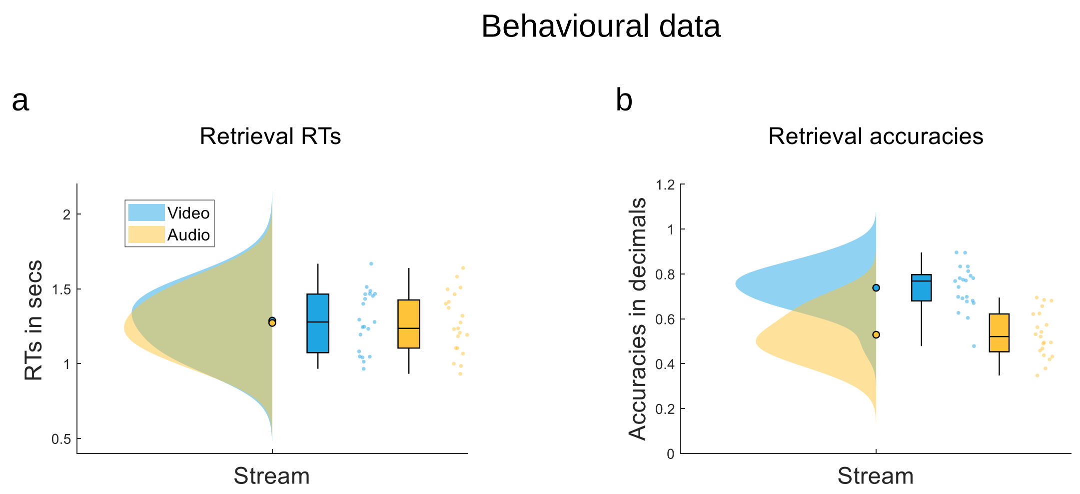

Figure 1. 3

Behavioural retrieval performance of visual and auditory retrieval. A) Retrieval reaction times (RTs) and b) accuracies for video and audio clips on average. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Blue represents video, orange audio retrieval performance. N = 21 independent subjects.

fMRI univariate results

As a first step, we explored whether we could find global hemodynamic activity differences within the brain when comparing auditory and visual processing during encoding and retrieval. We therefore performed a GLM analysis with subsequent t-contrasts between video and audio clips at encoding and retrieval (Fig. 1.4). At encoding (Fig. 1.4a), we found significantly higher activation for video clips than audio clips in areas along the visual stream ranging from occipital lobe to the middle temporal gyrus ($t(20) = 6.39$, $p < .05$ (FWE)). Audio clips in contrast elicited significantly higher BOLD responses in inferior and superior temporal gyrus ($t(20) = 6.39$, $p < .05$ (FWE)).

The visual activation of occipital and auditory activations of temporal regions were both in concordance with the previous findings (Griffiths, Mayhew, et al., 2019).

At retrieval (Fig. 1.4b), we found a higher activation for the videos in parahippocampal and perirhinal cortex ($t(20) = 6.39$, $p < .05$ (FWE)) but no higher activation for audio clips, similar to previous results (Griffiths, Mayhew, et al., 2019). When contrasting retrieval success versus failure for video trials (Fig. 1.4c), we additionally found univariate success effects (success > failure) in the occipital lobe, the insular cortex and putamen for video clips ($t(20) = 6.39$, $p < .05$ (FWE)); and success effects in the hippocampus for audio clips ($t(20) = 6.39$, $p < .05$ (FWE)). Our results thus show much overlap with the previous results (Griffiths, Mayhew, et al., 2019) with some minimal additional findings within the auditory condition.

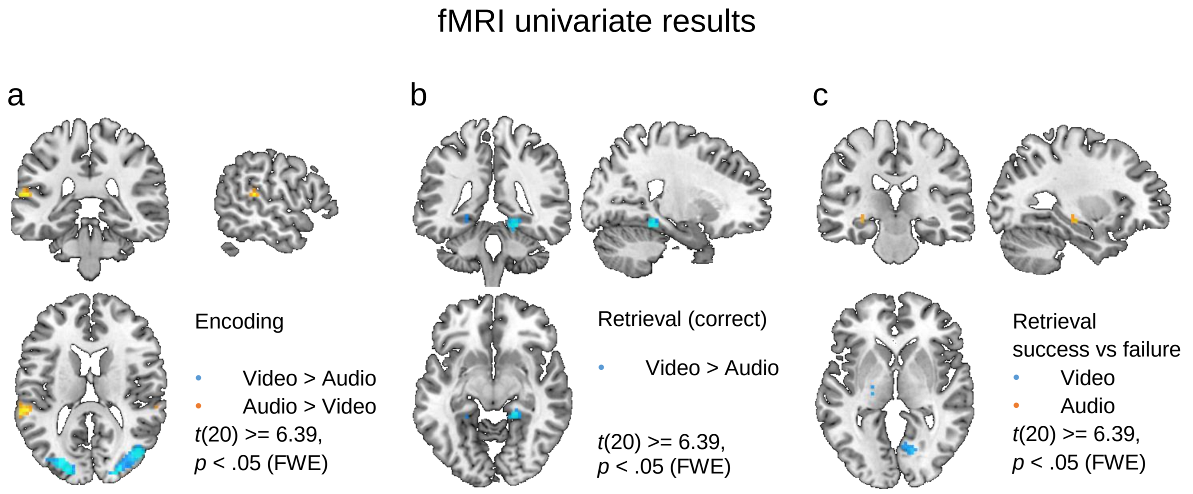

Figure 1. 4

Univariate t-contrasts results for encoding and retrieval. A) Contrasts at encoding depict blue: video > audio, orange: audio > video. B) Contrasts at retrieval depict blue: video > audio. C) Contrasts at retrieval depict blue: success > failure for video trials, orange: success > failure for audio trials. All contrasts were thresholded by the following values: T(20) = 6.39, p < .05 (FWE). N = 21 independent subjects.

fMRI multivariate results

Next, we took a closer look at modality-related information processing at the level of voxel activity patterns (Fig. 1.5). We therefore decoded the modality (video or audio) from fMRI activity patterns by a searchlight LDA during encoding and retrieval separately. At encoding (Fig. 1.5a), we found significant decoding accuracy spanning from early visual regions along the ventral stream up to fusiform gyrus and also expanding into superior temporal and inferior parietal cortex ($t(20) > 5.55$, $p < .05$ (FWE)). At retrieval (Fig. 1.5a), we similarly found significant decoding accuracy ranging from occipital regions over fusiform gyrus over inferior temporal gyrus to the hippocampus, and additionally expanding into insula ($t(20) > 5.55$, $p < .05$ (FWE)).

By means of a multiclass classifier, we then tried to decode individual video and audio clips from the voxel patterns. At encoding (Fig. 1.5b), individual videos could be classified in regions along the ventral visual stream from early visual cortex to fusiform gyrus. Audio clips could be classified in superior temporal gyrus and right inferior frontal gyrus ($t(20) > 5.24$, $p < .05$ (FWE)), however when using a more liberal threshold, also the left inferior frontal gyrus was involved ($t(20) > 3.55$, $p < .001$(uncorr)). Finally, within successful retrieval (Fig. 1.5c), individual dynamic clips could only be classified at a liberal threshold of p < 0.1 (uncorr). In particular, individual videos could be classified in small regions within the inferior temporal lobe and parahippocampal gyrus ($t(20) > 3.55$, $p < .001$ (uncorr)) and audio clips could be classified in the insula, left middle temporal and left ($t(19) > 3.55$, $p < .001$ (uncorr)) and right ($t(19) > 2.53$, $p < .01$ (uncorr)) inferior frontal gyrus.

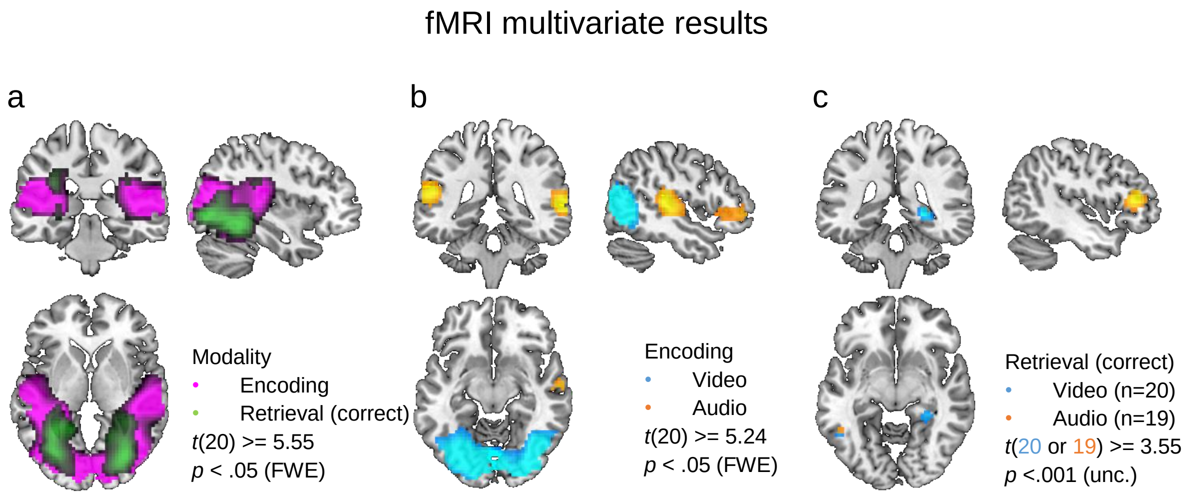

Figure 1. 5

Multivariate searchlight LDA t-contrasts for encoding and retrieval. A) Contrasts depict significant modality decoding at encoding (pink) and retrieval (green, using only correct trials), t(20) = 5.55, p < .05 (FWE). N = 21 independent subjects. B) Contrasts depict significant individual video (blue) and audio (orange) decoding at encoding, t(20) = 5.24, p < .05 (FWE). N = 21 independent subjects. C) Contrasts depict significant individual video (blue, t(20) = 3.55, p < .001 (uncorrected), N = 21 independent subjects) and audio (orange, t(19) = 3.55, p < .001 (uncorrected), n = 20 independent subjects) decoding at retrieval (using only correct trials). See methods for analysis.

EEG multivariate results

We then decoded modality and unique clips (Fig. 1.6) from the EEG patterns. Again, we first classified the modality (video vs audio clip) using a binary classifier, followed by a multiclass decoding of the individual video and audio clips within their modality. After computing classification accuracies over time, we tested whether the given accuracies are higher than chance, using a one-sample t-test (cluster-based correction with 1000 permutations, cluster-definition threshold *p* < .05, cluster size threshold *p* < .05).

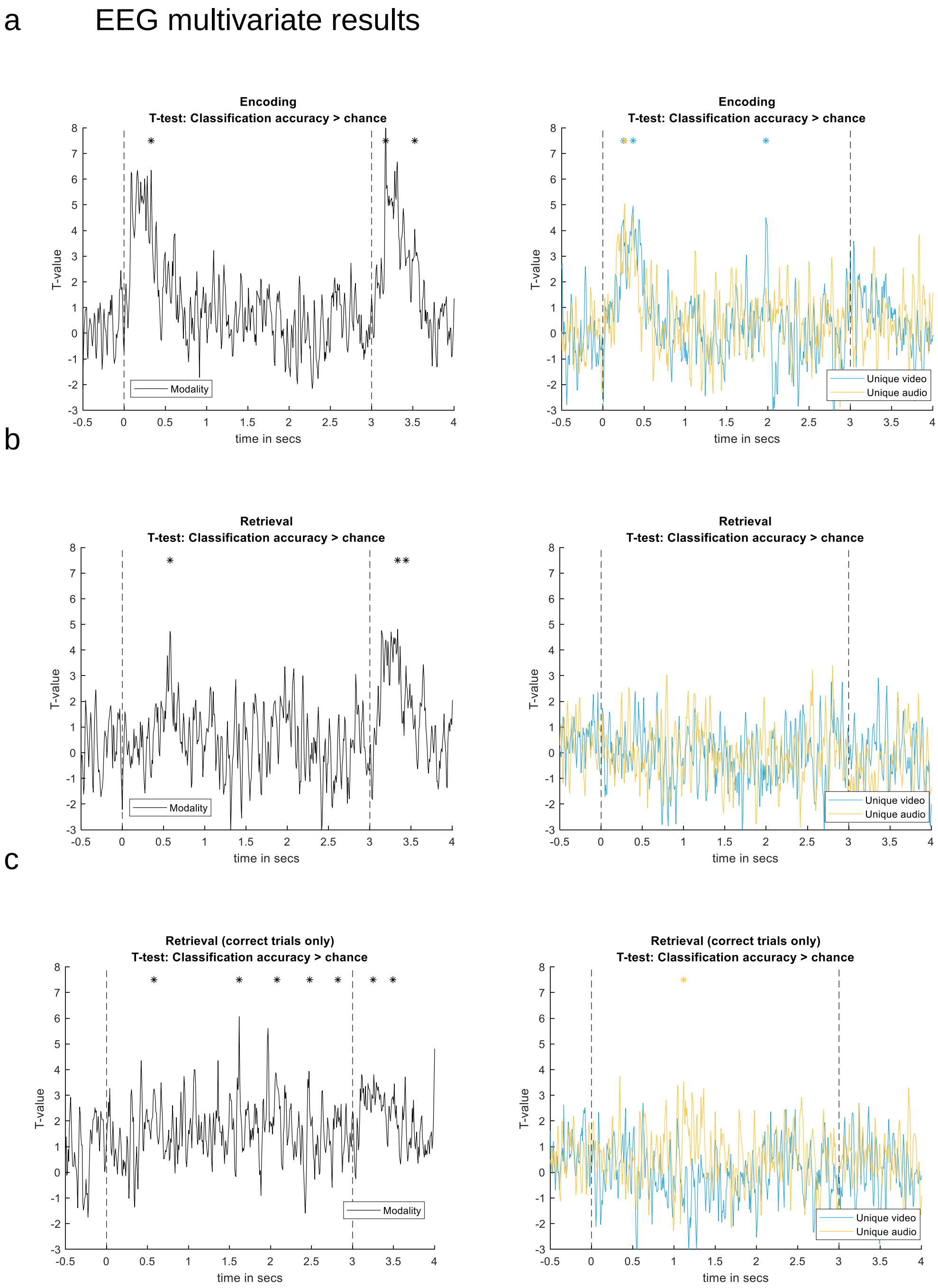

Figure 1. 6

EEG classification accuracy time courses during a) encoding (all trials), b) retrieval (all trials) and c) retrieval (only correct trials). Black line represents modality decoding accuracy, blue represents video decoding accuracy, and orange represents audio decoding accuracy. At encoding, time point 0 s marks clip onset, 3 s marks word onset. At retrieval, 0 s marks cue onset, 3 s marks clip choice. In all panels, *significant decoding accuracy is indicated by asterisk (p < .05 cluster). See Methods for details on cluster correction. N = 21 independent subjects.*

Within the encoding trials (Fig. 1.6a), we were able to classify modality after the presentation onset of the clip as well as after word encoding, indicated by significant classification peaks at 328 ms after clip onset, and 172 ms and 523 ms after word onset. Additionally, individual video clips could be classified at 250 ms, 367 ms and 1.98 s, and audio clips could be classified at 265 ms after clip onset, respectively (all at $p < .05$ (cluster)).

Classifying the modality of all retrieval trials (Fig. 1.6b), classification accuracy reached a significant peak at 578 ms after word onset, and 336 to 438 ms after clip choice onset (all at $p < .05$ (cluster)). However, the classification of individual video and audio clips at retrieval failed when using all responses in the analysis.

We then repeated the LDA on retrieval data including only correct trials (Fig. 1.6c). Classifying modality, we found one early significant accuracy cluster at 580 ms and several later clusters at 1.62 s, 2.08 s, 2.5 s and 2.8 s after word onset, as well as 250 to 500 ms after clip choice onset. Unique videos could still not be classified successfully. However, including only correct trials resulted in a significant cluster of audio clip classification at 1.12 s after word onset (all at $p < .05$ (cluster)).

EEG-fMRI data fusion

ROI fusion - encoding

After investigating the EEG and fMRI data separately to establish when in time and where in the brain modality and unique clips could be classified during encoding and retrieval, we then implemented the data fusion. For the data fusion, a second-order correlation has been computed between individual ROI RDMs and EEG RDMs at each time point to map the ROI representations on a timeline.

Inspecting the data fusion over both modalities, i.e. using video and audio trials (Fig. 1.7a), we found significant correlation clusters within visual regions at 188 ms, auditory regions at 203 ms, inferior parietal regions at 230 ms and superior parietal regions at 188 ms after clip onset ($p < .05$ (cluster)). Other peaks were found distributed over the encoding trial at a more liberal statistical threshold of $p < .01$ (uncorr.) (see Fig. 1.7a). Since we expected a sensory-specific to cross-modal information stream during encoding, we additionally analysed the ROI peak time differences of individual participants. First, a repeated measures ANOVA, using all five ROIs as within-subjects factor yielded an overall time difference between the regions that was marginally significant at a liberal statistical threshold ($F(4, 20) = 3.37$, $p = .01$). With a posthoc t-test we then compared the correlation peak times of visual regions against the peak times averaged across the cross-modal anterior temporal pole, inferior and superior parietal lobe. This contrast yielded that visual regions showed an earlier correlation peak within visual than cross-modal regions ($t(20) = -4.82$, $p < .0001$ (uncorr.)). Unexpectedly, auditory regions did not show an earlier peak than cross-modal regions ($t(20) = -0.29$, $p = .77$ (uncorr.)).

When looking at the fusion over video trials only (Fig. 1.7b), sensory-specific early visual and extrastriate regions show correlation peaks at 266 ms and 243 ms respectively ($p < .05$ (cluster)). Moreover, the inferior parietal lobe shows a significant correlation peak at 238 ms ($p < .05$ (cluster)). Other comparatively distributed peaks were found at a lower statistical threshold of $p < .01$ (see Fig.1.7b). A repeated measures ANOVA, using all six ROIs as within-subjects factor yielded no significant peak time differences between the ROIs ($F(5, 20) = 1.45$, $p = .21$). Further, performing a linear regression on the cumulative sums on the six ROI time courses at each time point (see Methods), we found non-significant slopes with values ranging between -$8*10^{-4}$ to $6*10^{-4}$ ($p > .01$ (uncorr.)). Sensory-specific and cross-modal regions thus seemed to activate around a similar time.

The data fusion over audio trials (Fig. 1.7c) did not reveal any significant clusters, but showed peaks at a liberal statistical threshold for inferior parietal lobe at 32 ms and anterior temporal pole at 600 ms and 918 ms after clip onset ($p < .01$(uncorr.)). The repeated measures ANOVA did not show a significant peak time difference between ROIs ($F(4, 20) = 0.36$, $p = .84$). A linear regression on the cumulative sums of the five ROI time courses did not yield a significant slope ($p > .01$ (uncorr.), ranging from $-1*10^{-3}$ to $2*10^{-3}$).

Summarizing the encoding data, the two fusion approaches within modalities, i.e. using only video or only audio trials, did not reveal any information stream across ROIs. However, the fusion over both modalities, i.e. using both video and audio trials replicates an information stream from sensory-specific visual to cross-modal regions confirmed by a contrasting t-test.

ROI fusion - retrieval

The same data fusion approach has then been applied to the retrieval data. Again we first performed a fusion over the trials of both modalities and then over video and audio trials separately. Importantly, in the retrieval data, we discarded all correlation peaks before 500 ms after word cue onset, respecting this time as processing period of the cue where no memory-related reactivation is thought to occur (Staresina & Wimber, 2019). Since our main hypotheses focused on retrieval, a more detailed description of correlation peaks within the retrieval data follows.

The fusion over both modalities, i.e. including both video and audio trials (Fig. 1.8a), only showed a significant cluster within visual regions at 613 ms s after cue onset ($p < .05$ (cluster)). Other peaks were found at a more liberal threshold within early visual regions at 1.84 s and 2.16s, auditory regions at 600 ms and 1.87 s, inferior parietal lobe at 600 ms, 1.84 s and 2.16s, and the superior parietal lobe at 630 ms after cue onset. As we had a specific hypothesis about the temporal order in which a modality-independent to sensory-specific reinstatement effects occur, we performed an additional repeated measures ANOVA on the individual correlation peak times with ROI as within-subject factor. This analysis did not show any significant differences in correlation peak times between the ROIs in terms of a main effect of ROI ($F(4, 20) = 0.76$, $p = .56$).

The fusion over video trials (Fig. 1.8b) only showed a significant correlation peak at 626 ms within extrastriate visual regions ($p < .05$ (cluster)). Interestingly, more peaks were found within a similar time frame at a lower statistical threshold. These peaks were seen in early visual regions at 540 and 600 ms, inferior temporal lobe at 630 ms, temporal pole at 550 and 630 ms, and inferior parietal lobe at 550 ms after cue onset (p < .01 (uncorr.)). Inferior parietal lobe showed another peak at 1 s (p < .01 (uncorr.)). After 2 s, several regions showed a reverberation of information (p < .01 (uncorr.); see Fig. 1.8b). The repeated measures ANOVA on the peak times did not yield a significant effect of ROIs (*F*(5, 20) = .34, *p* = .89). Performing a linear regression on the cumulative sums on the six ROI time courses at each time point, slopes were ranging between -10*10^{-4} to 2*10^{-4} and were not significantly different from zero (*p* > .01 (uncorr.)).

The fusion over audio trials (Fig. 1.8c) only showed peak correlations at a liberal threshold for A2 and A3 at 532 ms, temporal pole at 600 ms, and A1 at 690 ms, 1.42 s and 2 s after cue onset. None of these peaks survived the cluster correction. The repeated measures ANOVA on peak times did not yield a significant effect of ROI (*F*(4, 20) = .23, *p* = .93). Finally, also the linear regression on the cumulative sums of the five ROI time courses did not show a significant slope (*p* > .01 (uncorr.), ranging from -12*10^{-4} to 6*10^{-4}).

Summarizing the retrieval data, neither the ROI fusion over trials of both modalities, nor the fusion over individual modalities separately confirmed an information stream from cross-modal to sensory-specific regions. Instead, both cross-modal and sensory-specific regions descriptively reactivated for the first time within a similar time frame around 550 ms after cue onset. Interestingly, some sensory-specific regions descriptively showed reverberating later peaks (Fig. 1.8a-c).

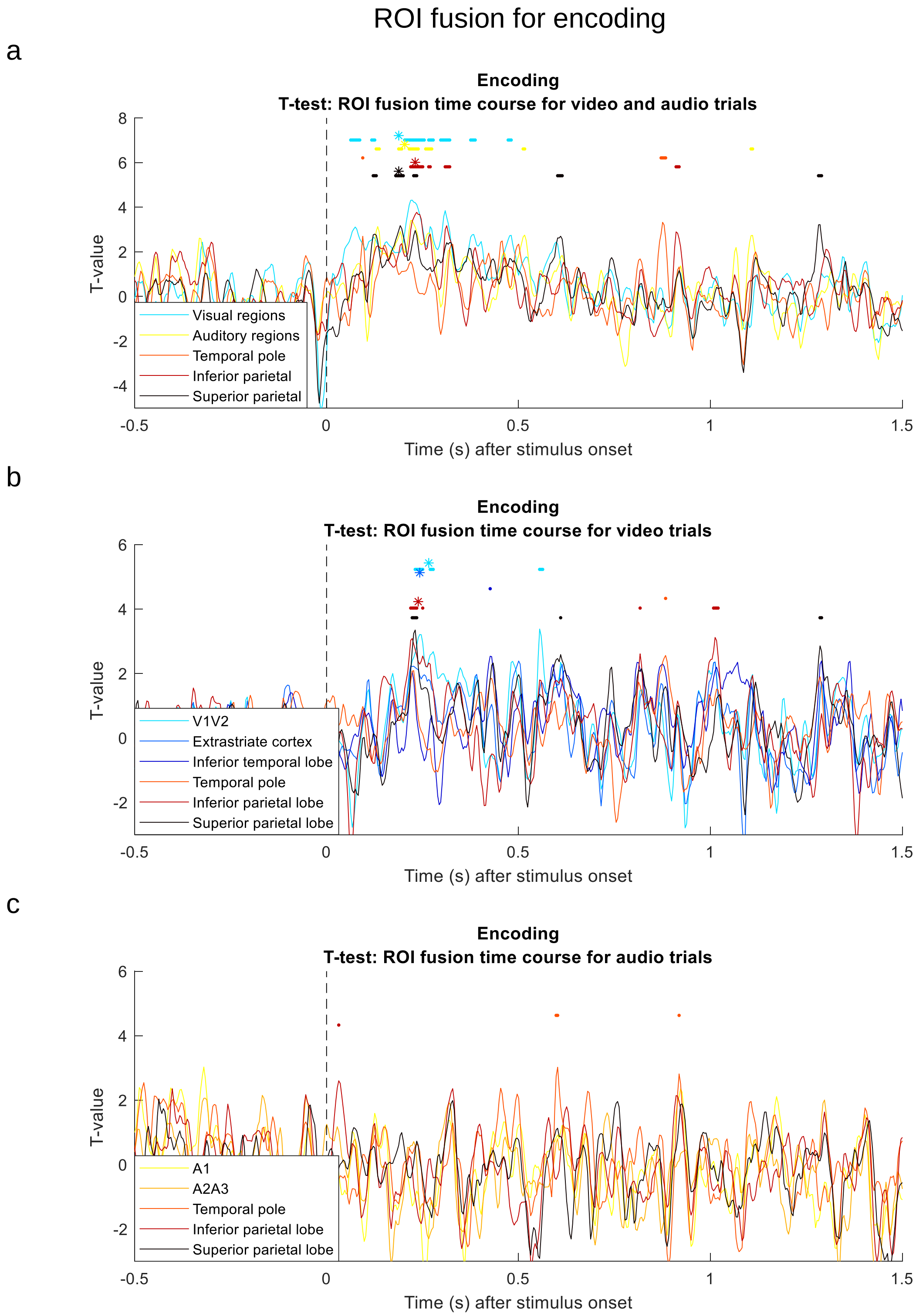

Figure 1. 7

Time courses of encoding ROI fusion in t-values for a) all trials, b) video trials, and c) audio trials. ROIs are colour-coded as indicated in legends. Time point 0 s marks clip onset, 3 s marks word onset. Significant decoding accuracy at individual time bins is indicated by points (p < .01 uncorrected) and asterisks (p < .05 cluster). See Methods for details on cluster correction. N = 21 independent subjects.

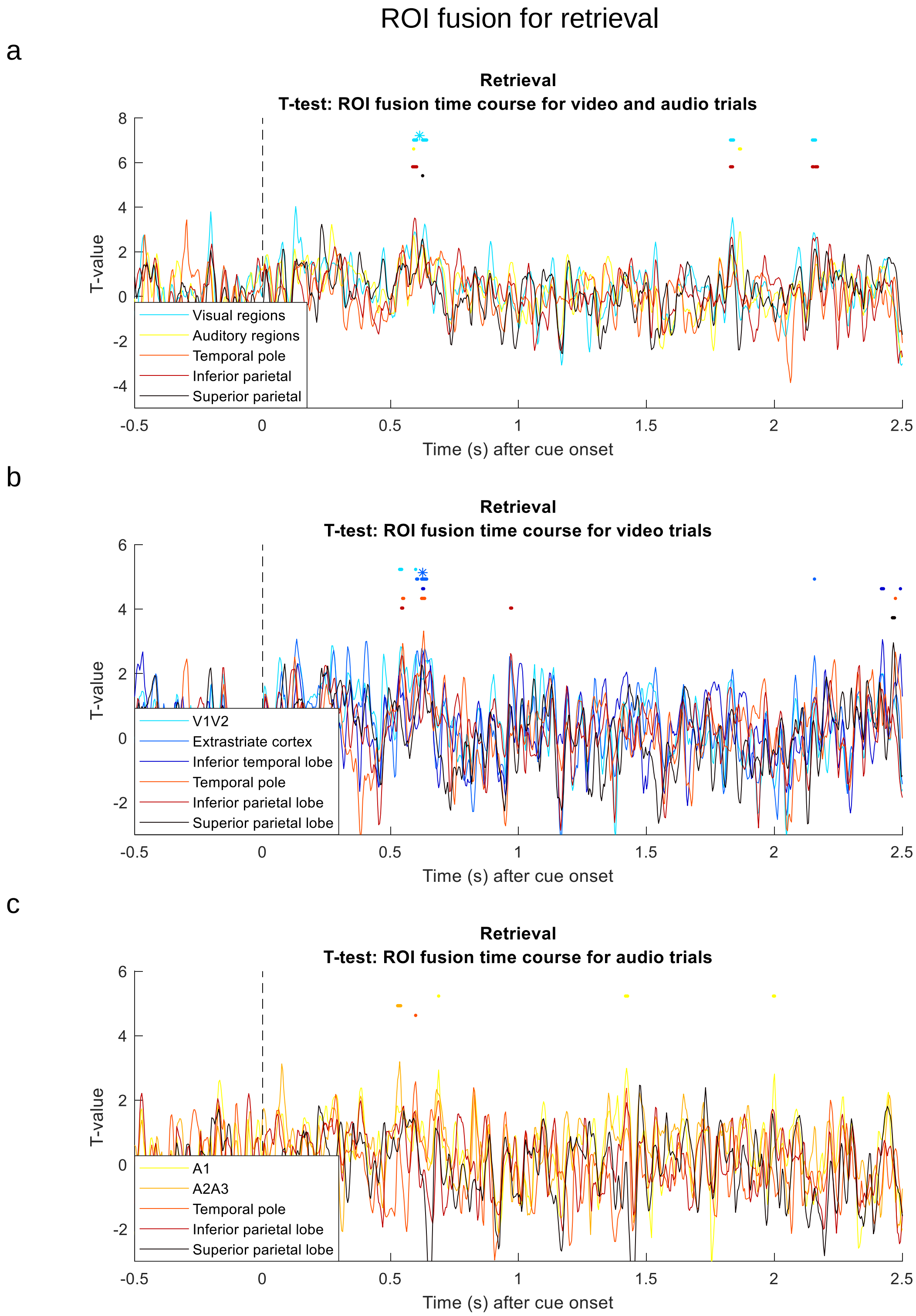

Figure 1. 8

Time courses of retrieval ROI fusion in t-values for a) all trials, b) video trials, and c) audio trials. ROIs are colour-coded as indicated in legends. Time point 0 s marks cue onset, 3 s marks clip choice. Significant decoding accuracy at individual time bins is indicated by points (p < .01 uncorrected) and asterisks (p < .05 cluster). See Methods for details on cluster correction. N = 21 independent subjects.

Searchlight fusion - encoding

The analyses above combined the EEG and fMRI data in a ROI-based fashion. Complementing these analyses targeted at pre-selected regions, we also used a whole-brain searchlight to reveal which regions in the brain correlated significantly with the similarity structure of a given time point (in the EEG). This approach essentially results in a statistically thresholded fusion movie.

Fusing EEG and fMRI data over both modalities within encoding (Fig. 1.9), we observed that high EEG-fMRI similarity started to evolve approximately 70 ms after stimulus onset in early visual and extrastriate regions. Within the next 100 ms information travelled further along the ventral visual stream, reaching fusiform gyrus und inferior temporal cortex. At 230 ms, superior temporal regions additionally showed significant EEG-fMRI similarity, with minor spread towards inferior parietal regions. After 300 ms similarity decreased in visual regions, and smaller clusters in fronto-parietal and medio-frontal areas appeared relatively late, around 490 ms. The encoding fusion thus shows the expected forward stream from posterior visual and auditory to more anterior temporal and parietal regions.

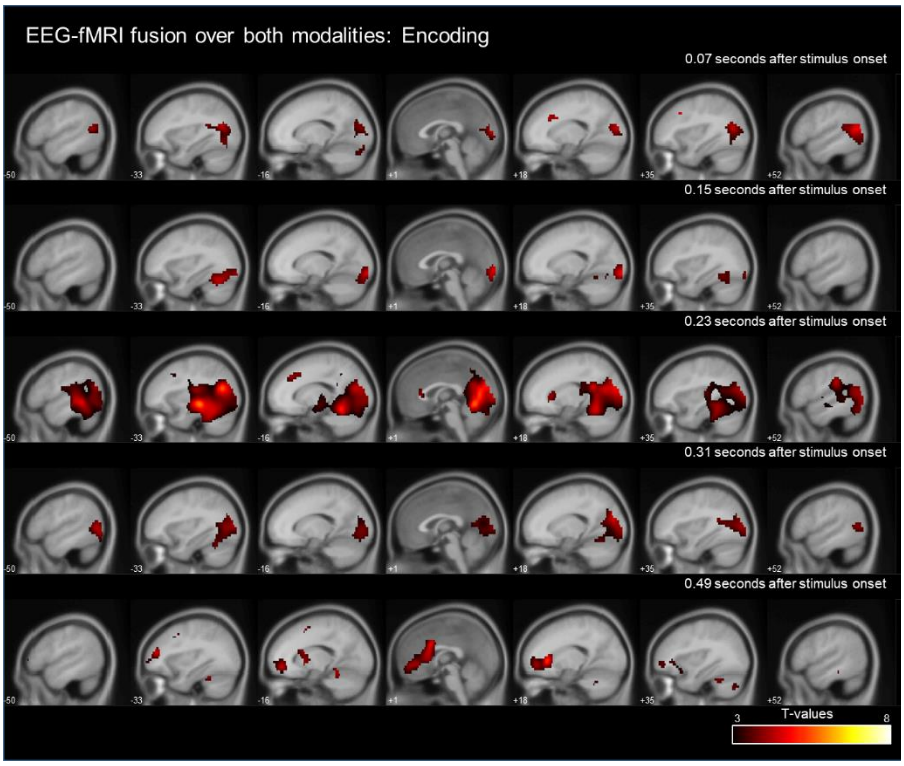

Figure 1. 9

T-maps of EEG-fMRI correlations at encoding, for both modalities together (i.e., full-matrix fusion), showing time points in the trial time course where significant spatial clusters (p < .05 cluster) emerged. See Methods for details on cluster correction. N = 21 independent subjects.

Searchlight fusion - retrieval

Again, the same searchlight-based fusion approach has been applied to the retrieval data. During retrieval, we expected reactivation-related clusters to emerge from approximately 500 ms following cue onset, and to evolve in a cross-modal to sensory-specific fashion. The EEG-fMRI fusion over both modalities (Fig. 1.10) within our TOI (> 500 ms) showed an early correlation cluster at 590-600 ms located in hippocampal and parahippocampal areas, and spreading over to medial prefrontal, inferior and superior temporal gyrus. A second correlation peak was then observed within the visual and inferior parietal cortex late, around 1.83 seconds after cue onset. Finally, at 2.79 s after cue onset, small parts of the superior, inferior, anterior and medial temporal cortex showed significant correlations with the EEG similarity structure.

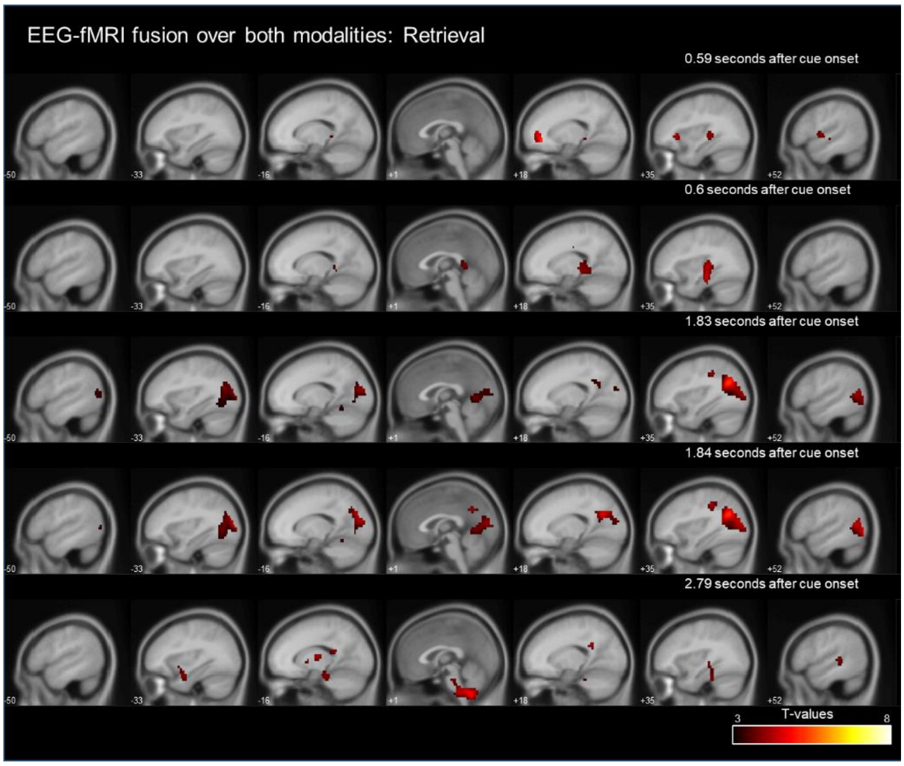

Figure 1. 10

T-maps of EEG-fMRI correlations at retrieval, for both modalities together (i.e., full-matrix fusion), showing time points in the trial time course where significant spatial clusters (p < .05 cluster) emerged. See Methods for details on cluster correction. N = 21 independent subjects.

To spatially resolve visual and auditory processing during retrieval separately, we conducted another data EEG-fMRI data fusion within each modality (Fig. 1.11). The analysis within the visual modality (i.e., video trials) revealed high correlations approximately 550 ms after cue onset in the visual cortex. Late clusters emerged in superior anterior temporal lobe at 2.42 s, and further inferior and medial temporal lobes at 2.78 s after cue onset. While the later clusters of sensory-specific correlations are consistent with the idea of a generic-to-detailed reactivation stream, we did not expect early time points to reflect video-specific activity patterns.

Looking at the audio trials only, we observed significant hippocampal, parahippocampal and superior temporal correlations around 600 to 690 ms. Later sensory-specific clusters were found in medial prefrontal and inferior, medial and anterior temporal areas at 1.43 s after cue onset, consistent with the later sensory-specific pattern observed in the visual modality (see above). Unexpectedly, inferior temporal areas along the ventral visual stream were also significantly correlated with the EEG structures later, at 1.54 s after cue onset, which might have been related to a visualisation of the auditory material.

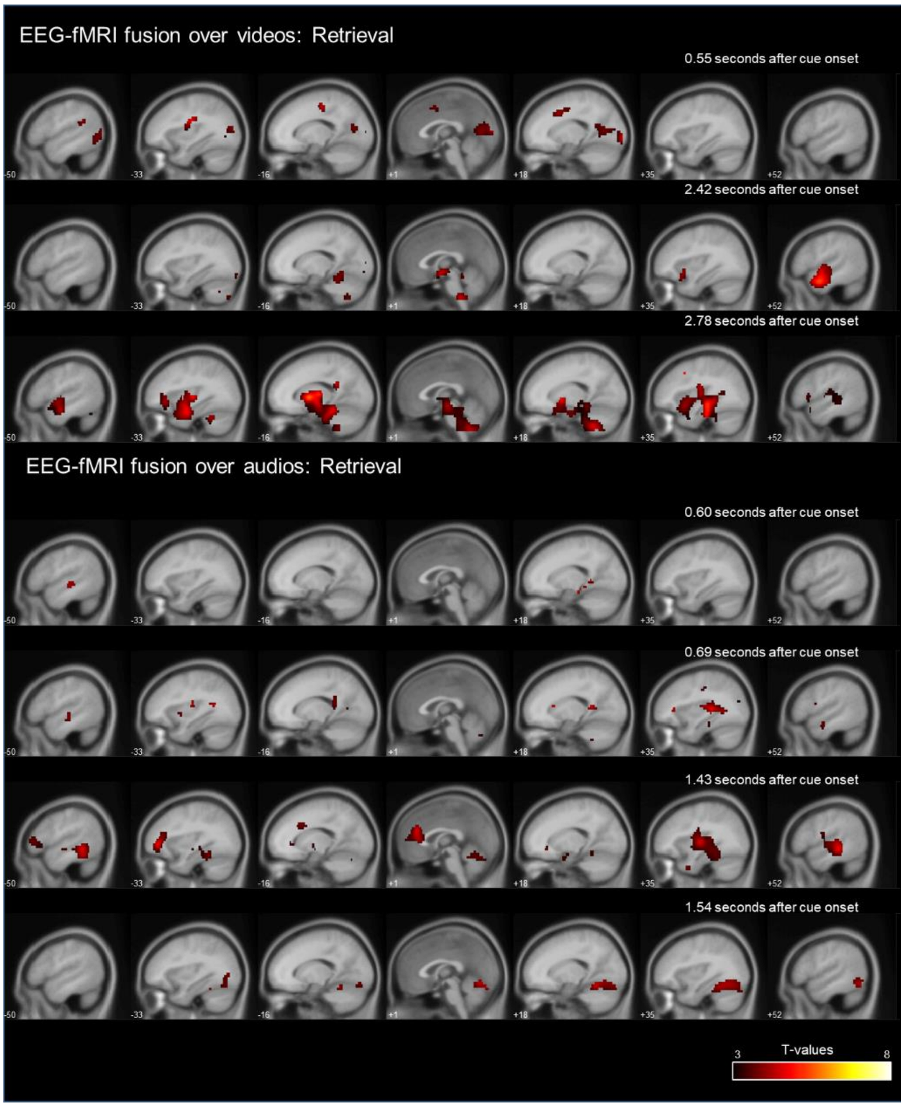

Figure 1. 11

T-maps of EEG-fMRI correlations at retrieval, for video and audio clips separately, showing time points in the trial time course where significant spatial clusters (p < .05 cluster) emerged. See Methods for details on cluster correction. N = 21 independent subjects.

Discussion

Neuroscientific research has demonstrated that auditory and visual perception follows a feedforward processing stream from sensory-specific to more abstract modality-independent information coding (T. Carlson et al., 2013; Cichy et al., 2014, 2016; Costanzo et al., 2013; Li et al., 2019; Lowe et al., 2020; Martin et al., 2018) and assumed that such a forward cascade feeds information to the hippocampus for the encoding of novel stimuli (Danker et al., 2017; Rolls, 2010). In comparison, our understanding of the spatio-temporal processes supporting the retrieval of memories from different modalities is still extremely limited. Here, using simultaneous EEG-fMRI recordings together with a multivariate fusion approach, we investigated the dynamic information processing cascade during the cued recall of short video and audio clips. We hypothesized that in contrast to the initial perception and encoding of these clips, the retrieval cascade progresses inversely from cross-modal to sensory-specific representations. Our findings offer insight into the dynamic neural representations supporting memory retrieval. Since our hypothesis were mainly based on the neural mechanisms of retrieval, we will mostly focus on the retrieval results in the discussion.

First, we replicated that during recall, spatial fMRI patterns represent audio- and video-unique processing, and these patterns are found in a subset of the regions involved in the initial perception of those stimuli (Fig. 1.5). Second, temporal EEG patterns show that during retrieval, generic modality information is established early around 550-600 ms, before clip-specific patterns are re-instated approximately half a second later (Fig. 1.6). Fusing the EEG and fMRI data in two different attempts, we find that the early processing of general modality information (Fig. 1.6b-c) is accompanied by simultaneous reactivation of both cross-modal and sensory-specific areas early in time

(Fig. 1.8), which stands opposed to our cross-modal to sensory-specific stream hypothesis. Further, episode specific features are represented in sensory specific areas at a relatively later time point (Fig. 1.6c, 1.8c). Finally, we show that the spatio-temporal information processing stream during retrieval generally progresses from medial temporal areas towards cross-modal and sensory-specific regions during retrieval (Fig. 1.10-1.11).

Using multivariate decoding analyses on regional voxel patterns of the fMRI data, we were able to offer insight into the spatial location of generic modality as well as clip-specific representations. The imaging data provides evidence for the reactivation of some brain regions already engaged during encoding on the one side, and showed additional regions during retrieval non-coinciding with encoding on the other side. Modality could be decoded from a set of sensory-specific regions. This set included areas in extrastriate to inferior temporal cortex along the ventral visual ('what') stream, presumably reflecting a reactivation of visual representations in those areas (Borowsky et al., 2007; Valyear et al., 2006). Additionally, modality information during retrieval could be decoded from superior temporal and insular cortex, likely representing auditory memories (Danker et al., 2017; Renier et al., 2009). Finally, voxel patterns in the hippocampus coded for modality, suggesting that this core region of the episodic memory network (Tulving & Markowitsch, 1998) recapitulates generic modality information during retrieval.

In comparison to the decoding of modality, the decoding of individual dynamic clips only succeeded at a liberal statistical threshold. Although we expected stronger classification accuracies, the data is in agreement with a substantial set of literature regarding the reactivation of encoding patterns, as described in the following paragraphs.

Individual video information could be decoded, during retrieval, in small parts of the inferior temporal lobe, a region representative of superordinate semantics (Cichy et al., 2014), which also coincides with the univariate finding showing higher activation of the same inferior temporal fraction for video than audio clips during retrieval. The found reactivation in the fusiform area also coincides with the previously reported encoding-retrieval similarity analysis on the same dataset (Griffiths, Mayhew, et al., 2019). Not surprisingly, the retrieval of the dynamic visual sceneries also elicited decodable activity patterns in the parahippocampal gyrus, which is commonly known to be central for the representation of visual scenery (Epstein & Kanwisher, 1998; Mormann et al., 2017). These findings show that as expected, individual video processing can be pinpointed to visual regions along the ventral stream.

In comparison, information about individual auditory clips was decoded in the insula, an area previously shown to process auditory stimulus identity (Renier et al., 2009; Danker et al., 2017), and to middle temporal lobe, which has been shown to be involved in controlled semantic retrieval (Davey et al., 2016). Additionally, the left inferior frontal gyrus was more engaged in individual auditory clip processing than the right inferior frontal gyrus, which stands contralateral to the encoding pattern. Similar left frontal representations have been found in the previously reported encoding-retrieval similarity results on the same dataset (Griffiths, Mayhew, et al., 2019). On the one hand these findings stand opposed to the hemispheric encoding/retrieval asymmetries that report a reversed lateralisation pattern (Habib et al., 2003; Nyberg et al., 1996). On the other hand, a lot of research also describes the role of the left inferior frontal gyrus in retrieval of contextual, conceptual and episodic information and auditory stimuli in particular (Badre et al., 2005; Badre & Wagner, 2007; Watanabe et al., 2008). Further, the left inferior temporal gyrus holds Broca's area (Keller et al., 2009), and its activation which could suggest the mental verbalization of the audio material during retrieval. Importantly, choosing a more liberal threshold at encoding and retrieval revealed bilateral involvement of the inferior frontal gyrus. Together, individual audio processing during retrieval could be related to the related to auditory regions also involved at encoding.

Even though the classification methods used here do not directly compare encoding to retrieval activity patterns, they provide evidence for similar information processing in overlapping brain locations between encoding and retrieval. Moreover, as indicated above, both the visual and auditory reactivation analysed here are complementary to and show consistency with previous encoding-retrieval similarity analyses on the same dataset (Griffiths, Mayhew, et al., 2019). The results also agree with previous literature on sensory-specific, retrieval related reinstatement (Danker & Anderson, 2010). Together, these mainly visual and auditory networks found during memory retrieval set the foundation for our next step of mapping the audio and visual mental representations of onto the dynamic EEG patterns.

On the electrophysiological level, multivariate classifiers enabled us to pinpoint the time points of maximum decodability of the retrieved contents, both on a gross (generic modality) and finer-grained (individual clips) scale. Specifically, we showed evidence for modality processing as early as 580 ms after cue onset, which was particularly prominent when using correct and incorrect trials, but also evident when using only correct trials. These peaks were followed by subsequent decoding peaks at approximately 1.6, 2, 2.5 and 2.8 s after cue onset. Individual video decoding based on the EEG patterns was not significant at any time point during retrieval. In contrast, individual audio content was decodable also around 1.1 s after cue onset. Importantly, the findings indicate that some, most likely modality-related, features of recalled memories are already represented in the brain around 550 ms after cue presentation, a time frame in line with previous findings that show reinstatement in the entorhinal cortex from 500 ms onwards (Staresina et al., 2019). Only about 500 ms later, specific individual clip representations evolve, but based on the EEG patterns alone these are only seen in the auditory domain.

By contrast, during encoding, we observed very early representation of modality that gradually increased within the first 100 ms and started to peak before the video-unique and the audio-unique decoding peak (Fig. 1.6a). The earlier decodability of modality is not surprising given the fact that visual and auditory information already enter the brain along completely separate routes, starting with the information relay from optical tract to lateral geniculate nucleus and auditory nerve to the cochlear nucleus respectively (Sefton et al., 2015; Malmierca, 2015). Interesting however is that individual videos and audio clips were maximally decodable at a relatively late processing stage, at which meaningful semantic processing is thought to take place (Cichy et al., 2014). This observation suggests that the decodability of individual clips might not be based on differences in low-level perceptual details, and that the neural representations distinguishing the specific content of the clips only emerged at a relatively late time point when meaning is assigned to these dynamic sensory clips. It is notable that within this experimental design, we cannot test which feature dimensions contribute to classification during encoding or retrieval, as there is no controlled manipulation along perceptual or any other dimension (see Chapter 3 for a study addressing this gap). Future studies should take particular manipulations of different hierarchical features into account, to properly decompose information processing along the sensory streams (Schyns et al., 2020). Nevertheless, we were able to show when in time information differentiating individual auditory and visual clips was represented in the brain during encoding, and at which time points we can expect recall dependent reinstatement to happen.

The core analysis in this study was the fusion of EEG and fMRI data. Computing second-order representational similarity analyses in ROI-based fashion, we were able to map the temporal information processing onto the distinct brain areas, revealing how content-specific representations in the two modalities dynamically unfold in the brain. To shortly sum up our findings on memory encoding, the ROI and searchlight fusion data give indications for a forward stream in the visual modality. Particularly, the ROI fusion over both modalities, i.e. including video and audio trials, replicated a sensory-specific to cross-modal information stream, which was supported by a contrasting t-test between visual versus cross-modal ROI peak time points (Fig. 1.7a). Moreover, the searchlight fusion showed information progress from early visual and early auditory to more frontal areas along their respective ventral stream (Fig. 1.9). Parietal areas and frontal areas were activated relatively late, all in line with the previously shown feed forward hierarchical processing cascades (Cichy et al., 2014; Costanzo et al., 2013; Li et al., 2019; Lowe et al., 2020). In the light of the EEG classification results, these results suggest at the very least that low-level perceptual features between modalities are processed before meaningful clip-unique ones, which is in line with earlier findings (Cichy et al., 2014; Costanzo et al., 2013; Li et al., 2019; Lowe et al., 2020). Future studies looking deeper into spatio-temporal information processes during perception and memory encoding or retrieval should work with explicit feature manipulations along different perceptual and or conceptual dimensions, to be able to relate the processing stages to the representational content.

Looking at the retrieval data, the ROI-based fusion over both modalities descriptively (i.e. at a low statistical threshold) suggests that first content-related reactivation patterns can be observed around 550 to 600 ms after cue onset, including cross-modal parietal areas as well as sensory-specific visual and auditory areas (Fig. 1.8). Based on the timing of the different ROI reactivations, our data does not convincingly support the idea of a general reinstatement transition from cross-modal to sensory-specific areas, as both type of regions descriptively showed an early reactivation between 550 and 600 ms after cue onset. This time frame is in concordance with the first modality classification peak within retrieval (Fig. 1.6b-c). In contrast, neither the individual video nor the individual audio clip can be decoded within this time frame. The data therefore suggests that the early reactivation is mainly informative of generic modality features but does not contain more specific characteristics of the individual clips.

In the ROI-based fusion over video trials only, sensory-specific visual and cross-modal ROIs descriptively showed a first early reactivation between 550 and 650 ms after cue onset. Together with the EEG-classification results, where we found significant modality decoding around the same time, but no clip-specific decoding, these findings suggests that early cross-modal and sensory-specific ROI activations possibly contribute to the generic modality representation of the retrieved clip, whereas no evidence was found for a contribution to visual episode-unique processing.

In the ROI-based fusion over audio trials, cross-modal parietal regions show no obvious correlation peak with the EEG structures at any time point. Instead, at an early time point between A2 and A3 showed descriptive peaks at 530 and temporal pole at 600 ms after cue onset, whereas at a late time point, around 1.4 s and 2 s, A1 showed a descriptive peak. This later timeframe at 1.4 s is close in time with the individual audio classification peak at 1.1 s after cue onset that was found based on the EEG data alone. This lets us assume that a late recapitulation of modality-specific content in sensory regions is required for the brain to retrieve the diagnostic features of unique episodic events.

Taken together, the ROI fusion (over modalities and audio clips in particular) shows that instead of a cross-modal to sensory-specific reactivation stream, we find something that looks more like a generic modality to clip-specific retrieval stream. Initial reactivations involving both cross-modal and sensory-specific networks support the global reinstatement of the modality of an episode, whereas later reactivations specifically in sensory-specific regions reinstate the within modality clip-specific details of the recalled events.

Inspecting the fusion data in a more explorative voxel-resolved searchlight approach for videos and audios separately, we found additional regions involved during retrieval, as well as a descriptive indication of a reversed retrieval flow. The data fusion including clips of both modalities, most likely dominated by generic modality information, showed that around 600 ms after cue onset, EEG-fMRI correlations evolved in the hippocampus and from there progressed towards temporal and parietal areas. Similarly, the fusion of over audio trials showed a progression from medial-temporal towards various lateral temporal regions. These data points indicate a feedback processing stream from hippocampal, medial temporal towards semantic and sensory regions. The data fusion over video trials showed no significant medial temporal match with EEG representations during early time points. Instead, and unexpectedly, visual areas became instantly reactivated around 550 ms after cue onset. Since previous literature has shown that medial temporal areas do reactivate from 500 ms onwards during retrieval, it is possible that our null finding in this time window is due to a lack of sensitivity for picking up these reinstatements in medial temporal areas (Staresina et al., 2019; Staresina & Wimber, 2019). Apart from this lack of early medial temporal reactivation during video processing, the majority of our present findings point to a feedback reconstructive retrieval stream, as previously suggested (Linde-Domingo et al., 2019; Lifanov et al., 2021).

We would like to note that we disregarded any information peaks within the first 500 ms of the retrieval data due to two reasons. First, previous work has consistently shown that visual stimulus processing elicits transient decodable activity strongest within the first 500 ms (Cichy et al., 2014), giving us reason to discard some of the initial processing time from making conclusion about the retrieval process. Further, the decoding of our EEG data indicates that representations of recalled clips only establish after 500 ms. We were therefore particularly interested into the time frame just after 500 ms to find the source of these distinctive recall related activity patterns, that drive the high classification accuracies in the previous analysis. Third, and as previously mentioned, current evidence shows that retrieval processes only start at about 500 ms after cue onset (Staresina et al., 2019), additionally justifying our choice of TOIs. However, early information peaks of several ROIs within the first 500 ms during retrieval do not go unnoticed. This information processing is likely to be attributed to the processing of the cue. As we expect similarities between cues within the dataset of an individual participant to be represented both within the EEG and the fMRI data, a rising EEG-fMRI correlation at the time of cue processing is not surprising. However, the expected reactivations related to retrieval were found in the previously described window of memory reactivation. And together, previous findings and the results from the EEG classification as well as the data fusion provide evidence for very early reinstatement processes in modality-independent and sensory-specific brain regions.

A disadvantage in the design of the present study is related to the locking of all time dynamics to the memory cue. While encoding processes are computationally straight forward, and at least the initial forward sweep along sensory processing pathways occurs with little temporal variance across trials, retrieval processes are additionally influenced by other factors. For instance, the timing and strength of retrieval-related reactivation can be affected by previous encoding strength (Lynch, 2004), contextual cues (Abernethy, 1940; Dulsky, 1935), emotional load (Bradley, 1994) and focused attention (Prull et al., 2016) during retrieval. Not surprisingly, any of these factors would lead to higher temporal variability in the retrieval compared to perception, as obvious for example in standard deviations of reaction time and EEG classification data (Linde-Domingo et al., 2019). For this reason, reinstatement processes may begin as early as 500 ms, but rates of progress from modality-independent to sensory-specific regions strongly differ between subjects and trials, which makes it hard to consistently detect meaningful information in the data fusion. One attempt to resolve this issue could be to analyse the data in a retrieval-locked fashion (Linde-Domingo et al., 2019), which was not possible within this task design, as there was no button press indicating the time point of subjective memory recollection.

Taken together, we were able to map modality-generic and clip-specific content representations during memory retrieval onto circumscribed brain areas and onto a neural timeline. Our results do not speak for a cross-modal to sensory-specific reconstruction stream. Instead, we showed that from 550 ms after cue onset, both cross-modal medial temporal and parietal regions and sensory-specific visual and auditory regions recapitulate information about the generic modality of the retrieved content, whereas later sensory-specific reactivations contain event-specific features. Finally, the exploration of multivariate similarity-based searchlight fusion suggests a (possibly recurrent) feedback reactivation cascade from hippocampal to sensory-specific regions, as opposed to the previously reported feed-forward trajectory during initial object recognition.

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Author contributions

B.G. and S.H. conducted the experiments. B.G. and J.L. preprocessed the data. J.L. analysed the data. B.G., S.H., I.C., and M.W. contributed to the analysis approach. J.L. wrote the first version of the chapter under the supervision of M.W. J.L. and M.W. contributed to reviewing and editing.

Competing interests

The authors declare no competing interests.

Chapter 3 - Reconstructing Spatio-Temporal Trajectories of Visual Episodic Memories in the Human Brain

At the time of thesis submission, this chapter represents preliminary analyses that are being prepared for publication and have been presented at the two conferences, SfN (San Diego, USA, 2018) and CCN (Berlin, Germany, 2019, https://doi.org/10.32470/CCN.2019.1156-0) (Julia Lifanov, Ben Griffiths, Juan Linde-Domingo, Catarina Ferreira, Martin Wilson, Stephen Mayhew, Ian Charest, & Maria Wimber; see section "Publications and presentations"). The CCN abstract was published (https://doi.org/10.32470/CCN.2019.1156-0; https://creativecommons.org/licenses/by/3.0/) and has been modified for reasons of consistency of the various chapters.

Abstract

During object perception, the neural representation of a stimulus becomes increasingly abstract as the information progresses along the visual processing hierarchy. Retrieving an object from episodic memory is known to involve the reactivation of the same neural patterns present during the earlier encoding of an event. However, our understanding of how information unfolds as it travels through the brain when we recall information from memory remains limited. In this project, we make use of a multivariate, similarity-based fusion of EEG and fMRI data to investigate the spatio-temporal trajectories of visual memories during retrieval. Participants studied new associations between objects and semantically unrelated verbs in an encoding phase, and subsequently recalled the objects upon presentation of the corresponding verb cue. Multivariate pattern analyses were used to track the processing of perceptual and conceptual object features from fMRI activation patterns. As expected, we found that conceptual features were generally represented at later, more semantic processing stages than perceptual features, and that the retrieval patterns were generally dominated by semantics. Classification-based similarity analyses then allowed us to map the EEG time courses onto spatial fMRI patterns, demonstrating that the visual processing stages were recapitulated during memory recall in a reversed fashion with respect to encoding. Finally, a backward conceptual-to-perceptual processing stream was also reflected in reaction times. Together, the results shed light onto the dynamic nature of mental representations during the reconstruction of visual objects from memory.

Introduction

In contrast to the large amount of scientific literature on visual perception, there are still large gaps in our knowledge about the neural processing flow during the recall of episodic memories. A number of recent neuroscientific studies suggests that during retrieval, information processing is reversed with respect to encoding (Linde-Domingo et al., 2019; Staresina & Wimber, 2019; Lifanov et al., 2021). However, the neural trajectories of information processing during retrieval are currently unknown. We here use a multivariate EEG-fMRI fusion approach to investigate whether the reversed information flow during visual recall can be mapped onto the ventral visual stream, reflecting a backward propagation from conceptual medial and ventrolateral temporal regions to more posterior visual-perceptual areas of the brain.

Vision research has decomposed the processes of visual perception to a detailed extent, providing a relative complete picture of what image features are coded at each step of a first feed-forward sweep of information processing. When light waves reflected from an object hit the retinal cells of our eyes, visual information is relayed to neocortex via the thalamus, and object information enters the ventral visual stream (Kolb et al., 1995). With activity propagating along this stream, stimulus information is represented along a gradient of increasing abstractness (T. Carlson et al., 2013; Martin et al., 2018). Neocortical analysis of a visual stimulus starts about 50-100 ms after stimulus onset in low-level visual areas, where perceptual appearance, such as colour and shape are processed (Cichy et al., 2014), and then progresses within the next 200 ms ventrally along the visual stream to more anterior temporal areas, where higher-level conceptual features are processed. This processing stage is related to the categorization of objects and the assignment of meaningful information (Cichy et al., 2014). Finally, the information reaches the hippocampus around 200-300 ms. In the hippocampus, at least some cells represent an object as a highly abstract and individual concept (Cichy et al., 2014; Quiroga, 2012). And most importantly, this final processing stage within the hippocampus binds information from different sources (including the dorsal stream) together and serves its longer-term storage (Danker et al., 2017; Horner et al., 2015; Rolls, 2010).

In contrast, little is known about the source and the presumed back-propagation of the internally generated information when visual memories are retrieved from episodic memory. Tulving's reinstatement hypothesis suggested that cueing a person with partial information of a previously stored episode would induce a so-called ecphoric process, in which a cascade of activity pattern reactivations leads to the subjective re-experience of the episodic memory (Tulving et al., 1983). Classical computational theories explain the origin of the reinstatement cascade by pattern completion in the hippocampus (Marr, 1971; O'Reilly & McClelland, 1994; O'Reilly & Norman, 2002). From this perspective, it is believed that the hippocampus dictates the reactivation of reciprocally connected neocortical brain regions that re-instate the various features of the relevant episodic memories (Teyler & Rudy, 2007; Marr, 1971; Moscovitch, 2008).

Anatomical research has laid some fundamental cornerstones for our understanding of the possible processing pathways involved in this reinstatement process. Once an original memory trace is partially reactivated by an internal or external cue, it is assumed that pattern completion is initiated in the CA3 region of the hippocampus. After additional processing of competing traces in CA1, most of the information is relayed over the subiculum to the deep layers of the entorhinal cortex which in turn has back-projections to other cortical areas (Chrobak et al., 2000; Rolls, 2013; Staresina &

Wimber, 2019). The described pathway provides the gateway for a possible retrieval-related reconstruction flow from the hippocampus that indexes the relevant memory trace to the reinstating cortical structures that complete the content of the episodic memory representation. Since a majority of direct hippocampal and entorhinal efferents end in late visual areas, the idea evolves that memories are initially reinstated on a conceptual level, before low-level areas could be reached (Insausti & Muñoz, 2001; Linde-Domingo et al., 2019).

Cortical reinstatement during retrieval has been explored by various neuroimaging studies using multivariate analyses approaches, often assessing the similarity of activation patterns between encoding and retrieval (Danker & Anderson, 2010; Rissman & Wagner, 2012). Using this method, numerous studies could show that successful retrieval is associated with the interplay of hippocampal activity and cortical reinstatement of encoding patterns during retrieval (Bosch et al., 2014; Horner et al., 2015; Staresina et al., 2012). These findings support both the dictating role of the hippocampus and the representative role of cortical structures in memory retrieval.

Reinstatement patterns during retrieval have been discovered in perirhinal and parahippocampal regions (Staresina et al., 2012), some of the most proximal cortical structures to the hippocampus. In theory, this would speak for the fact that the ecphoric process, presumably starting in the hippocampus, first progresses towards its surrounding cortices. From there, activation could be spread to more distanced cortical regions along anatomical connections. In line with this assumption, neocortical encoding-retrieval similarity has been found for categorical content (like faces, objects and scenes) (Polyn et al., 2005) and individual episodes (Wing et al., 2014).

However, few studies have decomposed what features of an item dominate these reinstated representations during retrieval. One exemplar study, using decoding methods based on neural networks, uncovered hierarchical representational structures from fMRI activity patterns (Bone et al., 2020). The study demonstrated that high- and low-level features throughout the ventral and dorsal streams, and in frontal and parietal areas, all contribute to the vividness of memory recall. Another study decomposed hierarchical memory representations using a classification approach on EEG data to specifically decode perceptual and conceptual information representations from temporally resolved neural activity patterns (Linde-Domingo et al., 2019). During retrieval, perceptual information was decoded later in time than conceptual information, while the opposite pattern was found during visual perception, speaking in favour of the reversed information processing hypothesis. Supporting these neural findings on a behavioural level, two recent studies demonstrated that when participants recalled previously encoded visual objects, they answered conceptual questions faster than perceptual ones, while the opposite was found when participants perceived a new image on screen (Linde-Domingo et al., 2019; Lifanov et al., 2021). Together the results give reason to assume a retrieval-induced feedback propagation along the ventral visual stream.

The latter studies (Linde-Domingo et al., 2019; Lifanov et al., 2021) suggest a reversed information processing during retrieval, first reactivating core concepts and then reinstating sensory details. However, they do not provide any insight on the retrieval-related spatial trajectories of information flow within the brain. Contrary, the previously mentioned study by Bone et al. (2020) offers insight into spatial representations along the ventral visual stream during retrieval but does not provide information about the temporal progression of reinstatement.

To fill this knowledge gap and reveal the spatio-temporal neural processes during retrieval, we here investigated which stimulus features are represented during retrieval, that is, when the relevant representations evolve in time and where in the brain. We used a combination of EEG and fMRI in order to map the feature reinstatement to the presumed back-propagation stream, and specifically to see whether information indeed flows backwards to where it originated from, or whether retrieved content emerges from different brain areas. The findings described above led us to propose our central working hypothesis that the retrieval process propagates backwards along the ventral visual stream, starting with early representations of conceptual information in medial temporal and ventrolateral temporal regions before moving on to low-level visual areas representing perceptual details. However, much recent work suggests that mnemonic content can primarily be decoded from parietal lobe areas (Favila et al., 2020), and we were thus additionally interested in whether these parietal representations map onto early or late processing stages of the retrieval stream.

To test these research hypotheses, we based our work on the memory paradigm developed by Linde-Domingo et al. (2019). Participants first encoded novel associations between objects and action verbs, and at a later recall stage were asked to retrieve the objects upon the presentation of the verb. Importantly, object images varied along a perceptual (photographs versus line drawings) and a conceptual (animate versus inanimate) dimension, and participants had to answer either a perceptual (Was the object a photograph/line drawing?) or conceptual (Was the object animate/inanimate?) question after each recall. Using this paradigm in an fMRI environment, we aimed at pinpointing the retrieval-related reinstatement of different object features in the brain. To locate the perceptual and conceptual representations, we used a searchlight classification approach. The aim was then to map spatial representations onto a timeline on a trial-by-trial basis within subjects, using a simultaneous EEG-fMRI data acquisition. Since the within-scanner data was too noisy to decode the relevant object features, we instead used previously acquired out-of-scanner EEG data (Linde-Domingo et al., 2019) to map the spatial representations onto the memory reconstruction timeline. This was done by means of an EEG-fMRI data fusion, using a second-order representational similarity analysis (RSA).

Methods

Participants

We acquired fMRI data of 37 right-handed, fluent English-speaking participants of the local student population at the University of Birmingham (26 females, 11 males, mean age (M_{age}) = 23.33, standard deviation (SD_{age}) = 3.89, one participant did not indicate the age). The a priori planned sample size for the full EEG-fMRI dataset was n = 24 subjects. However, due to poor data quality and technical failures in 13 of the EEG datasets, additional subjects were recorded leading to a final sample size of 37 fMRI datasets. Three subjects were excluded from the fMRI analysis due to failed scanning sequences, and three additional subjects were excluded due to extensive motion within the scanner, exceeding the functional voxel size, such that 31 fMRI datasets remained for analysis.

All participants were informed about the experimental procedure, underwent imaging safety screening and signed an informed consent. The research was approved by the by the STEM ethics committee of the University of Birmingham.

We further included a previously published EEG dataset including a nearly identical paradigm (Linde-Domingo et al., 2019) in our data analyses. This additional dataset included 24 further participants with a clean, out-of-scanner EEG. For further information on the EEG data sample and the related ethical procedures, we refer to the previous work (Linde-Domingo et al., 2019).

Material

The paradigm was a visual verb-object association task (Linde-Domingo et al., 2019) adapted for fMRI measurements. We used visual stimuli including 128 action verbs and 128 pictures of everyday objects (for more detailed information about the source of the verbs and pictures see (BOSS database; Brodeur et al., 2010; Linde-Domingo et al., 2019; www.gimp.org). Importantly, all object images existed in two perceptual versions, a black line drawing or a coloured photograph (perceptual categories); and each object belonged to one of two conceptual classes, i.e. animate vs inanimate (conceptual categories). We drew 128 images per participant according to a fully balanced scheme, such that each combination of perceptual and conceptual categories included the same number of pictures (32 animate-photographs, 32 animate-drawings, 32 inanimate-photographs, 32 inanimate-drawings; Fig. 2.1a). With respect to the later fusion with the out-of-scanner EEG data, it is important to note that due to the pseudo-randomised image drawing, the same objects could appear in different perceptually manipulated versions between participants; for example, an image of a camel could be shown as a photograph to one participant, and as a line drawing to another. Action verbs were randomly assigned to images in each participant and were presented together with pictures centrally overlaid on a white background.

Procedure

Before the experimental session, participants were informed about the experimental procedure and asked to perform a training task block in front of the computer. After the completion of the training, the experimental session in the fMRI scanner included four runs with four task blocks each, summing up to a total of 16 task blocks. A typical block in the training and experimental task included eight association trials, a 20 s distractor task and 16 retrieval trials (two repetitions per association). A 3 min break was included after each fMRI run, in which participants were asked to close their eyes and have some rest. In total, it took the participants approximately 70 min to perform the entire task.

Encoding

In the encoding blocks (Fig. 2.1b), participants were instructed to study eight novel verb-object pairings in random order. A trial started with a fixation cross presented to the participants for a jittered period between 500 and 1500 ms. The action verb was presented for 500 ms before an object was shown for a maximum duration of 5 s. To facilitate learning, participants were instructed to form a vivid visual mental image using the verb-object pairing. Upon the formation of a strong mental image, participants were asked to press a button with their thumb, which moved the presentation onto the next trial.

Distractor

After each encoding block, participants performed a self-paced distractor task for 20 s, indicating as fast as possible whether each of the consecutively presented numbers on the screen was odd or even, using a button press with their index or middle finger, respectively. Feedback on the percentage of correct responses was provided at the end of each distractor phase.

Retrieval

In the retrieval blocks, participants were instructed to recall the previously associated objects upon presentation of the corresponding verb (Fig. 2.1b). Trials started with the presentation of a fixation cross, jittered between 500 and 1500 ms and followed by a previously encoded action verb, presented for 500 ms. Cued with the verb, participants had to recall the paired object within a maximum of 5 s, while a black fixation cross was presented on screen. Participants were asked to indicate with a button press by their thumb the time point when they recalled the corresponding image, at which the black fixation cross turned grey and was presented for an additional 3 s. This retrieval button press was meant to mark the time point of subjective recollection. During the remaining 3 s participants were asked to hold the mental image of the object in mind as vividly as possible. Last, they were asked about the perceptual (Was the object a photograph or a line drawing?) or the conceptual features (Was the object animate or inanimate?) of the recalled object, answering with their index or middle finger with a maximum response time of 5 s. During the presentation of the catch question, participants also had the option to indicate with their ring finger that they forgot the features of corresponding object. Importantly, each encoded stimulus was retrieved twice, once with a perceptual and once with a conceptual question. Trial order was pseudo-random within the first and second set of repetitions, with a minimum of two intervening trials before a specific object was recalled for the second time. The order of catch questions was counterbalanced across repetitions such that half of the associations were first probed with a perceptual question, and the other half was first probed with a conceptual question.

Paradigm

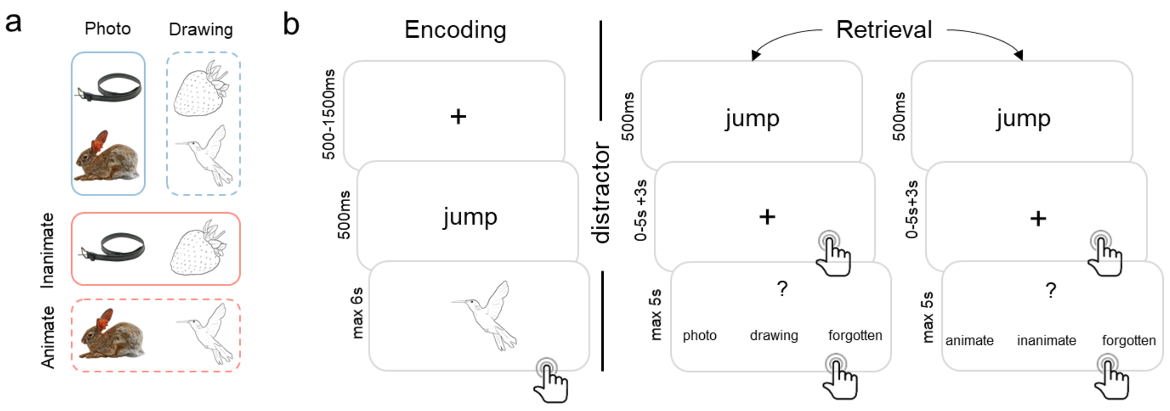

Figure 2. 1

Overview of stimuli and task. A) Design of the stimuli. The 128 pictures used in any given participant were orthogonally split into 64 drawings and 64 photographs, out of which 32 were animate and 32 inanimate objects, respectively. Each object could thus be classified along a perceptual (photo/drawing, blue) or conceptual (animate-inanimate, red) dimension. B) One prototypical task block of the paradigm. At encoding, participants were asked to associate verb-object pairings, and indicate the successful formation of an association by button press. After a 20 s distractor task, each of the associations was tested twice during retrieval, once with a perceptual, once with a conceptual question. Participants recalled the previously associated object upon presentation of a verb cue and indicated successful subjective recollection by button press (referred to as retrieval button press). Then participants were asked to hold the mental image of the object in mind for three further seconds, before answering a perceptual or conceptual catch question about the object. Participants performed 16 task blocks overall, with eight associations per block. Reaction times (RTs) were measured at each button press. Stimuli depicted are chosen from the BOSS database (https://sites.google.com/site/bosstimuli/home, https://creativecommons.org/licenses/by-sa/3.0/) and customized with free and open source GNU image manipulation software (www.gimp.org; see Linde-Domingo et al., 2019). Figure adapted from Lifanov et al. (2021) and Linde-Domingo et al. (2019).

fMRI data acquisition

FMRI scanning was performed in a high-field 3 Tesla Philips Achieva MRI scanner with a 32-channel sense head coil at the Birmingham University Imaging Centre (BUIC) in Birmingham. Slices covered the whole head. T1- weighted anatomical scans were collected with an MP-RAGE sequence (1 mm isotropic, 256 x 256 matrix, 176 slices, no inter-slice gap, repetition time (TR) = 7.5 ms, field of view (FOV) = 256 x 256 x 176 mm, flip angle (FA) = 7°, echo time (TE) = 3.5 ms). T2*-weighted functional images were acquired by a dual-echo EPI pulse sequence with a low specific absorption rate (SAR) to optimize the image quality in regions highly susceptible for distortions by a long readout gradient (3 x 3 x 3.5 mm, 64 x 64 matrix, 34 slices, no inter-slice gap, TR = 2.2 s, full head coverage, FOV = 192 x 192 x 119 mm, FA = 80°, TE1 = 12 ms, TE2 = 34 ms (for dual-echo information see also (Halai et al., 2014, 2015; Kirilina et al., 2016). Slices were acquired in a continuous descending fashion. Furthermore, we collected 200 resting state volumes, 50 after each of the four task runs, used for the later combining of images with the short and long TEs. During the acquisition of scans, the helium pump was switched off to prevent contamination of the EEG by the compressor artifact at about 20-30 Hz. The scans were acquired in a jittered fashion in relation to the stimulus timings. The task was presented to participants through a mirror system in the scanner and a JVC SX 21e projector with resolution 1280x1024 at 60 Hz. The participants´ heads were extra padded to minimize movement artefacts. The stimulus presentation and timing and accuracy information collection was controlled by scripts written in MATLAB 2016a (www.mathworks.com) and Psychophysics Toolbox Version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Responses were logged by NATA response boxes (https://natatech.com/).

Out-of-scanner EEG data acquisition

As previously stated, a simultaneous EEG dataset was acquired during the fMRI session but this EEG dataset was too noisy to decode retrieval-related information. We therefore decided to use an out-of-scanner EEG dataset. This out-of-scanner data used for all analyses reported here originated from a previous publication (Linde-Domingo et al., 2019). We give a short description of the EEG data acquisition in the following and of the EEG preprocessing further below.

For the EEG data collection, 128 electrodes of silver metal and silver chloride were used. Further, an Active-Two amplifier system and the ActiView acquisition program by BioSemi aided the data recording (BioSemi, Amsterdam, the Netherlands). Psychophysics Toolbox Version 3 and MATLAB 2014b (www.mathworks.com) were used for task presentation and response collection. For more specific details about the EEG data acquisition, we refer to the related manuscript and the corresponding author (Linde-Domingo et al., 2019).

Analysis

Behaviour

For the inspection of RTs and accuracies, the behavioural data were preprocessed as follows. For the RT analysis, all trials with incorrect responses to the catch question were removed first. Additionally, catch question RTs of correct trials were removed if they were faster than 200 ms or exceeding the average RT of a participant in a given set of repetitions (first or second cycle) by more than three times the standard deviation. For the analysis of the accuracy data, trials faster than 200 ms and objects with a missing response for either of the two questions were excluded in the corresponding cycle. The same procedures were applied to the data of the out-of-scanner EEG participants, who performed a nearly identical task. However, note that out-of-scanner EEG participants only went through one cycle of retrieval.

FMRI data preprocessing

We used MATLAB 2016a (www.mathworks.com) and SPM12 (*Statistical Parametric Mapping*, 2007; http://store.elsevier.com/product.jsp?isbn=9780123725608) for the preprocessing and the univariate analysis of fMRI data. All functional images were first realigned based on three motion and three rotation parameters, unwarped, and slice time corrected to the middle slice in time.

After these initial preprocessing steps, images obtained during the task at two echo times were combined as a weighted average. Importantly, the relative weights were obtained from the signal-to-noise ratio (SNR) of 200 resting state volumes per echo and its corresponding *TE*

$$w(CNR)_n = \frac{SNR_n{}^*TE_n}{\sum_n SNR_n{}^*TE_n} \qquad (1)$$

where *w* is the weight for an individual voxel, $SNR_n$is the signal to noise ratio here calculated as ratio of mean to standard deviation of the given voxel calculated over time at the *n*th echo, and *TE* is the readout time of the *n*th echo.

Weights obtained from the resting state were then used to combine task volumes from both echoes

$$S = w_1{}^*S_1 + w_2{}^*S_2 \qquad (2)$$

where S is the final signal of an individual voxel over time, calculated by summing the weighted signals of both echoes. These methods and equations were applied as described in work on BOLD contrast optimization by multi-echo sequences (Poser et al., 2006). Combined image structures were written to NIFTI files by Tools for NIfTI and ANALYZE image (https://uk.mathworks.com/matlabcentral/fileexchange/8797-tools-for-nifti-and-analyze-image by Shen, 2021; Tools for NIfTI and ANALYZE Image, n.d.).

Anatomical images were segmented, co-registered with the functional images and normalized into a standard MNI template in SPM. Then, after the combination of functional images, the T2* images were also normalized into MNI space, using the T1-based normalization parameters. Finally, EPI images were smoothed for the univariate GLM analysis with a gaussian spatial filter of 8 mm full width at half maximum (FWHM). Note that multivariate analyses were performed on unsmoothed data in native space.

ROIs

ROIs were created from templates in MNI space as available in the WFU PickAtlas (Maldjian et al., 2003, 2004; Tzourio-Mazoyer et al., 2002). These ROIs were then fitted to individual brains by applying inverted normalization parameters to the ROI masks. The anatomical masks used for our analyses included: an early visual mask, consisting of Brodmann areas (BAs ; Brodmann, 1909) 17 and 18, an human inferior temporal (hIT) mask, consisting of BAs 19 and 37; a temporal pole mask, consisting of superior and middle temporal pole regions as defined by automated anatomical labelling (AAL, Tzourio-Mazoyer et al., 2002); an MTL mask, consisting of BAs 28, 34, 35, 36 and AAL rhinal sulcus and parahippocampal gyrus; a hippocampus mask, as defined by AAL; a superior parietal lobe mask, consisting of BA 7; an inferior parietal lobe mask (Wernicke's area), consisting of BA 39 and 40; and another inferior parietal lobe mask (retrosplenial cortex) consisting of BA 29 and 30.

EEG data preprocessing

EEG data (Linde-Domingo et al., 2019) were preprocessed in MATLAB 2016a (www.mathworks.com) and Fieldtrip toolbox (Oostenveld et al., 2010; Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, the Netherlands. See http://www.ru.nl/neuroimaging/fieldtrip). During epoching, we used different temporal references for encoding and retrieval. Encoding epochs were stimulus locked to the onset of the object image, while retrieval timelines were locked to the subjective retrieval button press, in order to observe the reactivation stream leading up to the subjective experience of recollection. These epochs were created with a length of 2 s (-500 before to 1500 ms after object onset) for encoding and 4.5 s (-4 s before to 500 ms after retrieval button press) for retrieval. Line noise was removed by a FIR filter with a band-stop between 48 and 52 Hz. A high-pass filter with a cut-off frequency of 0.1 Hz was applied to remove slow temporal drifts, and a low-pass filter with a cut-off frequency of 100 Hz to remove high-frequency noise. Individual artifactual trials and bad electrodes were rejected manually. Remaining artifacts were removed by independent component analysis (ICA), after which any excluded electrodes were re-introduced by interpolation. The referencing of the data was set to the average across all scalp channels.

After this step, we implemented additional preprocessing steps to prepare data for the specific fusion analyses. The encoding data was baseline corrected by subtracting the average signal in pre-stimulus period from -0.2 to -0.1 s, separately per electrode. The retrieval data was baseline corrected by whole trial demeaning, since retrieval trials had no obvious, uncontaminated baseline period. The EEG time series data was then down-sampled to 128 Hz and temporally smoothed with a moving average with a time window of 40 ms.

fMRI univariate analyses

To investigate broad activations in the ventral visual stream, we modelled a GLM using the four main regressors (drawing-animate, photograph-animate, drawing-inanimate, and photograph-inanimate), independently for encoding, first retrieval, and second retrieval. We used stick functions locked to the object onset to model the onset of encoding trials and boxcar functions with a duration of 2.5 s locked to the cue onset to model the onset of retrieval trials. We added one regressor each for the presentation of verbs, button presses, and perceptual and conceptual questions as well as nuisance regressors for head motion, scanner drift and run means. After computing the GLM for each subject, a second sample-level ANOVA with the perceptual (photograph versus line drawing) and conceptual (animate versus inanimate) within-subjects factors was performed. Planned comparisons contrasting photographs versus drawings, and animate versus inanimate objects, were carried out in subsequent t-contrasts separately at encoding and retrieval. The t-contrasts for retrieval trials were performed using both the first and second retrieval trials together.

fMRI multivariate analyses

As preparation for the multivariate analyses, we performed another GLM, modelling individual object-specific regressors for encoding, and for each of the two retrieval repetitions separately (see above for details), again adding regressors of no interest for the presentation of verbs, button presses, and catch question onsets, as well as nuisance regressors (see above, one regressor per variable containing all onsets). The resulting beta weights were transformed into t-values for all subsequent multivariate analyses (Misaki et al., 2010).

fMRI searchlight LDA

To investigate where in the brain activity patterns differentiated between the two perceptual and the two conceptual categories, we performed a volumetric LDA searchlight analysis on the non-normalized and unsmoothed fMRI data of each participant individually using the searchlight function of the RSA toolbox (Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013; https://www.mrc-cbu.cam.ac.uk/methods-and-resources/toolboxes/). The LDA was performed at each centre voxel, while object-specific t-values of the voxels within a 3D searchlight radius of 12 mm were used as feature vectors. Using these feature vectors, we classified perceptual (photo vs drawing) and conceptual (animate vs inanimate) categories by a 5-fold LDA with 5 repetitions, preserving class proportions, for encoding and retrieval separately using the MVPA-Light toolbox (Treder, 2020; https://github.com/treder/MVPA-Light). Individual accuracy maps were then normalized to MNI space and spatially smoothed with a 10 mm full width at half maximum (FWHM) Gaussian Kernel, before second-level t-tests were performed to statistically compare voxel-specific classification accuracies against 50% chance performance. Finally, the results were plotted on an MNI surface template brain.

fMRI correlation-based RSA

As preparation for the fusion of EEG and fMRI data, we performed a representational similarity analysis (RSA, Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013; https://www.mrc-cbu.cam.ac.uk/methods-and-resources/toolboxes/) on the non-normalized and unsmoothed fMRI data. Object-specific t-maps corresponding to single objects were arranged in the same order for all participants. As mentioned earlier, object correspondence across participants was only given on the level of object identity (and thus also conceptual category), but not perceptual format. In other words, all participants saw an image of a camel (i.e. an animate object) at some point in the experiment, but the camel could be presented as a photograph in some participants, and as a line drawing in others. For each voxel and its surrounding neighbours within a radius of 12 mm, we extracted object-specific t-value patterns resulting from the appropriate GLM and arranged these as one-dimensional feature vectors. Using these feature vectors, we calculated the Pearson correlation distance (1-*r*) between each pair of objects at each voxel location, separately for encoding and retrieval. The resulting RDM maps were used at a later stage for the searchlight fusion.

In a similar fashion to the searchlight approach, RDMs were also calculated for the pre-defined set of anatomical regions of interest in the non-normalized and unsmoothed individual functional datasets (see section ROIs). The resulting ROI RDMs were used at a later stage for the ROI fusion.

EEG multivariate analyses

EEG cross-subjects classifier-based RSA

Our next step was to construct a representational dissimilarity matrix (RDM) for each time point of the EEG recordings, resulting in one timeline representing the similarity structure of our object dataset across all subjects. Cells of the RDM represented the pair-wise discriminability of object pairs, based on a cross-subjects classification of individual objects using the MVPA-Light toolbox (Treder, 2020; https://github.com/treder/MVPA-Light). To compute this matrix, we arranged object-specific trials in the same order between all participants, independent of their perceptual format, and the 24 repetitions of each individual object across participants were used for the pairwise classification. Specifically, we performed a time-resolved LDA using EEG amplitude values from the 128 electrodes, at a given time bin, as feature vectors, and participants as repetitions of the same object. We used these to classify object identity among each pair of objects at each time bin, again with a 5-fold cross validation, preserving class proportions. The resulting discrimination accuracies were entered in a single time resolved RDM structure representing the dissimilarity between individual objects of our stimulus pool across participants over time. This classification procedure was performed independently for encoding and retrieval.

Before using the EEG-based RDMs for our data fusion, we also wanted to assess statistically how much information about object identity can be decoded from the EEG signals themselves. We therefore first calculated the average classification performance across all pairwise accuracies as a descriptive measure. We then tested if the pairwise accuracies resulting from the ‘real’ classification with correct object labels were significantly larger than the pairwise accuracies that resulted from a classification with permuted object labels. This test was performed in two steps. First, we created 25 classification-based RDMs (same classification procedure as for the ‘real’ RDM time course) but each one with randomly permuted object labels, keeping a given label permutation consistent across time in order to preserve the autocorrelation of the EEG time series. The 25 permutations were averaged to form a single ‘baseline’ RDM time course.

As a second step, we used a cluster-based permutation test to find clusters with temporally extended above-chance decoding accuracy. This cluster-based permutation test compared the t-statistic of each time point evolving from a ‘real matrix’ versus ‘baseline matrix’ t-test with the t-statistics evolving from a ‘real matrix’ versus ‘baseline matrix’ comparison this time shuffling the corresponding ‘real’ and ‘baseline’ cells between the two matrices (again consistent across time, 1000 permutations, cluster-definition threshold of $p < .05$, as used in previous publications (Cichy et al., 2019; Cichy & Pantazis, 2017; Dobs et al., 2019). Note that the variance in the t-tests for each time bin comes from the pair-wise accuracies contained in the cells of the two (‘real’ and ‘baseline’) classification matrices. All remaining analyses were performed using the (‘real’) classification matrix with the correct object labels.

Then, we wanted to see whether object discriminability systematically differs between objects coming from the same or different conceptual classes (i.e. animate and inanimate objects) within the classification with correct labels. We thus calculated the average accuracies of pairwise classes within – and between conceptual categories as a descriptive measure. Using another cluster-based permutation test (again 1000 permutations, cluster-definition threshold of p < .05), we then tested within- against between-category accuracies over time. This analysis was conducted for conceptual classes only, since there was no correspondence of perceptual class between subjects. The retrieval analyses focused on the time period from -3 s to -1 s before retrieval button press to have a similar long time window as for encoding. Moreover, we based the upper time limit on the previous findings (Linde-Domingo et al., 2019), which indicated perceptual and conceptual decoding peaks prior to -1 s before button press. All cluster permutation tests were implemented by means of the permutest toolbox (https://www.mathworks.com/matlabcentral/fileexchange/71737-permutest by Gerber, 2021; Maris & Oostenveld, 2007; *Permutest*, n.d.).

EEG-fMRI data fusion

ROI fusion

Two distinct approaches were used for the fusion analyses, with either the fMRI data or the EEG data serving as starting point (similar to previous chapter). The first approach started with the fMRI patterns from a given ROI, and we thus refer to it as ROI fusion. One RDM was created per participant per ROI, representing the similarity structure in a given (functional or anatomical) brain region. This ROI RDM was then correlated with the RDM from each time bin of the single, EEG-based RDM that represents the pooled similarity structure across subjects (see cross-subject classification of described above). Correlations and classification accuracies were

Fisher's z-transformed before the data fusion. This analysis resulted in one correlation time course per individual ROI per subject who took part in the fMRI experiment (*n* = 31). The EEG-fMRI correlations were only computed for those cells of the matrix that an individual participant from the fMRI study remembered correctly. To test for statistical significance, we then contrasted the 31 correlation time courses against zero, using a cluster-based permutation test with 1000 permutations and a cluster-definition threshold of p < .05, as used in other studies (Cichy et al., 2019; Cichy & Pantazis, 2017; Dobs et al., 2019).

To test for a sequential information progression over the ventral visual stream, we implemented a linear regression on the cumulative sums of the ROI time courses of the five ventral regions (based on Michelmann et al., 2019). To do so, we first calculated the cumulative sum of the ROI time courses over the time period 0 to 1.5 s for encoding and -3 to -1 s before button press for retrieval. For an easier comparison, the cumulative sum of each ROI time course was normalized to an area under the curve that equals 1. For each time point, a linear regression was fitted across the cumulative correlation values of the ROIs within subjects. The resulting slopes of all subjects were then tested against zero in a one-sided cluster-based permutation test (again with 1000 permutations and a cluster-definition threshold of p < .05). This method enabled us to test for a forward stream during encoding and a backward stream during retrieval (Fig. 2.10). An example of the rationale is depicted in figure 2.3. In the case of a forward stream, the ROIs along the ventral visual stream activate sequentially from early towards late regions. Therefore the cumulative sums of earlier regions (e.g. V1-hIT) show a higher cumulative sum than later regions (e.g. temporal pole - hippocampus) at 0.5 s after stimulus onset (and other time points). A linear fit across ROIs at 0.5 s will therefore show a significantly negative slope. According to this rationale, a backward stream would result in a significantly positive slope. Since we expected a forward stream at encoding and a backward stream at retrieval, we used one-sided tests to see if the slope differs from zero (< 0 at encoding, > 0 at retrieval). The sequential ordering of our ROIs was based on a collection of literature on the ventral visual stream from anatomical and neuroimaging studies (e.g. Cichy et al., 2016, 2017; Felleman & Essen, 1991). Since some computational models propose that the role of the hippocampus is more related to association or indexing instead of feature representation (Eichenbaum, 2001; McClelland et al., 1995; Teyler & DiScenna, 1986), we computed the analysis once with and once without the hippocampus.

Searchlight fusion

The second, complementary fusion approach was meant to offer a higher spatial resolution and a more spatially focused perspective on the data. Here, we used the EEG-based RDMs from each time point as starting point, and then searched for matching similarity structures across the entire brain, using a volumetric searchlight analysis on each individual's fMRI data (Kriegeskorte, 2009; Kriegeskorte et al., 2006, 2008; Kriegeskorte & Kievit, 2013). We therefore refer to this method as a (time-resolved) searchlight fusion. To do so, a second-order correlation was computed between the classification-based EEG RDM from each time bin, and the correlation-based fMRI RDMs for each centre voxel and its neighbours within a searchlight radius of 3 voxels, separately for encoding and retrieval. This analysis results in a "fusion movie" (i.e., a time-resolved brain map) for each participant who took part in the fMRI experiment. The searchlight fusion for retrieval data was performed for correct trials within the fMRI data only (same as above). The fused data was Fisher's z-transformed. The searchlight fusion was performed using pyRSA (https://github.com/Charestlab/pyrsa) which works on Python (van Rossum, 1995), using the sys and os module, SciPy (Virtanen et al., 2020), NumPy (Harris et al., 2020), and nibabel (https://github.com/nipy/nibabel/releases).

To test for significant EEG-fMRI pattern similarity at individual voxels, we normalized the correlation maps to MNI space, smoothed them with 10 mm FWHM Gaussian kernel and then tested them in a one-sample t-test against zero at each single time bin. The t-test included a spatial maximal permuted statistic correction combined with a threshold free cluster enhancement (Nichols & Holmes, 2002; Smith & Nichols, 2009). This cluster-based analysis was performed using the toolbox MatlabTFCE (http://markallenthornton.com/blog/matlab-tfce/) with 1000 permutations, a height exponent of 2, an extent exponent of 0.5, a connectivity parameter of 26 and a step number for cluster formation of .1 as suggested by Smith & Nichols (2009). The analysis resulted in time-resolved spatial t-maps, depicting significant EEG-fMRI correlations.

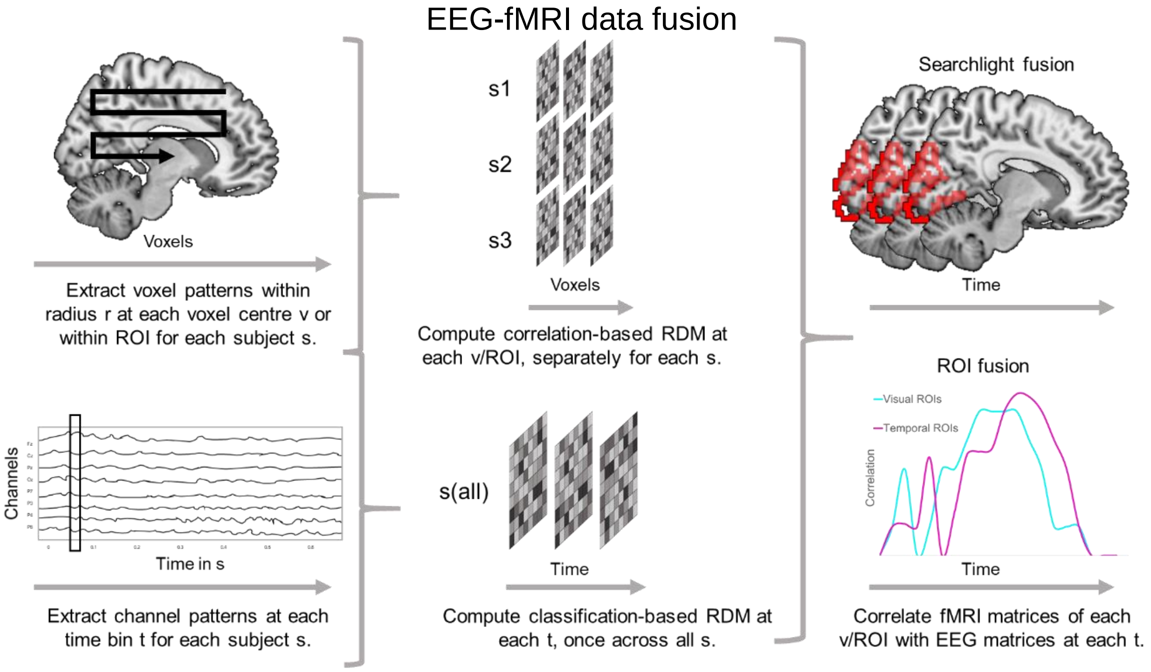

Figure 2. 2

Overview of ROI and searchlight fusion approaches. First, brain activity patterns are extracted from fMRI and EEG to create representational dissimilarity matrices (RDMs) in the spatial and temporal domain respectively. Then, second-order correlations of the RDMs from the two imaging modalities are computed for the data fusion. Importantly, the EEG RDMs are computed by performing a binary classifier on each pair of stimuli across all participants. FMRI RDMs in contrast are computed within participants and are correlation-based. FMRI RDMs can be performed at each voxel centre including voxels within a specific radius, or for larger regions of interest (ROI). Depending on this choice, the data fusion will be searchlight- or ROI-based.

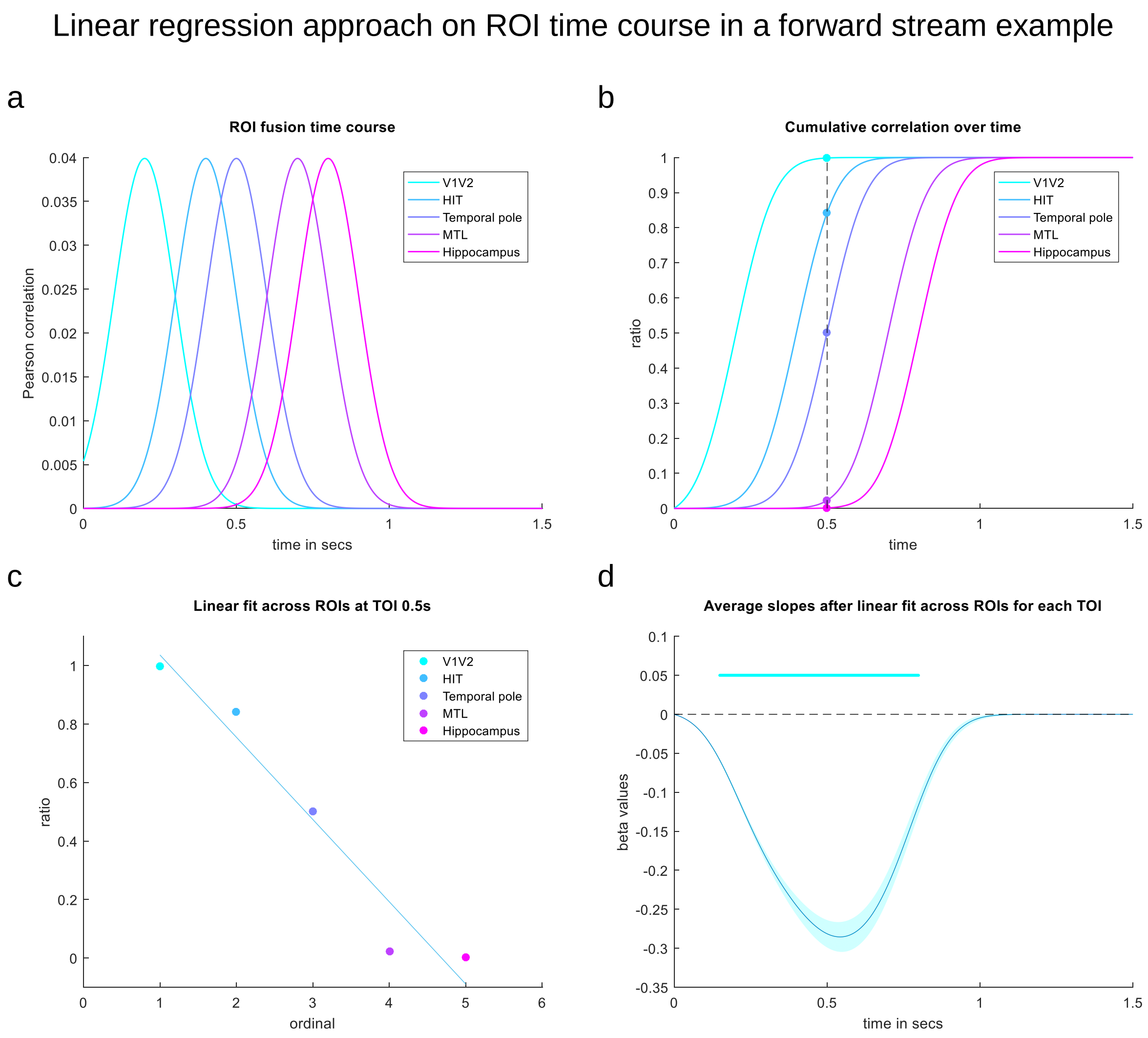

Figure 2. 3

Linear regression approach on ROI time courses in a forward stream example. A) Modelled ROI time courses of the ventral visual stream depict a hypothetical forward stream. B) Normalized cumulative sum of each ROI time course. At time point 0.5 s, earlier visual regions show a higher cumulative sum than later regions along the ventral visual stream. C) A linear regression is fitted across ROI values at 0.5 s and results in a negative slope. D) Average slopes and standard error are depicted for each time point across the window 0-1.5 s and tested against zero. Significant time points are indicated by points (p < .01 uncorrected). Method and figures adapted from Michelmann et al., (2019).

Figures

Figures were created using the raincloud plots Version 1.1, ColorBrewer 2.0 (from www.ColorBrewer.org by Cynthia A. Brewer, Geography, Pennsylvania State University), colorbrewer schemes 2.0 for Matlab (https://www.mathworks.com/matlabcentral/fileexchange/34087-cbrewer-colorbrewer-schemes-for-matlab by Charles, 2021; *Cbrewer*, n.d.), Inkscape 1.0.1 (https://inkscape.org/), WFU PickAtlas v3.0 (Maldjian et al., 2003, 2004), MRIcron (www.mricro.com, Rorden & Brett, 2000) and a colin 27 average brain template (http://www.bic.mni.mcgill.ca/ServicesAtlases/Colin27, Holmes et al., 1998).

Results

Behaviour

At encoding, participants in the fMRI study took an equal amount of time to learn a new verb-object pair (*M* = 3.01 s; *SD* = 0.91 s) in comparison to the EEG study (*M* = 2.82 s, *SD* = 1.56 s). At retrieval, we found similar average accuracy rates between participants who took part in the fMRI (*M* = 84.65 %, *SD* = .07) and participants who took part in the EEG study (*M* = 86.75 %; *SD* = .06). However, looking at the retrieval times, participants in the fMRI study (*M* = 1.75 s; *SD* = 0.66 s) were 1.24 s faster on average to push the retrieval button than participants in the EEG study (*M* = 2.99 s; *SD* = .81s). This RT difference was not only a result of the repeated retrievals in the fMRI group, since RTs of the fMRI group were substantially shorter than those of the EEG group for both the first (*M1* = 1.93 s; *SD1* = 0.67 s) and second (*M2* = 1.58 s, *SD2*

= 0.66 s) retrieval repetition. This observation might have implications for the results reported in the following paragraph.

After an explorative inspection of the behavioural data, we compared accuracies and reaction times between perceptual and conceptual questions with posthoc paired-sample t-tests and found that participants in the fMRI study performed more accurately ($t(30) = -6.63$, $p < .01$ (uncorr.)) and faster ($t\,(30) = 8.31$, $p < .01$ (uncorr.)) at answering conceptual ($M_{RT} = 1.06$ s, $SD_{RT} = 0.25$ s; $M_{Accuracy} = 0.88$, $SD_{Accuracy} = 0.07$) than perceptual questions ($M_{RT} = 1.30$ s, $SD_{RT} = 0.35$ s; $M_{Accuracy} = 0.82$, $SD_{Accuracy} = 0.08$), in line with the reverse reconstruction stream observed in earlier behavioural studies where the catch question preceded the memory cue (Lifanov et al., 2021; Linde-Domingo et al., 2019). In the EEG study, participants answered conceptual ($M_{RT} = 1.36$ s, $SD_{RT} = 0.30$ s; $M_{Accuracy} = 0.88$, $SD_{Accuracy} = 0.07$) and perceptual questions ($M_{RT} = 1.38$ s, $SD_{RT} = 0.35$ s; $M_{Accuracy} = 0.86$, $SD_{Accuracy} = 0.07$) equally fast ($t(23) = .5$, $p = .62$ (uncorr.)) and accurately ($t(23) = -1.80$, $p = .09$ (uncorr.)). This finding could be related to the reaction time difference described above and suggests that participants in the fMRI study often pressed the subjective retrieval button before recall was complete, such that a reverse memory reconstruction stream (Linde-Domingo et al., 2019) was still visible in the answers to catch questions following the retrieval button press (also see discussion).

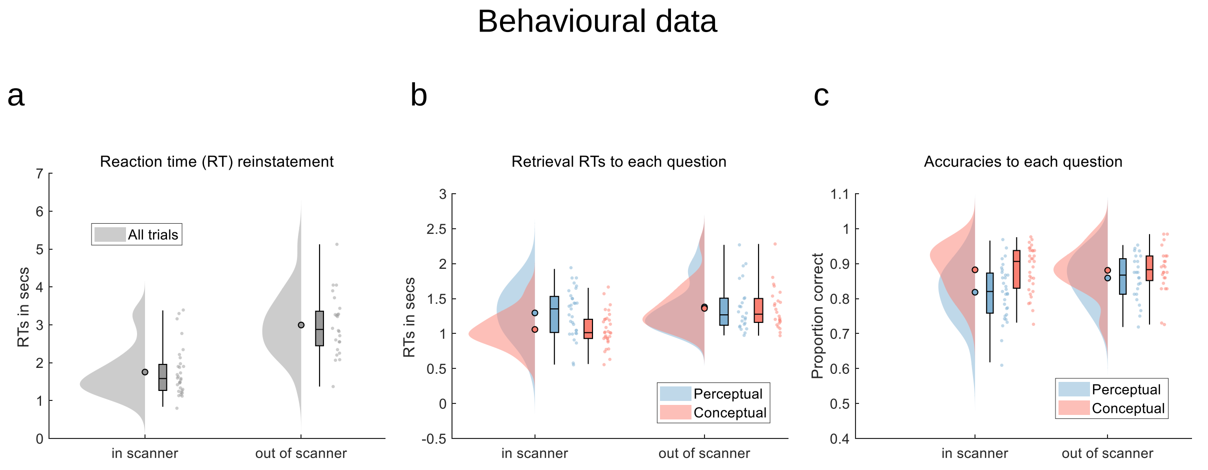

Figure 2. 4

Behavioural data acquired within and out of scanner. A) Reinstatement reaction times (RTs), b) retrieval RTs and c) accuracies for both question types. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Grey represents all trials, blue represents perceptual, pink conceptual responses. In-scanner data represents n = 24 independent subjects, out-of-scanner-data represents n = 31 independent subjects.

fMRI univariate results

We first performed a univariate GLM analysis and subsequent t-contrasts on the fMRI data to reveal activation differences between the two perceptual and the two conceptual categories (Fig. 2.5). At encoding, photographs and line-drawings showed average activity differences primarily in ventral visual regions. Photographs elicited significantly higher BOLD responses in regions V1, V2 and fusiform gyrus, ($t(30) = 4.56$, $p < .05$ (FWE)). Drawings only triggered slightly stronger activity in the middle and inferior occipital gyrus ($t(30) = 3.11$; $p < .001$ (unc.)). When contrasting conceptual categories, animate objects were associated with significantly higher activity in the lingual gyrus, middle occipital gyrus, fusiform gyrus and inferior temporal gyrus ($t(30)$

= 4.56; $p < .05$ (FWE)) and inanimate objects in middle occipital gyrus and fusiform gyrus ($t(30) = 4.56$; $p < .05$ (FWE)). These contrasts thus show the expected pattern that perceptual categories differed in regions earlier along the ventral visual stream than conceptual categories.

During retrieval, no voxels survived family-wise error correction or even a very liberal threshold of $p_{uncorr} < .01$ when contrasting perceptual or conceptual categories.

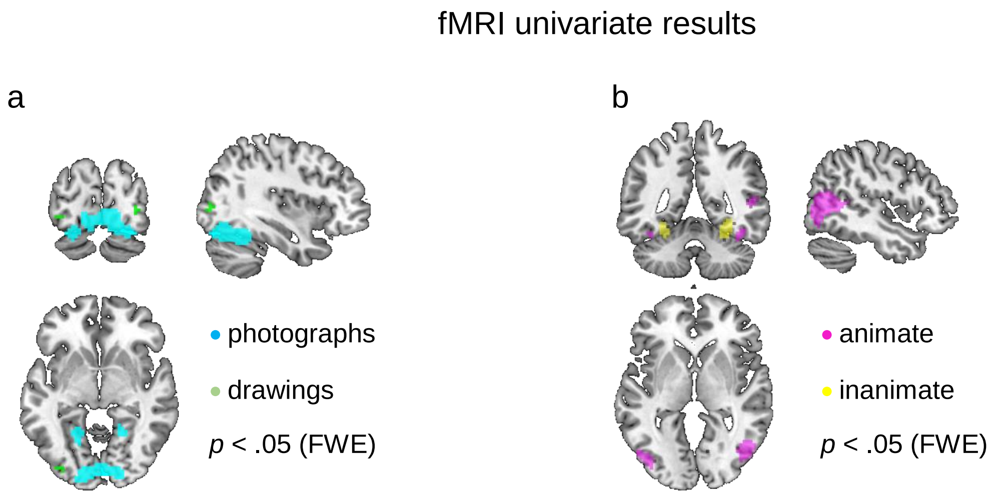

Figure 2. 5

Univariate t-contrasts results for encoding. A) Cyan: Photograph > drawing, green: drawing > photograph. B) Pink: animate > inanimate, yellow: animate< inanimate. All contrasts are thresholded at t(30) = 4.56, p < .05 (FWE). N = 31 independent subjects.

fMRI multivariate results

fMRI searchlight LDA

Searchlight LDAs were performed on the fMRI data to map the representation of perceptual and conceptual information during encoding and retrieval onto the brain

(Fig. 2.6a). Here, we classified photographs versus drawings, and animate versus inanimate objects, from object-specific t-value patterns of the fMRI data. During encoding, information about perceptual classes could be decoded in posterior regions along the ventral visual stream including V1, V2, lingual and fusiform gyrus (*t*(30 = 4.92, *p* < .05 (FWE)). Conceptual information was mapped to more anterior areas along the lateral temporal lobe, including inferior, mid and superior temporal gyrus, and additionally also to the precuneus, and inferior and dorsolateral prefrontal cortex (*t*(30) = 4.76, *p* < .05 (FWE)). Together, this mapping generally reflects a posterior-to-anterior perceptual-to-conceptual processing gradient while the object is visually presented on the screen. The results complement the univariate analyses reported above, but also show additional activity especially in frontal and parietal regions, suggesting that these areas code information in fine-grained voxel patterns that univariate analyses are unable to capture.

During retrieval (Fig. 2.6b), perceptual features were most strongly decodable in the right precentral gyrus (i.e. premotor cortex), but also in V2, precuneus, mid and inferior temporal lobe, parahippocampal gyrus, cingulate gyrus and middle frontal gyrus (*t*(30) = 4.74, *p* < .05 (FWE)). Conceptual information was classified with highest accuracy from fusiform gyrus, precuneus, angular gyrus, and dorsolateral prefrontal cortex, inferior and middle frontal gyrus, and temporal pole (*t*(30) = 4.54, *p* < .05 (FWE)). Hence, in addition to the ventral visual areas dominating encoding/perception, we also found extensive frontal and parietal areas engaged during retrieval, in line with previous work suggesting that mnemonic as opposed to sensory content can often be decoded from these areas (Favila et al., 2018, 2020; Kuhl & Chun, 2014).

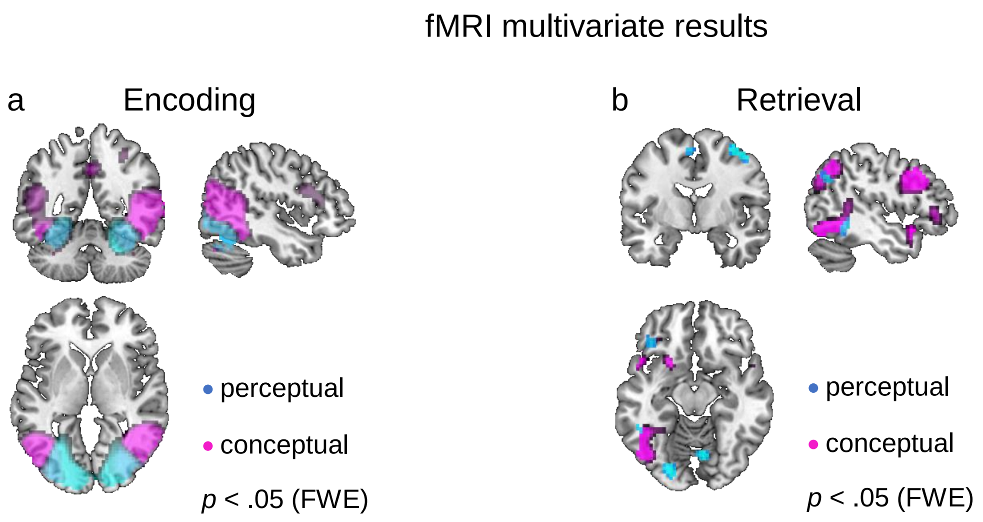

Figure 2. 6

Searchlight LDA results. Encoding and retrieval accuracies significantly higher than 50 % for perceptual (cyan) and conceptual (pink) classifications. All contrasts are thresholded at p < .05 (FWE). N = 31 independent subjects.

EEG multivariate results

EEG cross-subjects classifier-based RSA

Before fusing the EEG and fMRI data, we also wanted to see how much information about object identity can be decoded from the EEG signals themselves, and whether objects from different conceptual classes would show more pronounced pairwise distances than objects from the same conceptual class (Fig. 2.7). Plots below therefore show the overall average decoding accuracy as well as the average decoding accuracy within and between conceptual classes, with corresponding statistics (see methods).

Individual object decoding accuracy gradually increased from approximately 60 ms after stimulus onset, with a first smaller peak around 127 ms (p < .05 (cluster)), and a second temporally extended cluster from 224 ms until the end of the trial (p < .05 (cluster)). Moreover, objects from conceptually different classes (animate vs inanimate) were classified significantly better than objects from the same class, starting from 222 ms after stimulus onset until 1.3 s ($p < .05$ (cluster)).

During retrieval, overall classification accuracies remained relatively low in comparison to encoding, showing peak decoding accuracy of 51 % at around -2.8 s before retrieval button press. Five significant accuracy clusters were found with peaks located at times -2.74 s, -2.63 s, -2.54 s, -2.16 s and -1.46 s relative to the time of subjective recollection ($p < .05$ (cluster)). When comparing classification accuracy for conceptually different, between-class object pairs to within-class pairs, no test survived cluster correction. However, the maximum between- versus within-class difference was identified -2.5 s before the retrieval button press ($p < .01$ (uncorr.)).

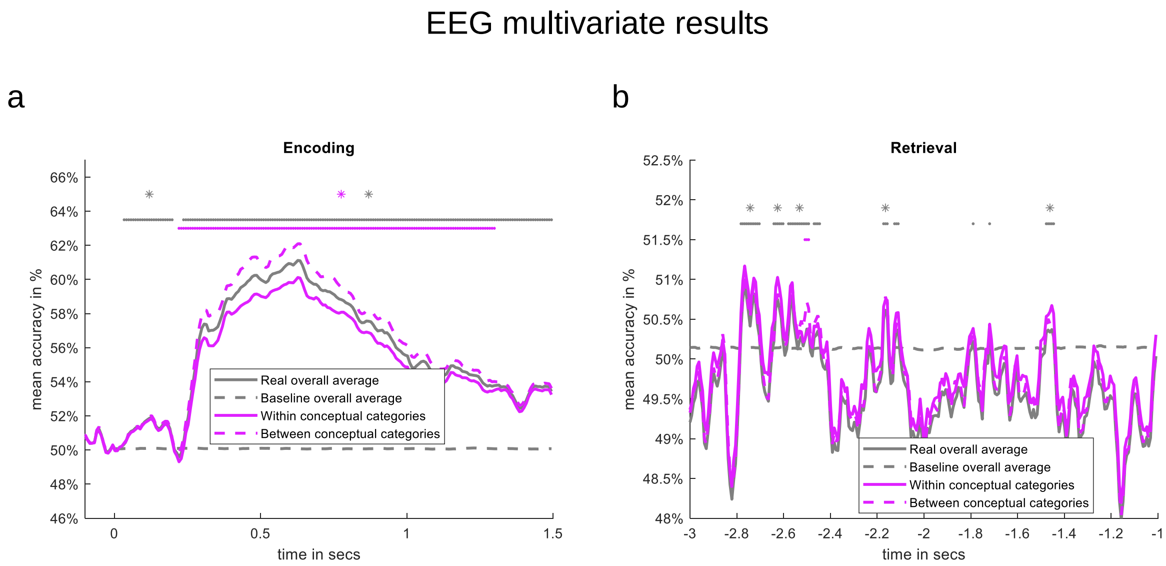

Figure 2. 7

Average EEG classification accuracy over time and average classification accuracy within- versus between conceptual classes during a) encoding and b) retrieval. At encoding, time point 0 s marks object onset. At retrieval, time point 0 s marks button response, but is not included in figure as it does not lie within the time of interest (see methods). Solid grey line represents overall average accuracy, dashed grey line represents baseline average, and grey markers indicate significant overall classification accuracy against chance through random label permutation. Solid pink line represents the average accuracy within conceptual categories, dashed pink line represents average accuracy between conceptual categories, and pink markers indicate significant between- versus within conceptual classes with correct labels. Specifically, significant decoding accuracy is indicated by points (p < .01 uncorrected) and asterisk (p < .05 cluster). See Methods for details on cluster correction. N = 24 independent subjects.

EEG-fMRI data fusion

ROI fusion

For a first fusion step, we used the representational geometries (i.e. the RDMs) from a pre-defined set of ROIs and tested when in the timeline of a trial they would correlate most strongly with the geometries obtained from the EEG data. In each of the below figures (Fig. 2.8-2.9), correlation time courses are plotted for each individual ROI as t-values against baseline. V1 and V2 show two first descriptive peaks at -50 and -30 ms before stimulus presentation ($p < .01$(uncorr.)), likely as response to the previous cue presentation. After stimulus presentation at encoding (Fig. 2.8), posterior regions including V1 and V2 start to show a rising correlation with the EEG representations from approximately 130 ms ($p < .01$ (uncorr.)). A significant cluster is seen at 240 ms ($p < .05$ (cluster)), followed by a correlation increase of later ventral visual areas (hIT) around 300 ms ($p < .01$ (uncorr.)), reaching a significant peak at 430 ms ($p < .05$ (cluster)). Later lateral and medial temporal as well as parietal regions do not show a significant correlation with the EEG time series during encoding.

As a proof of principle, we then tested for a forward stream within the ventral visual stream. Performing a linear regression on the cumulative sums of all ventral ROI time courses at each time point (see Methods and Fig. 2.3), we found negative but non-significant slopes for time points after 500 ms. Importantly excluding the hippocampus from this linear regression, the slopes decreased to a larger extent and reached significance 500 ms after stimulus onset ($p < .05$ (cluster)). This speaks for the fact that earlier regions along the ventral visual stream code relevant information before later regions, supporting the idea of the previously established forward stream (Fig. 2.10).

When looking at the ventral visual ROIs during retrieval (Fig. 2.9), MTL regions show a descriptive peak correlation with the EEG representation series -2.17 s prior to the retrieval button press ($p < .01$ (uncorr.)). Next, descriptive correlation peaks were found for early visual regions (V1/V2) shortly after, -1.90 s before the button press ($p < .01$) and again at -1.32 s before button press, before reaching a significant peak at -1.20 s (p < .05 (cluster)). At the latter peak, hIT also showed a peak correlation with the EEG geometry at -1.24 s (p < .01 (uncorr.)). The retrosplenial cortex showed a descriptive correlation peak in a similarly late time window, at -1.25 s and -1.13 s before button press (p < .01 (uncorr.)), however not surviving the cluster correction. This peak in the inferior parietal, but no other parietal regions, coincided with the peak times of early ventral visual areas. Unexpectedly, the hippocampus shows a correlation peak at -1.80 s (p < .01 (uncorr.)), possibly reflecting reverberating activation, which is only speculative at this point.

Importantly, our main aim was to test if the memory reactivation followed a backward processing stream. After replicating the forward stream during encoding, we therefore also performed a linear regression on cumulative sums of ventral visual regions within retrieval. This analysis including all five ventral ROIs revealed a significantly positive slope from -2.1 to -1.3 s before retrieval button press (p < .05 (cluster)). Also, when leaving out the hippocampus from the analysis, a significantly positive slope was found from -2.1 to -1.2 s before button press (p < .05 (cluster)), speaking in favour of a backward stream along the ventral visual pathway and thus confirming our main hypothesis (Fig. 2.10).

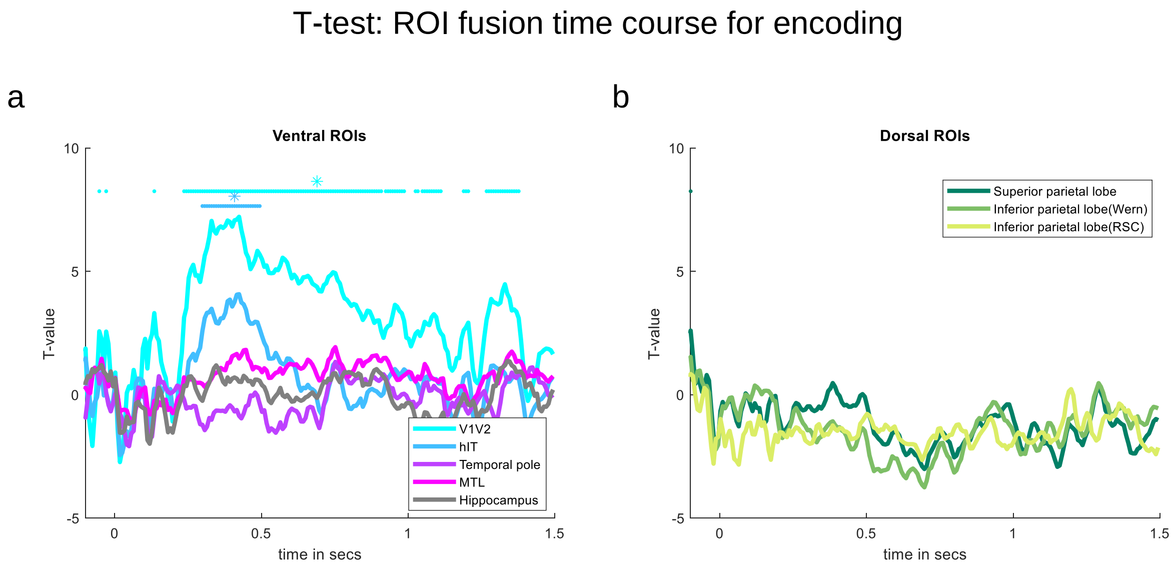

Figure 2. 8

T-values of correlation time course with EEG for a) ventral visual and b) dorsal regions of interest (ROIs) at encoding. Regions of interest (ROIs) are colour-coded as depicted in the legends. Time point 0 s marks object onset. Significant time points are indicated by points (p < .01 uncorrected) and asterisk (p < .05 cluster). See Methods for details on cluster correction. Variance comes from n = 31 independent subjects.

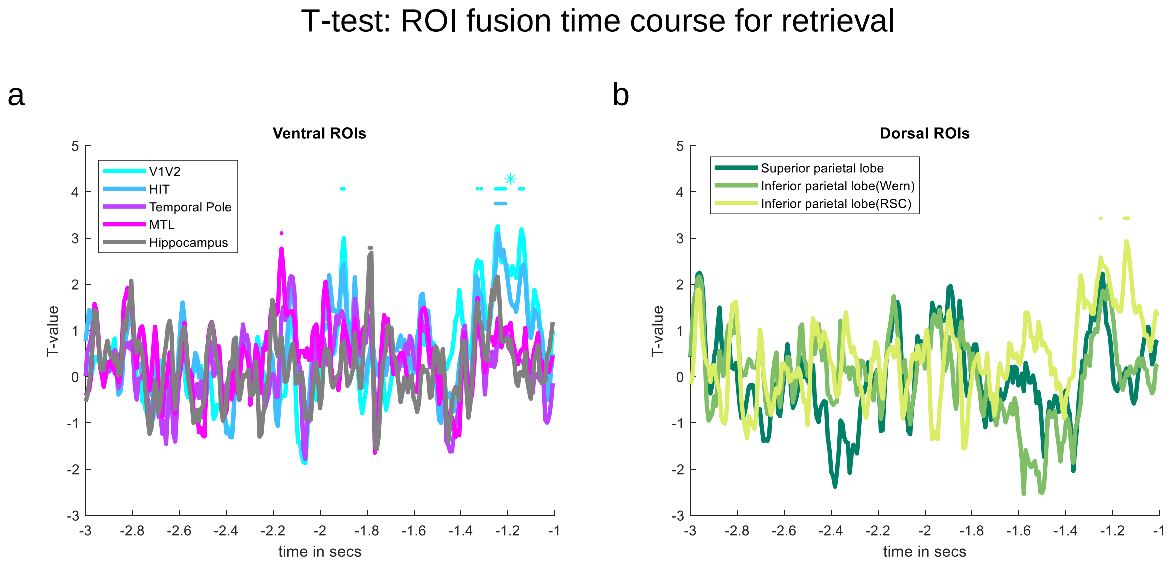

Figure 2. 9

T-values of correlation time course with EEG for a) ventral visual and b) dorsal regions of interest (ROIs) at retrieval. Regions of interest (ROIs) are colour-coded as depicted in the legends. Time point 0 s marks button response, but is not included in figure as it does not lie within the time of interest (see methods).

Significant time points are indicated by points (p < .01 uncorrected) and asterisk (p < .05 cluster). See Methods for details on cluster correction. Variance comes from n = 31 independent subjects.

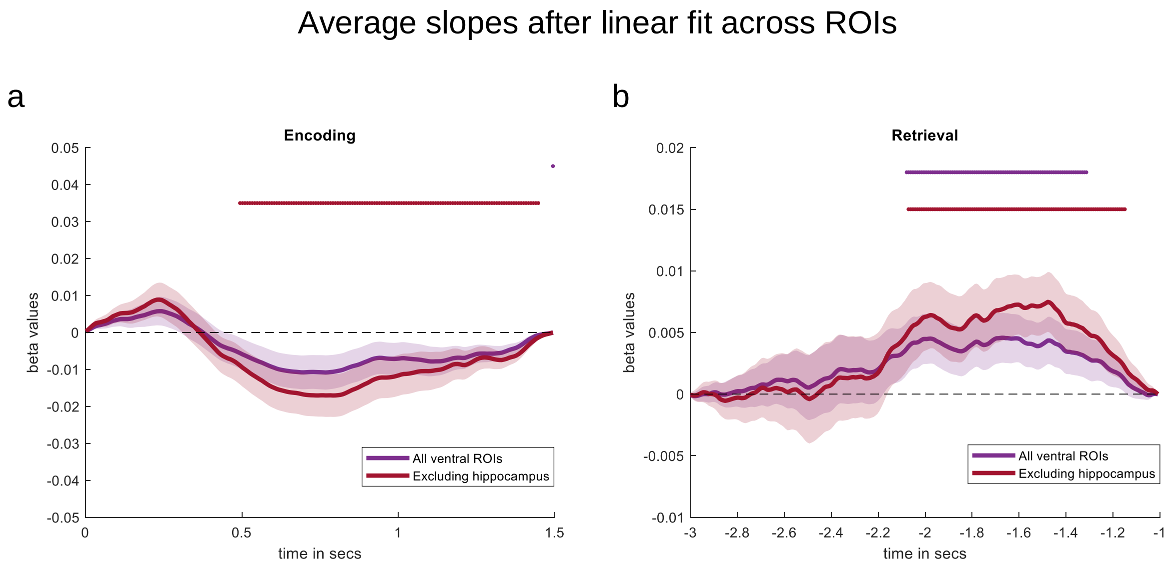

Figure 2. 10

Test for sequential processing using average slopes of linear fit across ROIs within the ventral visual stream using all ventral ROIs, or all ROIs except hippocampus at a) encoding and b) retrieval. Average slopes and standard errors are depicted for each time point and tested against zero. Slopes are colour-coded as depicted in the legends. At encoding, time point 0 s marks object onset. At retrieval, time point 0 s marks button response, but is not included in figure as it does not lie within the time of interest (see methods). A negative slope suggests that earlier ROIs along the ventral visual stream have a higher cumulative sum than later ROIs, indicative of a forward stream. According to the same logic, a positive slope indicates a backward stream. Significant time points are indicated by cyan points above the curve (p < .05 cluster). See Methods for details on cluster correction. Variance comes from n = 31 independent subjects.

Searchlight fusion

Next, we conducted a whole-brain searchlight fusion to inspect where across the brain the fMRI-based representational geometries matched the EEG geometries from any given time point. The figures below thus depict spatial t-maps representing significant EEG-fMRI RDM correlations in each searchlight radius for a given time bin, separately at encoding and retrieval. Only time points where significant spatial clusters emerged are shown. During encoding (Fig. 2.11), the searchlight fusion revealed a significant cluster in early visual regions from 300 to 800 ms after stimulus onset. Around 400 ms, the EEG-fMRI similarity in more ventral and lateral areas, including fusiform and inferior temporal gyrus, additionally increased. Correlations in early and ventral visual areas were sustained until around 700 ms, after which they gradually decreased. This more explorative searchlight approach shows overlapping results with the ROI fusion approach and mainly reveals ventral visual stream activation progressing in a forward manner. The missing engagement of early visual regions are most likely attributable to the cross-subject classification approach in the EEG data where the perceptual format of perceived objects differed between subjects.

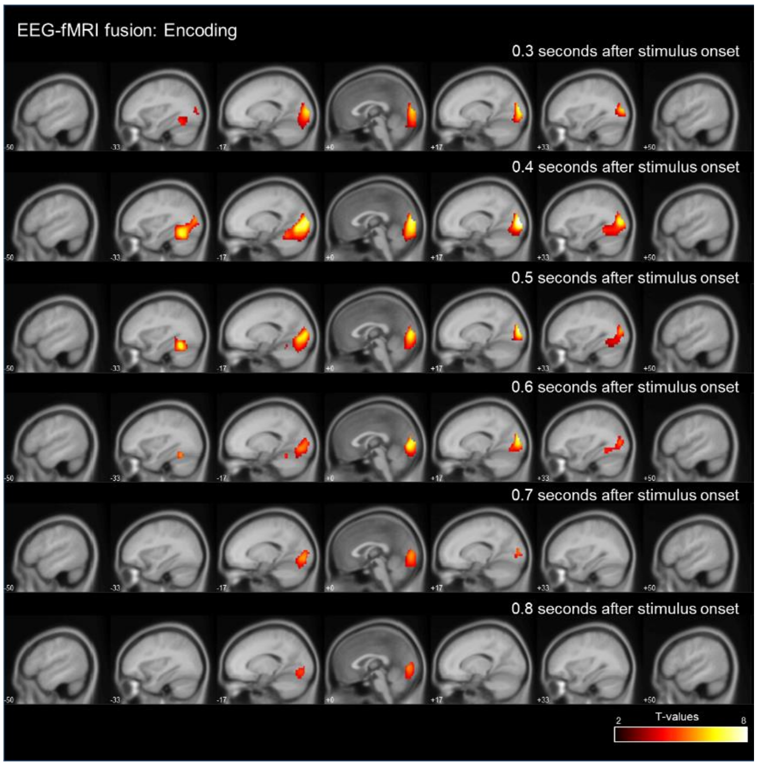

Figure 2. 11

T-maps of EEG-fMRI correlations at encoding showing time points in the trial time course where significant spatial clusters (p < .05 cluster) emerged. See Methods for details on cluster correction. N = 31 independent subjects.

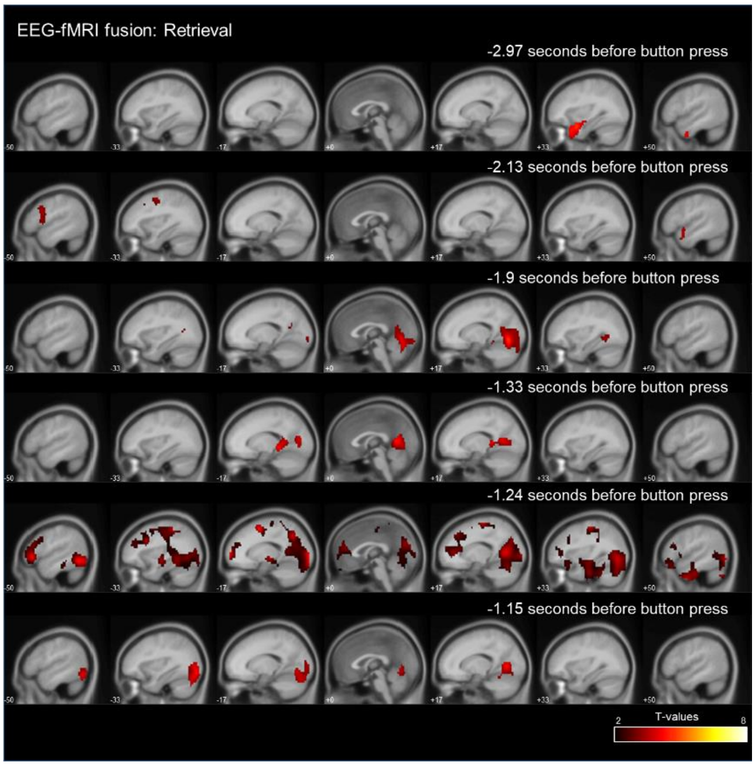

Figure 2. 12

T-maps of EEG-fMRI correlations at retrieval showing time points in the trial time course where significant spatial clusters (p < .1 cluster) emerged. See Methods for details on cluster correction. N = 31 independent subjects.

During retrieval (Fig. 2.12), the earliest significant EEG-fMRI correlation was found in the temporal pole around -2.97 s before the retrieval button press. This region also showed a significant correlation around -2.13 s, together with clusters in the precentral and inferior frontal gyrus. Then, from -1.9 s prior to the retrieval button press, ventral and early visual regions showed a significant correlation peak. Visual regions also emerged again between approximately -1.35 s and -1.15 s before the retrieval button press. At -1.24 s, a larger set of frontal and parietal regions showed significant correlations with the EEG representations. Together, also the retrieval data shows overlapping findings between the ROI- and searchlight fusion approach, showing a late temporal to visual activation processing and thus confirming our backward stream hypothesis, with additional engagement of fronto-parietal areas.

Discussion

A plethora of work on object recognition has shown that neural information about a visually perceived object progresses along the ventral visual stream following a feed-forward gradient with increasing levels of information abstraction (T. Carlson et al., 2013; Cichy et al., 2014; Martin et al., 2018). Contrary, recent memory research suggests that the information processing hierarchy is reversed during the recall of an object from memory (Linde-Domingo et al., 2019; Lifanov et al., 2021). Here, we investigated whether this presumed reversed information processing cascade during memory reconstruction maps onto the same ventral visual stream areas that carry the information forward during perception, but now following a feedback trajectory. Using a word-object association task and multivariate analyses on fMRI and EEG data, we first decomposed sensory and mnemonic processes into spatio-temporal feature representations. Then, using an EEG-fMRI fusion approach, we provide evidence for a reversed retrieval stream.

On the one hand, we showed that encoding follows a feed-forward perceptual-to-conceptual information flow, progressing from posterior visual to ventrolateral regions along the ventral visual stream (Fig. 2.8, 2.10, 2.11). On the other hand, while retrieved information was also reactivated in regions along the ventral visual stream, its trajectory followed a backward progression from anterior temporal to posterior parietal and visual cortices (Fig. 2.9, 2.10, 2.12). Decoding the two features built into our experimental design from fMRI activity patterns showed that these regions represented conceptual and perceptual representations, respectively (Fig. 2.6). In addition, also lateral and inferior parietal and inferior frontal regions contained information about the retrieved objects. Finally, reaction times of this study (Fig. 2.4) supported and replicated the conceptual-to-perceptual information processing during retrieval (see also Linde-Domingo et al., 2019; Lifanov et al., 2021).

Acquiring an fMRI dataset with a previously used visual learning paradigm (Linde-Domingo et al., 2019) provided us the missing information on spatial representational patterns of recalled episodic memories. Using both univariate and multivariate analysis approaches, we first set out to map the processing of perceptual and conceptual object features during encoding onto the brain. As expected, these features largely mapped onto the ventral visual pathway, where early visual areas processed the perceptual features (coloured photos versus black-and-white line drawings, irrespective of semantic content), and later visual areas processed the higher order, conceptual information (animate versus inanimate objects, irrespective of perceptual format). This general perceptual-to-conceptual gradient is in line with a multitude of findings in the basic vision literature (T. Carlson et al., 2013; Cichy et al., 2014; Kravitz et al., 2013).

Univariate analyses were not powerful enough to detect differential activations between our categories along the perceptual and conceptual dimension when objects were reconstructed from memory. Activity patterns at the finer-grained voxel level, however, represented the different features of the retrieved images. The memory-related reactivation of these features comprised some of the encoding-related regions, in particular in late visual areas. On a basic level, this finding confirms a body of previous work showing that posterior visual areas are not only involved in visual perception but also in internally generated processes, such as mental imagery (Dijkstra et al., 2021; Kosslyn et al., 1993) or in our case, memory representations. Moreover, the fMRI findings in themselves speak for the hypothesized reversed reconstruction stream, which also implies a pattern reinstatement during retrieval in areas that are active at encoding. The reinstatement of encoding-related patterns is a basic assumption of many computational models (O'Reilly & Norman, 2002), and has been reported in a wealth of empirical studies (Bosch et al., 2014; Polyn et al., 2005; Staresina et al., 2012; Staudigl & Hanslmayr, 2019; Wing et al., 2014). It is also commonly observed that stronger reinstatement of encoding-related patterns is associated with memory strength or successful retrieval (Ritchey et al., 2013; Tulving & Thomson, 1973) and the vividness of remembering (St-Laurent et al., 2015; Wheeler et al., 2000), suggesting an important functional role of sensory reactivation.

Although some of the retrieval-induced processing resembled the feature representations during encoding, it is important to note the partial mismatch between encoding and retrieval activity representations. Most notably, we were able to decode conceptual information from middle frontal gyrus, which has previously been related to the semanticization of memories and unique object identity processing (Ferreira et al., 2019), and fronto-parietal regions also commonly found in memory related processing and conceptual object representations (Favila et al., 2018; Xiao et al., 2017; Jeong & Xu, 2016; Levy, 2012). This transfer from visual to fronto-parietal regions has recently gained attention, and has been described as a spatial transformation of memories compared to their original representations during the actual physical experience (Favila et al., 2020). It was recently suggested that depending on an attentional bias in functional networks towards an encoding or retrieval state, content representations are rather exhibited in visual or parietal cortices, respectively and mediated by differential connectivity with the hippocampus (Long & Kuhl, 2021; Ritchey & Cooper, 2020). Why reconstructed information is primarily represented in parietal cortex is currently unclear, but our findings in principle support this encoding-retrieval distinction. They also suggest that it is primarily conceptual information (Fig. 2.6b) that is represented in these regions during retrieval, most likely explained by a general dominance of semantic information during memory recall. Further ideas about the involvement of parietal networks are discussed further below in relation with the timing of the reactivation.

Going beyond a simple spatial mapping of perceptual and conceptual representations, our fusion of the EEG and fMRI data allowed us to inject time information into these spatial maps, and to ask how the memory reconstruction stream evolves from cue presentation to the time of subjective recollection (i.e., the retrieval button press). We used two complementary approaches for data fusion, both comparing the representational geometries found in the EEG patterns at each time point with the fMRI geometries found in a given brain region. We did this once in a spatially focused ROI-based fashion, and once in a more exploratory searchlight fashion. Both approaches showed a mainly feedforward sweep of information processing during the first few hundred milliseconds of encoding, starting within early visual regions approximately 120 ms after image onset (ROI fusion), and then spreading to more ventral visual regions within the next 200 ms (ROI and searchlight fusion).

Relating the fusion maps above to the EEG decoding results, we found that representations in early visual areas evolve with individual object processing. In comparison, more ventral representations coincide with increasingly distinctive processing of different conceptual categories. Given the object recognition literature (Cichy et al., 2014), it was surprising that the accuracy of object-identity decoding was comparatively low (but still significant) within the first 100 ms compared to the time period after 200 ms. This might have to do with specifics of our fusion approach, combining data from two different groups who saw the stimuli in different formats. Across participants, the objects corresponded in terms of image content but not perceptual format, which potentially suppressed some patterns that reflect similarity on the level of early visual features. However, since the photographic and drawn versions of the object overlapped in shape, orientation and disparity, at least some of the representational structures should have been preserved. In fact, the main information cluster during encoding lies in early visual areas, which are also known to represent features such as contrast, orientation, spatial frequency and disparity (Tootell et al., 1998; Henriksson et al., 2008; Henriksen et al., 2016). Thus, even if some perceptual information was supressed within our cross-subject EEG classification, other early features should have contributed to decoding performance at these earliest time points. Apart from the unexpectedly small early onset of the perceptual processing stream in the ROI fusion (and the missing early onset in the searchlight fusion), however, we were able to replicate the forward visual processing cascade, which was statistically supported by a sequence analysis (Fig. 2.10).

Most critically, the same fusion approaches and the sequence analysis applied to the retrieval data revealed a largely feed-back information processing trajectory. Specifically, the data shows an information flow from medial temporal lobe (see ROI fusion) and temporal pole (see searchlight fusion) to early visual regions (both fusion approaches). The earliest correspondence between EEG and fMRI representations in the searchlight approach (Fig. 2.12) was found 2.97 s prior to the retrieval button press, and was confined to the anterior temporal lobe. Caution is needed when interpreting this earliest time point, since some participants had retrieval button press times shorter than 3 sec, where this time point would overlap with cue presentation. Reassuringly however, later time points around 2.2 to 2.1 s before subjective recollection mark the onset of a backwards propagation and show the same anterior temporal reactivation together with reinstatement in MTL structures (Fig. 2.9). The temporal pole has previously been associated with the modality-independent processing of semantic information in general, and semantic retrieval in particular (McClelland & Rogers, 2003; Noppeney & Price, 2002; Patterson et al., 2007; Rice et al., 2018; Visser et al., 2010). Moreover, temporal pole reactivation around -2.1 s before button press was close in time to the time point when objects from two different conceptual classes were decoded with significantly higher accuracy than objects from two similar conceptual classes (based on the EEG classification alone). Together, these findings indicate that the conceptual features we explicitly manipulated are among the first to be reactivated in semantic networks.

More posterior areas including inferior temporal, inferior parietal and visual cortex, and frontal regions reached their information representation peaks considerably later, at the earliest around -1.9 s and more strongly at -1.2 s, the latest time window leading up to subjective recollection (Fig. 2.9 & 2.12). While the visual and extrastriate activations are assumed to represent low-level perceptual content, the parietal regions have been shown to play a role in contextual processing and memory-related imagery (Cichy et al., 2016; Lundstrom et al., 2005; Fletcher et al., 1995; Chrastil, 2018). The late timing of these reverberations might be indicative of a final reinstatement likely underlying working memory and memory-related imagery, as preparation for the upcoming categorisation task (Christophel et al., 2012, 2017; Ganis et al., 2004). Together, the information reactivation from frontal anterior pole to posterior parietal and visual regions with additional frontal involvement revealed by the EEG-fMRI data fusion overlaps with the regions found when classifying retrieved mnemonic features from the fMRI data alone and suggest a conceptual-to-perceptual processing stream with a final activation of a task-relevant imagery buffer.

The EEG classification methods used in our data fusion differed from previously used classification methods (Linde-Domingo et al., 2019), which mainly served to decode categorical information within-subjects in order to find the peak times where conceptual and perceptual features are represented in the EEG data (Linde-Domingo et al., 2019). Evidence from these previous analyses provided the confidence that conceptual and perceptual representational structures are encoded in the electrophysiological data and could be used to find related representations in an EEG-fMRI data fusion. In contrast, our cross-subject, object-specific classification approach served the goal of subsequent fusion with fMRI data, which requires representational geometries (i.e. dissimilarity matrices) that are resolved on an individual object level, in order to then correlate the EEG and fMRI data on the level of these representational dissimilarity matrices. The different classification approaches might contribute to some of the outcome differences described below.

The present study revealed a reinstatement timeline that slightly differs from the categorical classification peaks identified in Linde-Domingo et al. (2019). More anterior temporal and more posterior visual areas showed a representational match around -

2.2 s and 1.9 s before button press respectively, while the previous study found conceptual and perceptual information processing peaks at 1.8 and 1.6 s prior to subjective recollection. The most obvious reason for these differences in timing is the decoding approach used for the data fusion, capitalizing on individual object representations. This could mean that object-level information is retrieved even before conceptual-classes-level information. Importantly, the findings do agree on the reversed reconstruction aspect of memory retrieval and add the missing spatial information about the loci of reconstructed content to previous work. Together these results imply an information reactivation cascade during memory retrieval that starts with late semantic networks that are close to the hippocampus, coding more abstract object features, and which then back-propagates to early visual regions representing perceptual characteristics of an object.

The fMRI classification and the RSA-based EEG-fMRI data fusion in this study offer complementary information. While the data fusion tells us how information progresses in brain space over time, it does not provide information about the content that is driving the match in representations. In contrast, classifying two explicitly manipulated feature dimensions from fMRI activation patterns yields information about where specific representational content is most dominant in the brain, but does not provide any information on the temporal evolution of such content representations across the trial time course. The two analyses together thus provide complementary information on the representational information processing streams at encoding and retrieval. In this respect, it can be deducted that during encoding, feature processing increases in abstractness as information travels along the ventral visual stream over time. In contrast, retrieval follows a feedback propagating stream along the ventral visual stream reflecting a conceptual-to-perceptual information reconstruction. Moreover, as in Chapter 2, we find that the backward reconstruction flow is not limited to ventral visual brain areas, but involves frontal and parietal regions likely serving as an episodic memory or imagery buffer for the retrieved representations (Baddeley, 1998; Levy, 2012; Wagner et al., 2005).

RSA is a highly useful tool to enable the comparison of brain activity representations measured by different neuroimaging modalities as fMRI and EEG (Kriegeskorte & Kievit, 2013). By creating similarity structures from both EEG and fMRI activity patterns, it is possible to directly correlate the two measures and find commonalities between the spatial and temporal representational geometries, because they are now available in the same format. As stated above, however, the data fusion in itself does not provide any content information. Our present design allowed us to complement the spatio-temporal representations with content information by using categorical classification. Here, explicitly manipulating low- vs high-level features of the object stimuli offered us insight into the level of processing at different temporal stages and within different brain regions. This attempt complements studies that use early vs late deep neural network layer outputs to model low- vs high-level processing (e.g. Bone et al., 2020). Though in contrast to the black box of such DNN layers, the controlled stimulus manipulation used here offers more transparency. However, we acknowledge that the dimensions of memory representations in the brain extend beyond the features (i.e., colour and animacy) that we were able to explicitly manipulate here. In fact, it has been previously argued that to tap into content information contained in a signal, explicit manipulations in a predefined set of dimensions is required (Schyns et al., 2020). This is important as we found some correlation peaks in the searchlight fusion maps during retrieval that did not overlap with the perceptual or conceptual classification results in the fMRI data. Similarly, some individual stimulus classification peaks in the EEG data do not coincide in time with the ROI fusion peaks. It has thus been suggested to make use of richer study designs with more stimulus variations on a trial-by-trial basis (Schyns et al., 2020). We agree that such studies with better feature resolution are an important future step in order to identify what dimension are contained in, and dominate, reactivated memory representations.

Finally, the behavioural performance of the fMRI study supported a conceptual-to-perceptual information processing during retrieval, reversed with respect to encoding. Note, that it was not the purpose of our study to find differential conceptual and perceptual reaction times in question type. The paradigm was designed such that after verb cue onset, participants were instructed to first reinstate objects fully and indicate this by a retrieval button press. At this stage, we expected participants to have a fully reconstructed image of the recalled object in mind, and answering either perceptual or conceptual question should thus take equally long, as found in the behavioural responses of the EEG dataset (also see Linde-Domingo et al., 2019). Our fMRI participants, however, responded more rapidly to conceptual than perceptual questions, and we believe that this is related to a significantly faster average timing of the subject recollection button presses in this group. If participants in this group pushed the retrieval button prematurely, while still in the process of reconstructing the object from memory, this would explain why the reconstruction process carried over into the catch question period, making the reverse reconstruction stream visible in behaviour. The comparably high accuracies show that the recall process itself did not suffer from overly rapid button presses. Our reaction results are thus in line with the reversed feature access during retrieval compared to encoding as shown in previous work (Linde-Domingo et al., 2019; Lifanov et al., 2021).

It is important to consider the differences in reaction times between the EEG and fMRI datasets, and possible effects on the results. As discussed above, these reaction time differences are suggestive of different memory processing stages at the time of button press between the studies. All analyses of the out-of-scanner EEG data are response locked and the reverse reconstruction stream is likely to be relatively complete at the time of this button press. The fusion results should thus reflect differential representational patterns aligned to the subjective button presses. Button presses in the fMRI sample did occur on average 1.3 s earlier and possibly at a time where the memory reconstruction process was less complete. However, due to the sluggishness of the BOLD response (Friston et al., 1994; Kruggel & von Cramon, 1999), this temporal delay should only have minor effects on the fusion analyses. Moreover, cue-locked boxcar regressors were used to cover the entire reconstruction period in a trial, to make sure that both the perceptual and conceptual reconstruction stages were equally covered in the dataset. Since the fMRI data in our setting is mainly used to derive the spatial representational patterns, while the time resolution is provided by the EEG data, the difference in reaction times should thus only minimally affect the outcomes of the retrieval fusion analyses.

Reaction times and accuracies have previously been shown to be highly related to neuroimaging results and thus indicative of the timing of the underlying brain processes (T. A. Carlson et al., 2013; Cichy et al., 2017; Linde-Domingo et al., 2019; Ritchie et al., 2015). Our reaction time results by themselves are suggestive of a feedback neural processing stream, which is strongly in line with previous findings (Linde-Domingo et al., 2019; Lifanov et al., 2021). Complementary to the hierarchical reaction time pattern, accuracies also show a better retention of conceptual in contrast to perceptual features, supportive of a prioritization of conceptual information during retrieval. The fMRI-based categorical decoding analyses support such a prioritization (Fig. 2.6b), showing that reactivated mnemonic information is dominated by conceptual information. One important neural theory here is that closer reciprocal connections from the MTL to semantic than to perceptual regions shorten the processing time and thereby favour the reactivation of semantic features during retrieval, which ultimately leads to a stronger retention of semantic features, a possibly a semanticization of memories over time (Linde-Domingo et al., 2019; Lifanov et al., 2021). This notion could also indicate that repeated remembering, and retrieval-based practice of recently acquired memories, play a major role in the process of memory semanticization. The question whether the semanticization of memories is a naturally occurring effect, independent of practice strategy or whether retrieval particularly affects memory representations and contributes to the conceptualization and a long-term retention is further investigated and discussed in the next chapter (and published in Lifanov et al., 2021). Taken together, the RT and accuracy data highlight the prioritisation of conceptual over perceptual features during retrieval. The behavioural results therefore complement the spatial and temporal prioritisation of conceptual over perceptual representations during retrieval (as seen in the fMRI and EEG patterns respectively).

Summarizing the present study, we decomposed hemodynamic activation representations into two pre-specified feature dimensions, and were able to map these dimensions onto the brain. A multivariate RSA-based EEG-fMRI data fusion then allowed us to map stimulus-specific information representations in neural time and space. These complementary analyses, supported by additional reaction time measures, provide evidence for the backwards propagation of reconstructed episodic memory representations along the ventral visual stream, following a reversed information processing gradient with respect to encoding.

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Author contributions

J.L. and M. Wimber designed the experiments. J.L. and J.L.D. conducted the experiments. B.G. and C.F. helped with the scanning acquisition. J.L. and J.L.D preprocessed the data. J.L. analysed the data. J.L., J.L.D., S.M., M. Wilson, I.C. and M. Wimber contributed to the analysis approach. J.L. wrote the first version of the chapter under the supervision of M. Wimber. J.L. and M. Wimber contributed to reviewing and editing.

Competing interests

The authors declare no competing interests.

Chapter 4 – Feature-specific reaction times reveal a semanticisation of memories over time and with repeated remembering

At the time of thesis submission, this chapter has been as published online as an early preprint version: BioRxiv, 2020.09.11.292813. https://doi.org/10.1101/2020.09.11.292813 (https://creativecommons.org/licenses/by-nc-nd/4.0/); and in Nature Communications: Nat Commun 12 (1), 1–10. https://doi.org/10.1038/s41467-021-23288-5 (https://creativecommons.org/licenses/by/4.0/), but has been modified for reasons of consistency of the various chapters (Julia Lifanov, Juan Linde-Domingo, Maria Wimber).

Abstract

Memories are thought to undergo an episodic-to-semantic transformation in the course of their consolidation. We here test if repeated recall induces a similar semanticisation, and if the resulting qualitative changes in memories can be measured using simple feature-specific reaction time probes. Participants studied associations between verbs and object images, and then repeatedly recalled the objects when cued with the verb, immediately and after a two-day delay. Reaction times during immediate recall demonstrate that conceptual features are accessed faster than perceptual features. Consistent with a semanticisation process, this perceptual-conceptual gap significantly increases across the delay. A significantly smaller perceptual-conceptual gap is found in the delayed recall data of a control group who repeatedly studied the verb-object pairings on the first day, instead of actively recalling them. Our findings suggest that wake recall and offline consolidation interact to transform memories over time, strengthening meaningful semantic information over perceptual detail.

Introduction

One powerful way to protect memories against forgetting is to recall them frequently. Decades of research on the testing effect have shown such a protective effect, suggesting that repeated remembering stabilizes newly acquired information in memory (Abott, 1909; Butler & Roediger, 2007; Dunlosky et al., 2013; Gates, 1917; Roediger & Butler, 2011; Roediger & Karpicke, 2006). It is unknown, however, whether all aspects of a memory equally benefit from active recall. The aim of the present work was to investigate the qualitative changes in memories that occur with time and repeated remembering. We used feature-specific reaction time probes to measure such changes in lab-based visual memories. Specifically, we expected to observe a transformation along a detailed-episodic to gist-like-semantic gradient, based on several strands of research indicating that memories become "semanticised" in the process of their stabilisation.

Dominant theories of the testing effect make the central assumption that active recall engages conceptual-associative networks more so than other practice techniques such as repeated study (Bjork, 1975; Carpenter, 2011; Kolers & Roediger, 1984). The elaborative retrieval account suggests that during recall, a conceptual relationship is established between initially separate episodic elements to unify them into a coherent memory[9]. Similarly, the mediator effectiveness hypothesis (Pyc & Rawson, 2010) states that testing promotes long-term retention by evoking mediator representations, which are concepts that have meaningful overlap with a memory cue and target (Carpenter, 2011). Together, this work suggests that remembering co-activates semantically related concepts, more than restudy, and can thereby contribute to the long-term storage of newly acquired memories by linking them to already established, related concepts.

Other authors have made similar assumptions from a more neurobiologically and computationally motivated perspective (Antony et al., 2017), drawing a parallel between the processes stabilizing memories via online recall, and the processes thought to consolidate memories via offline replay, including during sleep. In this online consolidation framework of the testing effect, active recall activates a memory's associative index in the hippocampus, together with the neocortical nodes representing the various elements contained in the memory. As a result of this simultaneous activation, links between the active elements are strengthened (HEBB, 1949). Moreover, because recall tends to be somewhat imprecise, more so than re-encoding, activation spreads to associatively or conceptually related elements, providing an opportunity to integrate the new memory with related information. This presumed stabilization and integration is strongly reminiscent of the hippocampal-neocortical dialogue assumed to happen during sleep-dependent memory replay (Frankland & Bontempi, 2005), resulting in the integration of new memories into existing relational knowledge, and the strengthening of conceptual/schematic links between memories (Káli & Dayan, 2004). Critically, many consolidation theories assume that this reorganization goes along with a “semanticisation” of memories, such that initially detail-rich episodic memories become more gist-like and lose detailed representations over time and with prolonged periods of consolidation (Dudai et al., 2015; McClelland et al., 1995; Sekeres et al., 2018; Winocur & Moscovitch, 2011). Based on these parallels between wake retrieval and offline consolidation, the present study tested whether repeated recall specifically induces a behaviourally measurable “semanticisation” that goes beyond the effects that naturally occur over time.

In the human memory consolidation literature, much of the empirical evidence for semanticisation comes from neuroimaging studies showing a gradual shift in the engagement of hippocampus and neocortex during recent and remote recall, or studies tracking representational changes in memories over time (Dudai et al., 2015; Tompary & Davachi, 2017). Recent work even suggests that the neocortical changes that accompany such shifts can occur rapidly, across repeated exposures to episodic events on the same day (Brodt et al., 2016, 2018), and that these changes are then further stabilized through subsequent periods of sleep (Himmer et al., 2019). Behavioural studies, on the other hand, have largely relied on scoring of autobiographical or other descriptive verbal memory reports for central gist versus peripheral details, and yielded robust evidence for a detail-to-gist gradient (Moscovitch et al., 2016; Sekeres et al., 2016). The present study used a different approach, asking if semanticisation via recall can be observed in reaction times (RTs) that specifically reflect the speed with which participants can access higher-level conceptual and lower-level perceptual features of visual object memories.

This method was recently introduced by Linde-Domingo, Treder, Kerrén, & Wimber (2019). They showed that when participants are retrieving visual objects from memory, conceptual aspects (e.g., Does the recalled image represent an animate or inanimate object?) are accessed more rapidly than perceptual aspects (e.g., Does the recalled image represent a photo or a drawing?). In sharp contrast, RTs were consistently faster to perceptual than conceptual questions when the image was physically presented on the screen. This flip suggests that recalling a memory progresses in the opposite direction from visual perception, reactivating the core meaning first before back-propagating to sensory details. Such semantic prioritisation is plausible considering that the hippocampus is most directly and reciprocally connected with late sensory processing areas assumed to represent abstract concepts (Felleman & Essen, 1991; Suzuki & Amaral, 1994). Both online retrieval and offline replay of hippocampus-dependent memories can therefore be assumed to preferentially activate conceptual features of a memory, and this prioritisation may over time produce a semanticized memory compared with the one originally encoded. With this background in mind, and an adapted version of the described RT paradigm, we here investigate whether repeated retrieval enhances the semanticisation of memories over time compared to repeated study.

In this work, two groups of participants learn novel verb-object pairings at the beginning of day 1 (Fig. 3.1), and then immediately practice the associations six times overall. Subjects in the retrieval group practice by actively recalling the object image from memory when cued with the verb, and answering conceptual and perceptual questions about the recalled object as fast as possible. Subjects in the restudy group instead practice by re-encoding the intact verb-object pairings, answering the conceptual or perceptual question while seeing the object on the screen. All participants return to the lab 48h later for a delayed cued recall test, where each verb-object pairing is probed once more with a conceptual and a perceptual question. Feature-specific reaction times (RTs) are used as a measure of accessibility to lower-level perceptual or higher-level conceptual object features. We show that the reaction time gap between perceptual and conceptual features increases across the two-day delay, indicative of time-dependent semanticisation, and that active retrieval plays a central role in this presumed semanticisation. Dependency analyses also suggest that object features are remembered and forgotten in a hierarchical fashion, and that recall becomes more dependent on conceptual object features over time.

Methods

Participants

Previously published work has found an effect size of *d* = .55 for the perceptual-conceptual gap in RTs during retrieval (Linde-Domingo et al., 2019). We expected an effect size at least as large on day 2 in the repeated retrieval group. A power analysis in G*Power (Faul et al., 2009) with *d* = .55, *α* = .05 and a power of 0.9 suggested that a sample size of at least 30 was required to detect an existing effect in the retrieval group. The effect of most interest in the retrieval group was a significant interaction between testing day and question type, specifically such that the gap between conceptual and perceptual RTs would significantly increase from day 1 to day 2. The power for this interaction contrast could not be estimated a priori from the work of Linde-Domingo et al. (2019). To have sufficient power to detect an increase in the perceptual-conceptual gap, we decided to double their sample size, aiming for 48 subjects in the retrieval group. A sensitivity analysis in G*Power (Faul et al., 2009) on a two-by-two repeated measures ANOVA with an alpha of .05, a power of 0.9 and a sample size of n = 49 (as we eventually acquired) revealed a required effect size of *f* = .47 for the within-factor effect (see results section for corresponding posthoc effect sizes).

The second comparison of interest in this study was a contrast between the perceptual-conceptual gap on day 2 (i.e., delayed test) in the retrieval and the restudy groups. Again, since the effect size could not be estimated directly from previous work, we aimed for *n*=24 participants in the restudy group based on Linde-Domingo et al. (2019) using *n*=24 within multiple groups to do between group comparisons. We thus aimed for a sample size of *n*=72 overall for the critical comparison of the retrieval and the restudy group. A sensitivity analysis on a two-by-two repeated measures ANOVA with an alpha of .05, a power of 0.9 and a sample size of n = 73 revealed a required effect size of *f* = 0.38 for the interaction effect (see results section for corresponding posthoc effect sizes).

Fifty-seven healthy volunteers from the local student population in Birmingham participated in the retrieval condition (45 female and 12 male, mean age (M_{age}) = 19.95, standard deviation (SD_{age}) = .79), of which eight were excluded due to absence on the second testing day or missing data. Another 26 volunteers participated in the restudy group (21 female and 5 male, M_{age} = 18.92, SD_{age} = .89), of which two were excluded due to absence on the second testing day. Our final sample thus consisted of 49 participants in the retrieval group and another 24 participants in the restudy group. All participants were informed about the experimental procedure, underwent a screening questionnaire (including sleep and consumption behaviour 24h before the experiment) and gave their written informed consent. The research was approved by the STEM ethics committee of the University of Birmingham.

Material

The paradigm was an adapted version of the visual verb-object association task designed by Linde-Domingo et al. (2019). Our stimulus materials consisted of 64 action verbs and 128 pictures of everyday objects, all presented on white backgrounds (see Fig. 3.1a and previous work (Linde-Domingo et al., 2019) for more detailed information about the source and manipulation of pictures (BOSS database, www.gimp.org (Brodeur et al., 2010)) and verbs). Importantly, objects were categorized into two conceptual classes, i.e. animate vs inanimate objects; and two perceptual classes, i.e. black line drawings vs coloured photographs. We pseudo-randomly drew 64 images per participant according to a fully balanced scheme, such that each of the two-by-two categories included the same number of pictures (16 animate-photographs, 16 animate -drawings, 16 inanimate-photographs, 16 inanimate-drawings). Action verbs were randomly assigned to images in each participant, and were presented together with pictures centrally overlaid on a white background. The stimulus presentation and timing and accuracy information collection was controlled by scripts written in Matlab 2017a (www.mathworks.com) and the Psychophysics Toolbox Version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

For the analysis we used customized Matlab code (https://www.mathworks.com/matlabcentral/fileexchange/64980-simple-rm-mixed-anova-for-any-design by Caplette, 2021; *Simple RM/Mixed ANOVA for Any Design*, n.d.); https://www.mathworks.com/matlabcentral/fileexchange/6874-two-way-repeated-measures-anova by Schurger, 2021; *Two-Way Repeated Measures ANOVA*, n.d.), G*power 3.1 (Faul et al., 2009). Figures were created using the raincloud plots Version 1.1 (M. Allen et al., 2019; Kirstie Whitaker et al., 2019), ColorBrewer 2.0 (from www.ColorBrewer.org by Cynthia A. Brewer, Geography, Pennsylvania State University) and colorbrewer schemes 2.0 for Matlab (https://www.mathworks.com/matlabcentral/fileexchange/34087-cbrewer-colorbrewer-schemes-for-matlab by Charles, 2021; *Cbrewer*, n.d.) and the Inkscape 1.0.1 (https://inkscape.org/).

Procedure

In both experimental groups, participants were informed about the experimental procedure, asked to sign an informed consent form, and to perform a training run. After completion of this training, participants continued to the experimental task (Fig 3.1.b). On day 1, participants performed eight task blocks, each including an encoding block with eight trials, a 20s distractor task and three practice cycles, each including two times eight practice trials. Returning after 48h, participants finished the experiment with a final test consisting of a single retrieval cycle (see below for details). Before leaving, participants completed a written cued recall test. Participants in both experimental groups had been clearly and repeatedly informed about the final recall on test day 2 before carrying out the task on test day 1. It took participants about 70 min to perform the task on day 1, and about 20 min on day 2.

Encoding

In each encoding block (Fig. 3.1b), participants were instructed to study 8 novel verb-object pairings. A fixation cross was presented to the participants for a jittered time period between 500 and 1500ms. An action verb was then presented for 1500ms before an object was shown for a maximum time period of 7s. To facilitate learning, participants were instructed to form a vivid visual mental image using the verb-object pairing. Once they had formed a strong mental image, participants were asked to press the up-arrow key, which moved the presentation on to the next trial. In the repeated retrieval group, it took participants 4.65s on average, and in the restudy group it took them 4.34s to proceed to the next trial ($SD_{retrieval} = 1.77$; $SD_{restudy} = 1.65$).

Distractor

After each encoding block, participants performed a self-paced distractor task for 20s, indicating as fast as possible whether each of the consecutively presented numbers on the screen was odd or even, using a left/right key press. Feedback on the percentage of correct responses was provided at the end of each distractor phase.

Practice

Repeated retrieval group

The retrieval trials started with the presentation of a fixation cross, jittered between 500 and 1500ms, and followed by the conceptual (animate/inanimate) or perceptual (photo/drawing) question that was displayed for 3s, enabling participants to mentally prepare to recall the respective feature of the object that was relevant on a given trial. The verb was then displayed above the response alternatives (e.g., animate/inanimate), and participants had to retrieve the associated object and answer the question as fast as possible. Verb and question were displayed for a maximum period of 10s or until the participant selected a response to the question. The questions were answered with left, downward and right-arrow keys.

Restudy group

In the restudy group, the paradigm was kept as similar to the repeated retrieval group as possible, including an attempt to equate average exposure times during practice (for which reason the restudy group data was collected after the retrieval group). The restudy trial was initiated with a fixation cross with the same jitter (500-1500ms) as in the retrieval group, and followed by the conceptual or perceptual question that was displayed for 3s. The verb cue and object then appeared together above the question. Again, participants were asked to use the 3s period to prepare mentally to answer the question. When the object appeared, participants were instructed to first answer the question about the object they saw on the screen as fast as possible, and then use the remaining time to restudy the verb-object pair. In order to equate exposure times between the two groups, we set the trial duration of each of the three restudy cycles to the average response time of each of the three individual retrieval cycles from the previously collected retrieval group (cycle 1: 2.2s, cycle 2: 1.9s, cycle 3: 1.8s).

Retrieval and restudy blocks setup

Participants of both groups completed three consecutive practice cycles, in each of which they practiced all eight verb-object associations they had learned in the previous encoding block twice, once answering a conceptual and once answering a perceptual question. This sums up to six practice trials per learned association, three with each question type. The order of the conceptual and perceptual questions within cycles was counterbalanced as follows: In each of the three cycles, one half of the stimuli was first probed with a conceptual question and the other half with a perceptual question first. Additionally, we controlled that each of the eight question-order possibilities occurred equally often for each object type (i.e., animate-photo, animate-drawing, inanimate-photo, inanimate-drawing). The percentage of correct trials was provided after the third practice cycle.

Final Test

After 48 hours, participants were asked to complete a final test, in which they performed one cued recall block with the same procedural set-up as on day 1 in the retrieval group. Participants were presented with a conceptual/perceptual probe, and asked to answer this question as fast as possible when cued with a verb. Each object was recalled once with each question type. Here, half of the stimuli was first probed with a conceptual question and the other half with a perceptual question, randomized independently with respect to the first testing day. Finally, participants were given a paper sheet, displaying all 64 action verbs, next to which they were asked to write down a verbal description of the associated object.

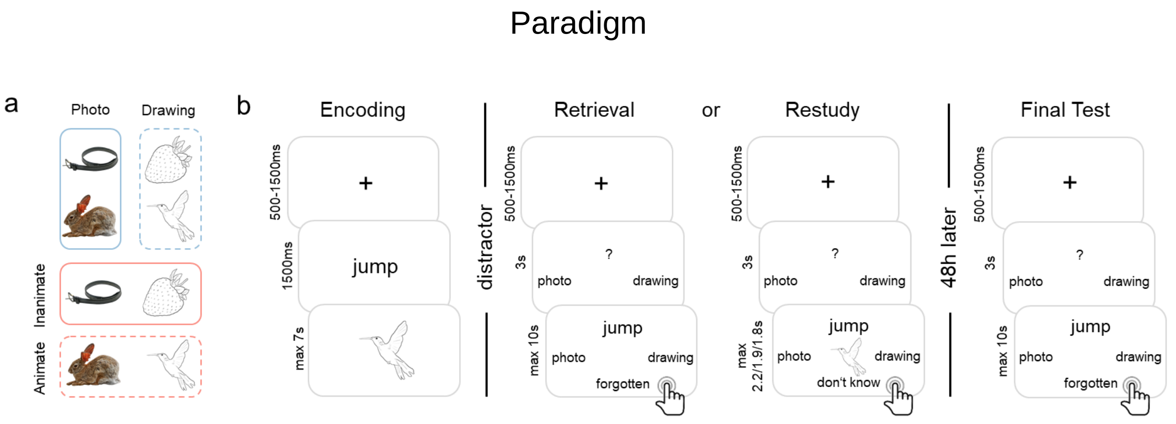

Figure 3. 1

Overview of stimuli and task. a) Design of the stimuli. The 64 pictures used in any given participant were orthogonally split into 32 drawings and 32 photographs, out of which 16 were animate and 16 inanimate objects, respectively. Each object could thus be classified along a perceptual (photo/drawing, blue) or conceptual (animate-inanimate, red) dimension. b) One prototypical task block of the paradigm within the repeated retrieval/restudy group. Both groups performed eight blocks, each starting with the encoding of eight novel verb-object associations. After a 20s distractor task, each of the eight associations was practiced twice in each of the three practice cycles, once with a conceptual, once with a perceptual question, and reaction times (RTs) were measured on each of the overall 6 practice trials. The maximum response time in each practice cycle of the restudy group was set to the average response time of the corresponding cycle in the retrieval group. After 48 hours, participants returned to complete a final test, where again each association was tested once with each of the two question types, with RTs being recorded, as indicated by the button press symbols. Finally, a written cued recall test was performed. Stimuli depicted are chosen from the BOSS database (https://sites.google.com/site/bosstimuli/home (Brodeur et al., 2010), https://creativecommons.org/licenses/by-sa/3.0/) and customized with free and open source GNU image manipulation software (www.gimp.org; see Linde-Domingo et al., 2019). Figure adapted from Linde-Domingo et al. (2019).

Data preprocessing

During data preparation, all RTs faster than 200ms were excluded from the study. For the main analyses, RTs of correct trials were averaged and the standard deviation was calculated for both conceptual and perceptual questions, separately for the retrieval and the restudy group, and separately for the trials of each individual practice cycle per subject. Trials exceeding the average RT of a given cycle by more than three times the standard deviation were excluded in further RT analyses (Linde-Domingo et al., 2019). In the repeated retrieval group, 98.16 % of the data remained after trimming the RTs of correct responses, whereas in the restudy group, 99.60% remained for our main analyses. Testing for a relationship between day 2 RTs and sheet responses, the RTs we used included correct, incorrect, and “don’t remember” button press responses and trials exceeding the average RT of the given cycle by more than three times the standard deviation were excluded after the categorization of RTs.

To prepare the accuracy data, trials with responses faster than 200 ms, and objects with a missing response for either of both questions on one cycle were excluded in the related cycle. After this accuracy trimming, 99.39% of the repeated retrieval data and 93.26% of the restudy data remained.

Analysis

In the past decades, there has been ongoing discussion about the validity of choosing mean RTs over medians (Miller, 1988, 2020; Rousselet & Wilcox, 2020). Here, we decided to use mean RTs similarly to previous work (Linde-Domingo et al., 2019) to easily compare our findings to the ones of Linde-Domingo et al. (2019). To counteract a biased estimation of central tendency of RTs on the first level (i.e. within subjects), we used a large number of repetitions per condition (64 responses to a perceptual and conceptual questions each within each repeated cycle) on the one hand and trimmed our data as described in the section above on the other hand. Finally, on the second level, participants' mean RTs within individual conditions met the normality assumptions to proceed to statistical analyses.

To assess our main hypotheses of interest, including RT differences over time and between groups, we performed repeated measures (rm) ANOVAs on the RTs. Testing for a semanticisation over time, we included cycles (cycle 3, cycle 4) and question type (perceptual, conceptual) as within-subjects factors. Control analyses were added that used the averaged day 1 data instead of cycle 3, such that the relevant factors were day (day 1, day 2) and question type (perceptual, conceptual). Exploring the RT gap between groups on day 2, we used question type (perceptual, conceptual) as within-subjects factor and group (retrieval, restudy) as between-subjects factor. To replicate a reversed stream, we again used an rmANOVA with question type as within-, and group as between-subjects factor. Additional rmANOVAs were carried out on accuracies to test for dependency between two features. Here, we used cycles and question type as within-subject factors. For posthoc analyses, we performed two-sided t-tests. Two-sided t-tests were also used on sheet response accuracies, to demonstrate a testing effect. Finally, two-sided t-tests were performed on RT gaps and task accuracies categorized according to sheet accuracies.

Results

Semanticisation over time

Participants in the retrieval group (*n = 49*) immediately practiced the newly learned verb-object associations via cued recall. They did so six times overall, in three pseudo-randomized cycles that each contained one perceptual and one conceptual feature probe. We first tested the retrieval group data for a time-dependent semanticisation, assuming that memory recall prioritises access to conceptual over perceptual features, and that this prioritisation increases over the two days with increasing semanticisation. Importantly, we wanted to isolate the transformation of episodic memories that occurs purely with passage of time, as opposed to the changes that occur already on the first day across the repeated practice trials. Using feature-specific reaction times, we thus compared the memory representation at the end of day 1 (i.e., cycle 3), after completed learning and practice, to the representation on day 2. We expected an increased perceptual-conceptual RT gap on the delayed day 2 test, compared to the end of day 1. A 2 (recall cycle: end of day 1 vs day 2) by 2 (question type: conceptual vs perceptual) repeated measures analysis of variances (rmANOVA) on the RT data of the repeated retrieval group only (Fig. 3.2) showed a main effect of recall cycle ($F(1,48) = 71.44$, $p < .01$) indicating slower responses on day 2 than day 1, and a main effect of question type ($F(1,48) = 29.58$, $p < .01$) with conceptual questions being consistently answered faster than perceptual questions. Critical to our first main hypothesis, the rmANOVA also revealed a significant interaction ($F(1,48) = 19.87$, $p < .01$) between the two factors, indicating that the conceptual-over-perceptual RT advantage changed across days. A posthoc power analysis in G*Power revealed an effect size of $f = .64$ for the interaction effect, which exceeds our required effect size of $f = .47$. Average

RTs confirmed that the interaction was produced by an increasing perceptual-conceptual RT gap from the end of day 1 (M_{day1} = 40 msec, SD_{day1} = 194 msec) to day 2 (M_{day2} = 290 msec, SD_{day2} = 359 msec), in line with the semanticisation hypothesis. Note that the interaction is equally robust when using the averaged day 1 reaction times within participants (F(1,48 = 20.11, p < .01), rather than the cycle 3 data. Together, these results suggest that semantic features preferentially benefit from passage of time after retrieval practice, in line with semanticisation.

We additionally tested whether the perceptual-conceptual gap in the retrieval group already changed across cycles on day 1, in line with a "fast consolidation" process (Antony et al., 2017). A 3 (cycle: 1, 2, 3) by 2 (question type: conceptual or perceptual) repeated measures ANOVA of the day 1 RTs (Fig. 3.2) revealed a significant main effect of cycle (F(2,96)) = 102.44, p < .01), with participants becoming faster over time, as well as a significant main effect of question type (F(1,48) = 5.01, p = .03), with conceptual questions being answered overall faster than perceptual ones, generally replicating the results of Linde-Domingo et al. (2019). However, the cycle by question type interaction was not significant (F(2,96) = .42, p = .66), indicating that the perceptual-conceptual gap did not change significantly across practice cycles. The immediate recall data of this study thus provide no behavioural evidence for a fast semanticisation.

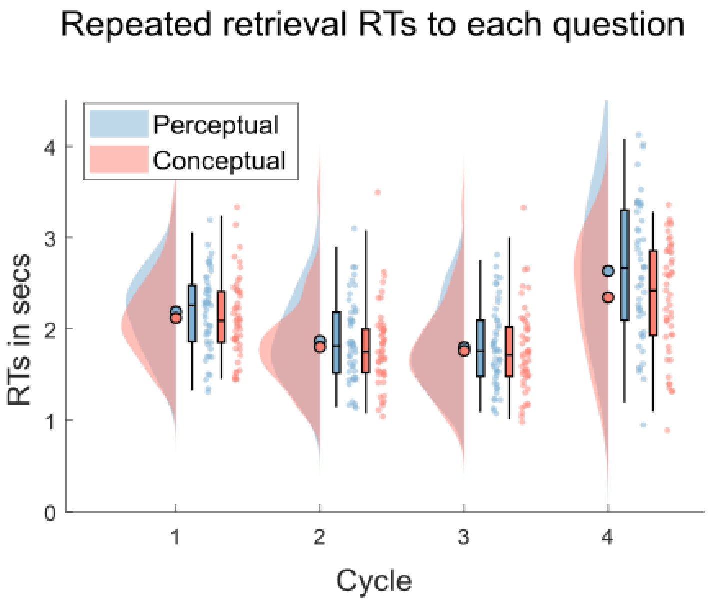

Figure 3. 2

Retrieval reaction times (RTs), separate by question and repetition. The gap between perceptual and conceptual RTs significantly increases from day 1 to day 2 (interaction between question type and repetition (F(1,48) = 19.87, p = .00, d = .64)), in line with a semanticisation process over time. RTs in the repeated retrieval group are depicted for each cycle and question type. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Blue represents perceptual, red conceptual responses. N = 49 independent subjects.

Stronger semanticisation after repeated retrieval than restudy

To test our second hypothesis, that repeated retrieval leads to a stronger delayed perceptual-conceptual gap than repeated study, we investigated the RT gap on the second testing day in both groups. If semanticisation over time is enhanced by retrieval practice, this should be reflected in a larger RT gap in the retrieval group (*n = 49*) in contrast to the restudy group (*n = 24*). A 2 (practice condition: retrieval vs restudy) by

2 (question type: conceptual vs perceptual) mixed ANOVA on the RTs of day 2 (Fig. 3.3) revealed no main effect of practice condition ($F(1, 71) = 1.41$; $p = .24$), and a main effect of question type ($F(1, 71) = 16.92$; $p < .01$) with overall shorter RTs for conceptual than perceptual questions. As hypothesized, a significant interaction was found between question type and practice condition ($F(1, 71) = 5.21$; $p = .03$). Our posthoc power analysis on the interaction effect revealed an effect size of $f = .27$, which does not exceed but is comparatively close to our required effect size of $f = .38$. This interaction was due to an effect in the expected direction, with a higher perceptual–conceptual difference in the repeated retrieval group ($M_{retrieval}$ = 290 msec, $SD_{retrieval}$ = 359 msec) than in the restudy group ($M_{restudy}$ = 83 msec, $SD_{restudy}$ = 372 msec), in line with the interpretation that repeated retrieval leads to more pronounced semanticisation than repeated study. Specifically, we found that perceptual questions are answered only slightly faster in the retrieval group ($M_{retrieval}$ = 2.63 sec, $SD_{retrieval}$ = .75 sec) in comparison to the restudy group ($M_{restudy}$ = 2.74 sec, $SD_{restudy}$ = .86 sec). In contrast, conceptual RTs show a comparatively stronger difference between repeated retrieval ($M_{retrieval}$ = 2.34 sec, $SD_{retrieval}$ = .61 sec) and restudy ($M_{restudy}$ = 2.66 sec, $SD_{restudy}$ = .84 sec), suggesting that the interaction is mainly caused by faster access to conceptual features in the retrieval group, in line with a retrieval-induced semanticisation.

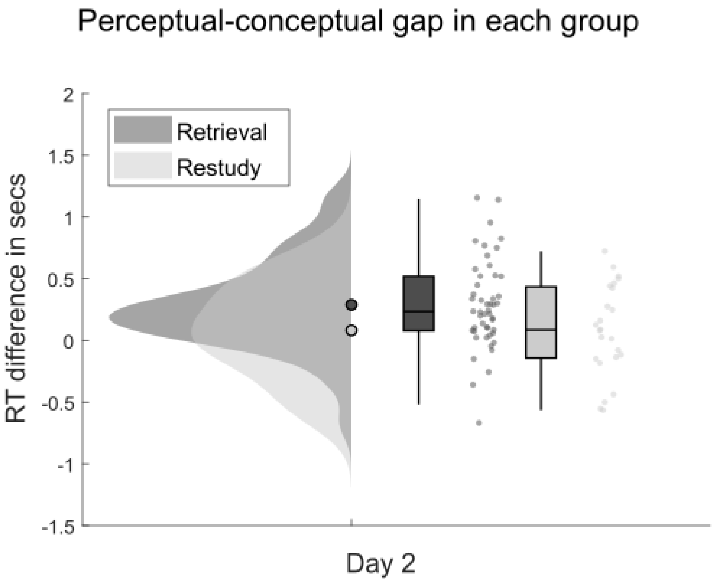

Figure 3. 3

Perceptual-conceptual reaction time (RT) gap in each group on day 2. Repeated retrieval yields a stronger perceptual-conceptual RT gap than restudy on the delayed test (two-sided t(71) = 2.28, p = .03, CI = [.03, .39]). Perceptual-conceptual RT gaps are depicted for retrieval and restudy on day 2. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Dark grey represents retrieval data, light grey represents restudy data. N = 49 independent subjects in the retrieval group, n = 24 independent subjects in the restudy group.

To assure that the differential RT gap between groups is not a consequence of the unequal sample sizes, we randomly drew 5000 subsamples of size n = 24 of the repeated retrieval group, to equalize the group size to the one of the restudy group (n = 24). We then computed the z-score between the mean RT gap in the restudy group and the distribution of mean RT gaps of the resampled retrieval groups. First, we confirmed that, not surprisingly, the mean RT gaps in the subsampled retrieval groups (n = 24) distributed around the mean RT gap observed for the larger sample (n = 49).

Across the 5000 sub-samples, the perceptual-conceptual RT gap in the retrieval group had a mean of 290 msec (95% *CI* = [203 msec to 376 msec]). Critically, the mean RT gap in the restudy group (*mean* = 83 msec) showed no overlap with this confidence interval, and in fact we found zero cases amongst the 5000 subsamples where the restudy RT gap was equal to, or larger than, the retrieval RT gap. Comparing the restudy gap to the empirical distribution of retrieval RT gaps thus resulted in a highly significant z-score (*z* = -3.95, *p* < .01) and an empirical p-value <.01. This result confirms that the stronger semanticization in the repeated retrieval than restudy group also holds with equal sample sizes (Fig. 3.4).

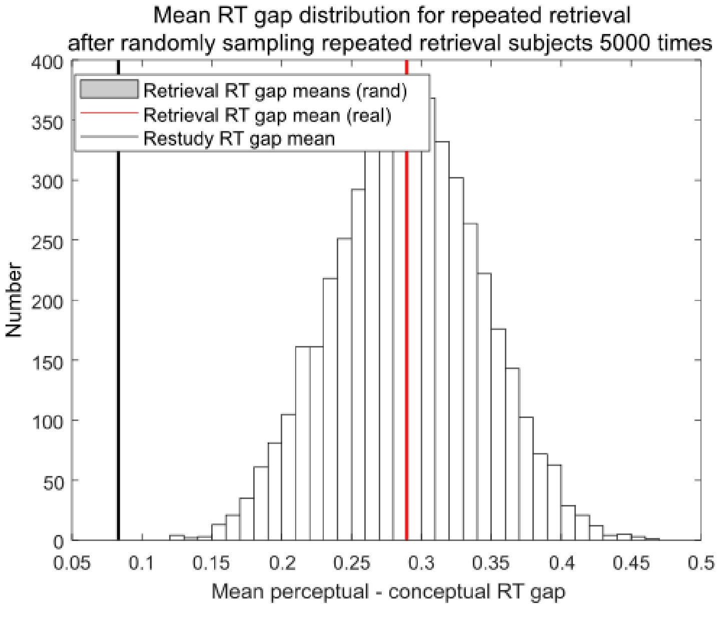

Figure 3. 4

Subsampling methods showing higher perceptual-conceptual reaction time (RT) gap in retrieval on day 2. The distribution of mean RT gaps after drawing subsamples of the repeated retrieval group 5000 times shows that repeated retrieval yields a stronger semanticisation than restudy in 100% of the cases, even when using equally sized samples (one-sided empirical p = .00; z = -3.95, p = .00). The black line represents restudy data, the red line retrieval data, and the distribution is created by randomly drawing *subsamples from the retrieval data with n = 49 independent subjects in the retrieval group and n = 24 independent subjects in the restudy group.*

A replication of the reversed retrieval stream

Next, we analysed the data of the first day to test if we could replicate a reversal of the RT patterns between memory retrieval and visual exposure, conceptually replicating previous results(Linde-Domingo et al., 2019). Based on these findings, we expected faster RTs to conceptual than perceptual questions (i.e. a reverse stream) in the retrieval group that practiced the associations via active recall (Fig. 3.2), and faster perceptual than conceptual RTs (i.e., a forward stream) in the restudy group that practiced the associations by visual re-exposure. We therefore performed a mixed 2 (practice condition: retrieval vs restudy) by 2 (question type: conceptual vs perceptual) ANOVA on the day 1 data, averaging RTs across the 3 cycles. Apart from a main effect of task ($F(1,71) = 71.13$, $p < .01$), and no main effect of question type ($F(1,71) < .01$, $p = .98$), this analysis revealed the expected, significant cross-over interaction ($F(1,71) = 9.24$, $p < .01$) with faster responses for perceptual questions than conceptual ones in restudy ($M_{per} = 1.13$ sec, $SD_{per} = 0.21$ sec; $M_{con} = 1.19$ sec, $SD_{con} = 0.19$ sec) and vice versa in retrieval ($M_{per} = 1.95$ sec, $SD_{per} = 0.42$ sec; $M_{con} = 1.89$ sec, $SD_{con} = 0.44$ sec).

Hierarchical relationship between remembered features

Two further analyses were conducted on accuracy data, rather than reaction times. First, we investigated a possible hierarchical dependency between perceptual and conceptual features as shown in recent work (Balaban et al., 2020) and how this relationship changed over time. All correct and incorrect recall trials with a response time above 200ms were sorted into four categories, depending on whether participants remembered both features, only perceptual features, only conceptual features or none. In line with previous work (Balaban et al., 2020; Joensen et al., 2018), we expected that over time, the majority of items would be forgotten in a holistic manner, such that items that were fully remembered ("both features correct") on day 1 would be fully forgotten ("none correct") on day 2. For the present purpose, we were however particularly interested in the two response categories indicating partial remembering (i.e., "conceptual only" and "perceptual only" recall trials). Here, a hierarchical dependence in a reverse memory reconstruction stream predicts a particular pattern: higher-level conceptual information would need to be accessed before the lower-level perceptual information can be reached. As a result, participants should be relatively likely to remember the conceptual feature ("Was it animate or inanimate") while forgetting the perceptual one ("Was it a photo or drawing"), but there should be very few trials where they remember the perceptual while forgetting the conceptual feature, except for random guesses. We thus expected to see a significant difference in the number of responses falling into these two categories already on the immediate day 1 recall. If semanticisation increases this hierarchical dependency, the gap in the proportion of conceptual-only and perceptual-only recalls should significantly increase across the 2-day delay.

We carried out a 2 (recall cycle: end of day 1 vs day 2) by 2 (features remembered: conceptual-only vs perceptual-only) rmANOVA to test this hypothesis. This analysis revealed a main effect of repetition ($F(1,48) = 53.97$, $p < .01$), and a main effect of features remembered ($F(1,48) = 27.10$, $p < .01$), the latter effect in line with hierarchical recall. Importantly, we also found the expected significant interaction ($F(1,48) = 8.21$, $p < .01$), reflecting the observation that over time, the number of objects for which the conceptual but not the perceptual feature could be remembered increased significantly more than the number of objects for which the opposite pattern was true (Fig. 3.5). The interaction is equally robust when using the averaged day 1 accuracies ($F(1,48) = 14.31$, $p < .01$), rather than the cycle 3 data.

Note that the data presented in Figure 3.5 is not corrected for estimated random guesses (Balaban et al., 2020), as such a correction would have turned most proportions negative, and therefore seemed to be an overestimation of guesses in our dataset. However, since the guesses of a particular cycle are assumed to be distributed equally across response categories within that cycle, correcting does not change the outcomes of the statistical analysis (corrected repetition effect $F(1,48) = 55.52$, $p < .01$), corrected features remembered effect ($F(1,48) = 27.10$, $p < .01$), and corrected interaction ($F(1,48) = 8.21$, $p < .01$)). Again, the interaction was also significant when comparing the average day1 data to day2 ($F(1,48) = 14.31$, $p <.01$).

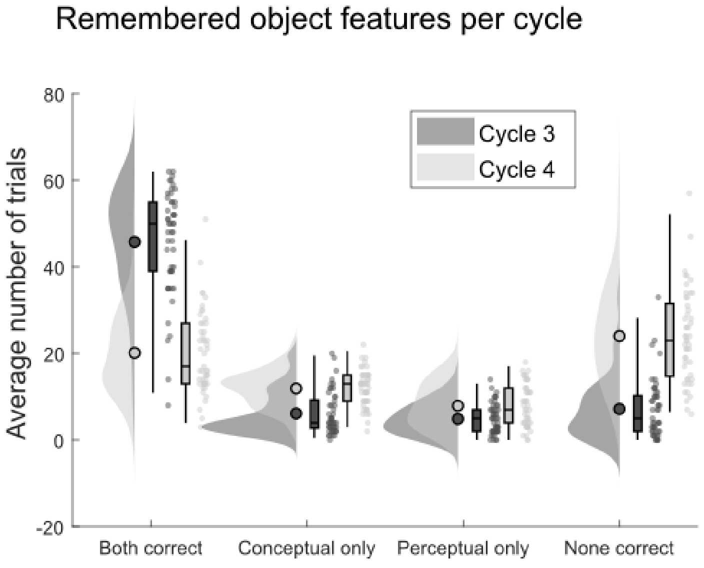

Figure 3. 5

Remembered and forgotten object features, separate for cycle 3 and 4. The data shows a hierarchical dependency between conceptual and perceptual memory features that increases over time (interaction between feature remembered and cycle F(1,48) = 8.21, p = .01, d = .41). The average number of objects in each response-category for cycle 3 (end of day 1) and cycle 4 (day 2) of all subjects in the repeated retrieval group are shown. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Dark grey represents cycle 3, light grey represents cycle 4. N = 49 independent subjects.

A replication of the testing effect

Finally, we also assessed the written cued recall responses on the second day to investigate if a general testing effect was found in our sample. To do so, we compared the accuracy in the written sheet responses between both experimental groups, using two independent sample t-tests. All written responses were categorized by two experimenters as “specific correct/incorrect” and “coarse correct/incorrect” responses. Here, specific correct includes retrieving the exact object label (e.g., parrot), whereas coarse correct responses also include correct descriptions of the object's category (such as "colourful bird" for "parrot"). Two-sided t-tests revealed that participants in the repeated retrieval group (M_{coarse} = .30, SD_{coarse} = .19; $M_{specific}$ = .25, $SD_{specific}$ = .18) recalled significantly more associations than restudy participants (M_{coarse} = .20, SD_{coarse} = .18; $M_{specific}$ = .16, $SD_{specific}$ = .17) using either scoring scheme, specific ($t(71) = 2.06$, $p = .04$, CI = [.00, .17]) and coarse ($t(71) = 2.16$, $p = .03$, CI = [.01, .19]).

We also wanted to make sure that the significant accuracy difference between groups, on the written paper and pencil test, is not influenced by the difference in sample sizes. We randomly drew 5000 subsamples from the repeated retrieval group with size n = 24, to equate the restudy group, and then computed the z-score between the restudy group mean and the retrieval sample distribution, both for specific and coarse responses. We found that the restudy accuracy significantly differed from the repeated retrieval accuracy distribution for both coarse (*z-score* = -3.63, $p < .01$, empirical $p < .01$) and specific accuracies (*z-score* = -3.45, $p < .01$, empirical $p < .01$). For both scoring methods, the mean accuracies of the restudy group (M_{coarse}= 0.20; $M_{specific}$= 0.16) were outside the 95% confidence intervals (CI_{coarse}= [0.25 to 0.34]; $CI_{specific}$= [0.21 to 0.29]), and in fact entirely outside the re-sampled retrieval distributions. This finding confirms that a robust testing effect is present in our data also when equating sample sizes, based on the commonly used cued recall accuracies (Fig. 3.6).

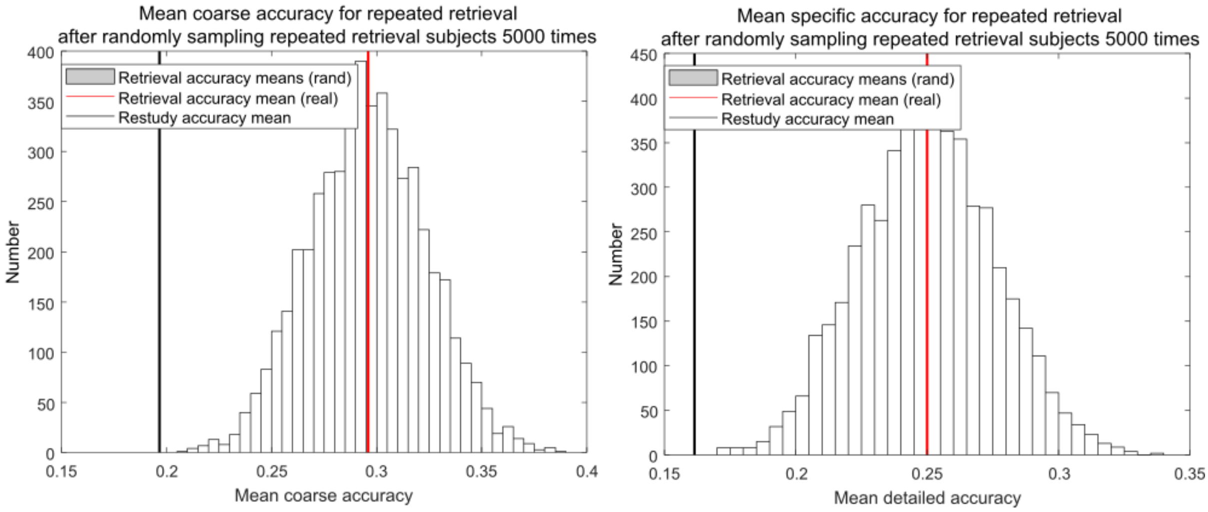

Figure 3. 6

Subsampling methods showing higher memory performance in retrieval on day 2. The distribution of mean sheet response accuracies after drawing subsamples of the repeated retrieval group 5000 times shows that repeated retrieval leads to better accuracies than restudy according to coarse (one-sided empirical p =.00; z = -3.63, p = .00) and specific scoring (one-sided empirical p =.00; z-score = -3.45, p = .00). The black line represents restudy data, the red line retrieval data, and the distribution is created by randomly drawing subsamples from the retrieval data with n = 49 independent subjects in the retrieval group and n = 24 independent subjects in the restudy group.

We were then interested whether the paper-and-pencil based cued recall performance was related to the size of the perceptual-conceptual gap in feature-specific reaction time probes. We thus tested whether, within participants, those items for which delayed memory performance is strong enough to support cued recall on the final sheet test show a larger RT gap. To do so, all RTs of day 2 were compared between trials where the corresponding object was remembered on the response sheets (specific/coarse correct), and those where the object was not remembered (specific/coarse incorrect). Results show that the perceptual-conceptual RT gap is significantly larger for correctly than for incorrectly recalled items (*t*(71) = 2.13, *p* = .04, *CI* = [.01, .33] with the specific scoring approach, *t*(71) = 2.65, *p* = .01, *CI* = [.05, .38] with the coarse scoring approach). Decomposing these differences in more detail, we found similar perceptual RTs for correct and incorrect sheet responses (for coarse scoring: M_{per_corr} = 2.54 sec, SD_{per_corr} = .87 sec, M_{per_incorr} = 2.52 sec, SD_{per_incorr} = .97 sec; for specific scoring: M_{per_corr} = 2.50 sec, SD_{per_corr} = .68 sec, M_{per_incorr} = 2.52 sec, SD_{per_incorr} = .97 sec) whereas the conceptual RTs for correct sheet responses (coarse scoring: M_{con_corr} = 2.23 sec, SD_{con_corr} = .59 sec; specific scoring: M_{con_corr} = 2.20 sec, SD_{con_corr} = .62 sec) are faster than those for incorrect sheet responses (coarse scoring: M_{con_incorr} = 2.42 sec, SD_{con_incorr} = .93 sec; specific scoring: M_{con_incorr} = 2.40 sec, SD_{con_incorr} = .89 sec). In contrast to the difference between correct and incorrect perceptual RTs (*t*(71) = .03, *p* =.98, *CI* = [-.19, .19]), the difference between conceptual RTs for correct and incorrect sheet responses is significant with the coarse scoring method (*t*(71) = -2.49, *p* = .02, *CI* = [-.38, -.04]) and thus seems to drive the changed RT gap on day 2 (the specific scoring method did not yield a significant difference for neither feature; t(71) = -.22, *p* = .83, *CI* = [-.21, .17] for perceptual; *t*(71) = -1.95, *p* = .06, *C*I = [-.39, .00] for conceptual questions; Figure 3.7). Again, these findings suggest that items for which a strong episodic trace exists show a larger RT gap, caused by relatively faster access to conceptual item features.

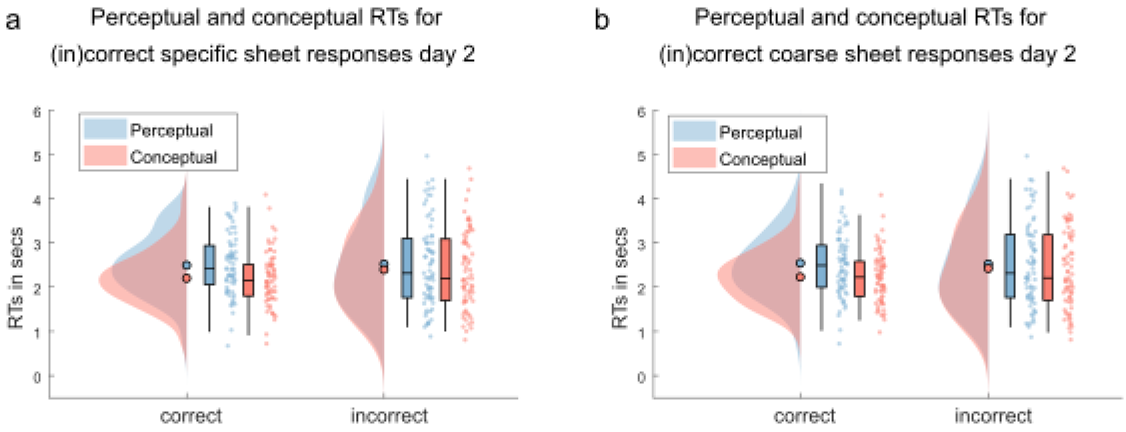

Figure 3. 7

Perceptual and conceptual reaction times (RTs) for (in)correct a) specific and b) coarse written cued recall responses on day 2. Only associations that are remembered in the cued recall test yield a perceptual-conceptual reaction time gap in the task (two-sided test for the gap difference between correctly and incorrectly remembered associations: t(71) = 2.13, p = .04, CI = [.01, .33] with the specific scoring approach, two-sided t(71) = 2.65, p = .01, CI = [.05, .38] with the coarse scoring approach). Perceptual and conceptual RTs are shown as categorized in correct and incorrect specific (a) / coarse (b) sheet responses. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Blue represents perceptual, red conceptual responses. N = 73 independent subjects.

Note that we found a mirrored effect for accuracies, such that participants who performed better on the paper-and-pencil test showed a larger accuracy gap in the button presses, when splitting according to specific (*t*(71) = 3.08, *p* < .01, *CI* = [.03, .15]) and the coarse (*t*(71) = 3.95, *p* < .01, *CI* = [.05, .16]) scoring method (Fig. 3.8).

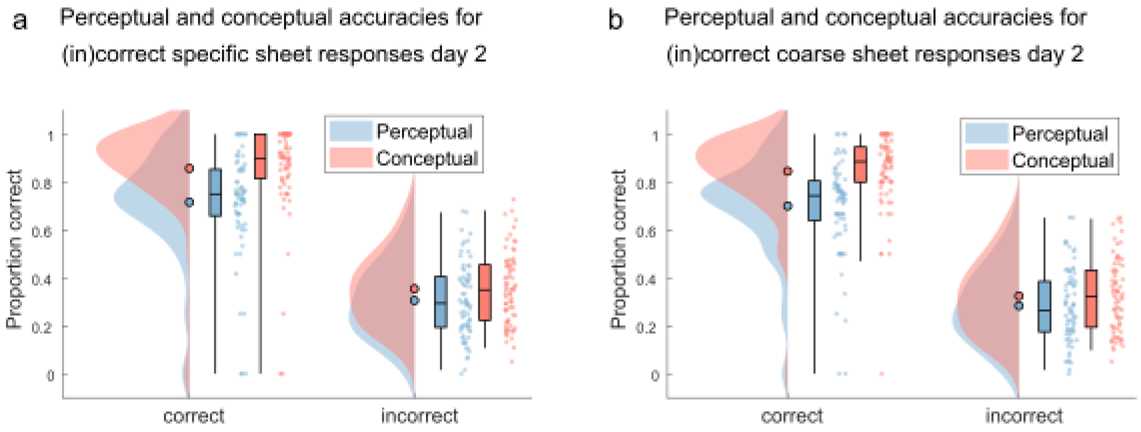

Figure 3. 8

Perceptual and conceptual accuracy performance for (in)correct specific and coarse written cued recall responses on day 2. Associations that are remembered in the cued recall test yield a stronger perceptual-conceptual accuracy gap in the task (two-sided t(71) = 3.08, p = .00, CI = [.03, .15] with the specific scoring approach, two-sided t(71) = 3.95, p = .00, CI = [.05, .16] with the coarse scoring approach). Task accuracies from cycle 3 in the repeated retrieval group have been categorized into correct/incorrect specific (a) and coarse (b) response sheets. Filled circles represent the overall mean, boxplots represent median and 25th and 75th percentiles; whiskers represent 2nd and 98th percentile; dots represent the means of individual subjects. Blue represents perceptual, red conceptual responses. N = 73 independent subjects.

Discussion

Do memories change every time we remember them? Cognitive (Carpenter, 2009; Pyc & Rawson, 2010) and neurobiologically motivated (Antony et al., 2017) theories assume that each active recall constitutes a distinct online consolidation event that systematically changes the nature of the memory, from an initially detail-rich episode to a “semanticised” version of the same event. Two questions were of central interest in the present study. First, we wanted to test if feature-specific probes can be used to reveal this presumed perceptual-to-conceptual transformation (semanticisation) of memories over an initial period of consolidation. Second, we were interested if repeated remembering specifically boosts this transformation compared with repeated study, preserving conceptual information relatively more over time.

To test our first hypothesis of a semanticisation over time, we measured how fast participants were able to recall perceptual and conceptual features of previously memorised objects on the first day, compared with how fast they accessed the same features 48h later. While conceptual information was consistently accessed faster on the immediate and the delayed memory test, the perceptual-conceptual gap significantly increased over the two-day retention period, suggesting that access to conceptual memory features was favoured over access to perceptual features across the temporal delay. This finding is consistent with at least two possible interpretations. High-level semantic information may be prioritised for active consolidation, an ongoing discussion in the consolidation literature (Dudai et al., 2015; Schreiner & Rasch, 2018). Or semantic information might be forgotten at a slower rate than perceptual information, a possibility we return to further below. As also elaborated below, hierarchical forgetting and prioritisation for active consolidation may in fact rely on the same mechanism.

Recent studies do support an active and selective consolidation view. For example, structured, categorical information shows above-baseline enhancement from sleep, compared with detailed, stimulus-unique features of the memorized stimuli (Schapiro et al., 2017). It has thus been suggested that structured information is subject to active consolidation. In terms of functional anatomy, the hippocampus is most directly connected with late sensory areas coding abstract-semantic features of objects

(Felleman & Essen, 1991; Suzuki & Amaral, 1994). Moreover, concept cells in the hippocampus are thought to form the building blocks of episodic memories (Quiroga, 2012). The elements (e.g., objects, people) that constitute an episode are thus likely bound together on the level of meaningful semantic units. During retrieval and offline replay, it is assumed that the linked elements belonging to the same episode are reactivated in a cascade that starts with pattern completion in the hippocampus, followed by a back-propagation into neocortex (Horner et al., 2015; Rolls, 2013; Staresina & Wimber, 2019). This back-propagation likely starts off with the information coded closest to the hippocampus, and then progresses backwards along the neocortical hierarchy (Linde-Domingo et al., 2019). The presumed hippocampal-neocortical dialogue during wake retrieval and sleep might thus prioritise conceptual features of the reactivated memories, relative to their perceptual features that are coded in brain areas further removed from the hippocampus. As a result, each replay event would strengthen semantic information more than perceptual, further exaggerating the gap that is already present on the immediate recall.

Alternatively, it is possible that the perceptual features of our visual objects were forgotten faster than their conceptual features. The nature of item-based forgetting is still under debate (Andermane et al., 2020). Some recent work suggests that the forgetting of perceptual features, such as colour, is independent of, and occurs faster than, forgetting of higher-level conceptual features such as item state or exemplar (Brady et al., 2013; Utochkin & Brady, 2020). In contrast, other research has shown that object memories are forgotten in a more holistic manner, with an interesting hierarchically dependent forgetting of perceptual and conceptual features (Balaban et al., 2020). Inspired by this work, we investigated a possible hierarchical dependency of forgetting in our own accuracy patterns. We indeed saw evidence for asymmetrical recall, such that if participants only recalled one of the two features, they were more likely to remember the conceptual but not the perceptual feature than vice versa. This asymmetry significantly increased over the two-day delay, again indicating an increasing dependence of remembering on conceptual features. Together with the reaction time results, our findings therefore support a view of hierarchically dependent remembering and forgetting of single item features, with lower-level perceptual features having a higher likelihood of being forgotten independently of higher-level semantic features.

To distinguish the contribution of active retrieval to such time-dependent consolidation effects, we further tested whether retrieval on the first day enhances the preservation of conceptual features more than restudy, a more visual type of practice that does not involve the same degree of intrinsic memory reactivation. In line with our second main hypothesis, we found a larger perceptual-conceptual RT gap on the second day in the retrieval group. Average reaction times indicate that this change is driven by a pronounced gain in conceptual feature access after repeated retrieval compared to restudy, rather than differences in how fast the two groups access the perceptual details of the stimuli. This pattern of results suggests that the semanticisation process is relatively stronger when the originally learned associations are immediately practiced by active cued recall, and it has at least two important implications.

First, our finding has implications for theories of the testing effect, showing that active recall disproportionally increases the access to conceptual aspects of a memory over perceptual aspects. This finding resonates with the idea that each memory recall tends to co-activate semantically related information (McDermott, 2006), in turn facilitating the integration of newly learned information into existing knowledge networks (Carpenter, 2009; Pyc & Rawson, 2010). In the long-term, such knowledge integration can then aid memory recall, as supported by the close relationship we found between paper-and-pencil accuracy and the RT gap on day two, such that participants with good episodic recall tend to show larger differences between perceptual and conceptual feature access on the delayed tests. Semanticisation thus seems to support episodic recall on delayed tests and is boosted by retrieval practice.

Second, our results suggest that repeated remembering could be an important factor for representational memory changes that interacts with a subsequent period of sleep (see also Cairney et al., 2018). Many sleep studies carry out a memory test before and after sleep to obtain a difference score within subjects (Gais et al., 2006), and it is thus important to distinguish retrieval's specific contribution to the observed consolidation effects. While the present study suggests that repeated recall can amplify time-dependent, qualitative changes in memories, we did not manipulate whether retrieval was followed by a period of wake or sleep, and our results can therefore not directly address the interaction between retrieval practice and sleep. One recent study found that sleep's benefits were indeed reduced when preceded by retrieval compared to restudy practice (Bäuml et al., 2014). These results, however, were interpreted as evidence that repeated recall can strengthen memories up to a point where they no longer benefit from sleep (Bäuml et al., 2014), an interpretation that is well in line with other reports that sleep prioritizes, or at least has a more measurable effect on, weaker memories (Petzka et al., 2020; Schapiro et al., 2018). In such cases, more sensitive tests like our feature-specific reaction time probes, or test conditions with higher demands (e.g. on interference control) can still be used to successfully uncover consolidation effects (Petzka et al., 2020). In future studies, sensitivity and the timing of tests will certainly play an important role in disentangling the differential contributions of repeated remembering and sleep to the long-term retention of memories.

Our findings support the idea that active testing, in terms of the neurobiological processes involved, mimics consolidation by relaying newly acquired information from hippocampal to neocortical structures (Antony et al., 2017). However, the perceptual-conceptual gap in the retrieval group did not change with repeated remembering on day 1, and our results do thus not provide evidence for a “fast” consolidation (Antony et al., 2017) process. A very similar finding was recently reported in a study investigating qualitative changes in memory-specific, multivariate neural patterns during recall (Ferreira et al., 2019). In contrast, recent neuroimaging studies report that functional and neuroplastic changes can occur within a single session of rehearsal (Brodt et al., 2016, 2018), speaking in favour of a fast consolidation process. Why then do the behavioural, feature-specific changes not become visible on a more rapid timescale, when the neurobiological changes presumably take place? After initial learning and practice, hippocampal and neocortical memory traces likely co-exist, with the hippocampus dominating immediate recall. Delayed recall has been shown to depend more strongly on neocortex (Ferreira et al., 2019; Gais et al., 2006; Takashima et al., 2009), in line with most consolidation theories (Marr, 1971; McGaugh, 2000; Nadel et al., 2012; Winocur & Moscovitch, 2011). Moreover, imaging work suggests that the rapid neurophysiological markers of plasticity may require a large number of, and more spaced, repetitions to evolve (Brodt et al., 2016, 2018), plus a further period of consolidation to become stabilised (Himmer et al., 2019). Retrieval practice might thus help to establish a neocortical trace rapidly, more so than restudy, but this trace will only become behaviourally relevant at longer delays, when remembering is more dependent on neocortex.

The present findings suggest that reaction times, paired with questions that differentially probe access to specific mnemonic features, are sensitive to the presumed time- and recall-dependent transformation of relatively simple, visual-associative memories. Our feature-specific reaction time method thus lends itself well to testing for qualitative changes of practice and sleep on memory, and it complements other approaches that are commonly used. These include the scoring of autobiographical memories according to how much gist or detailed information subjects report (e.g. used in recent work Moscovitch et al., 2016); recognition-based measures using familiarity as a proxy for gist, and recollection as a proxy for detail (Guran et al., 2020); and more recently, measures of access and precision (Berens et al., 2020; Cooper et al., 2019). Reaction times are rarely used in memory studies. Object recognition work, however, shows that the speed with which participants can categorize objects (e.g., animate/inanimate) is well aligned with the time points when the same categories can be decoded from brain activity (T. A. Carlson et al., 2013; Ritchie et al., 2015), and a recent study tracked the back-propagation of information during memory recall using such feature-specific RTs (Linde-Domingo et al., 2019).

On another important note, there is an ongoing discussion about the usage of means versus medians as to estimate the central tendency of RTs within subjects: While medians are usually closer to the centre of a skewed distribution, particularly low or unevenly distributed sample sizes across conditions can yield biased estimates with both measures (for more information see Miller, 1988, 2020; Rousselet & Wilcox, 2020). To suit the skewed distribution of RTs, generalized linear mixed models consider RTs on the single trial level and can serve as an alternative approach to general linear models on means and medians. Importantly, using this approach, previous behavioural work on perceptual-conceptual RT differences yields results that are in alignment with our findings (Linde-Domingo et al., 2019). Moreover, our behavioural results are further supported by the sequential reactivation of conceptual to perceptual neural processing as seen within EEG and fMRI patterns (see Linde-Domingo et al., 2019 and chapter 3). These findings suggest that the exact choice of statistical analyses did not affect the outcome of the results. Together, the present results indicate that differential mean RTs can directly tap into the qualitative changes that occur over the course of memory consolidation.

We have framed the qualitative changes as reflecting a transition along a perceptual-to-conceptual gradient, whereas the primary terminology in the consolidation literature is that of an episodic-to-semantic transition (Nadel & Moscovitch, 1997; Tulving, 1972). These gradients are clearly overlapping in our paradigm, where answering the perceptual questions requires more vivid and detailed recollection than answering the conceptual questions. Moreover, semantic features (e.g. that a dog is animate) are inherent in an object's identity, whereas our perceptual features are random bindings, and retrieving them should thus strongly engage episodic-associative memory processes. Having said that, if our reaction time task primarily measured an episodic-semantic distinction, we would expect to see that participants with good episodic memory show very fast reaction times to perceptual questions, diminishing the RT gap to conceptual questions. On the other hand, participants with a weak memory should show a greater conceptual prioritisation, while losing access to perceptual information. Contrary to this prediction, we found that better memory accuracy (based the paper-and-pencil cued recall test) was related to a larger RT gap, and to faster RTs for conceptual features in particular. Access to the episodic trace does therefore not seem to scale with access to the perceptual features, even though the two processes are certainly not independent. We instead argue that feature-specific reaction times reflect the neocortical back-propagation process that follows initial access to the episodic trace (Linde-Domingo et al., 2019).

In summary, using feature-specific probes, we provide evidence for the semanticisation of memories over time and specifically with repeated remembering. Our main results are consistent with a framework where the natural prioritisation of conceptual information during repeated retrieval (Linde-Domingo et al., 2019) has a lasting effect on what is being retained over time. We reconcile cognitive theories of the testing effect with neurobiologically motivated theories of memory retrieval, which posit that functional anatomy during retrieval dictates faster access to later, more abstract-conceptual stages of visual processing. Finally, our feature-specific RT probes provide a simple way to assess the qualitative changes of mnemonic representations over time, and might thus be useful for future consolidation studies using lab-based rather than autobiographical memories.

Statistics and reproducibility

Our methods and statistical results, especially the retrieval group results from day 1, reproduce and extend findings from one other study by Linde-Domingo et al. (2019) (Linde-Domingo et al., 2019, p.).

Data availability statement

The retrieval and restudy data files that support the findings of this study can be downloaded from the “Retrieval_group” and “Restudy_group” folders respectively, hosted on the Open Science Framework under the identifier https://doi.org/10.17605/OSF.IO/WP4FU (Lifanov, 2020). Stimulus material can be found in the BOSS database (https://sites.google.com/site/bosstimuli/home(Brodeur et al., 2010)).

Code availability statement

The custom code used in this study is available on the Open Science Framework with the identifier https://doi.org/10.17605/OSF.IO/WP4FU (Lifanov, 2020).

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Author contributions

J.L. and M.W. designed the experiments. J.L conducted the experiments. J.L. analysed the data. J.L., JL.D. and M.W. contributed to the analysis approach. J.L and M.W. wrote the first version of the manuscript and all authors contributed to reviewing and editing.

Competing interests

The authors declare no competing interests.

Chapter 5 - General discussion

Objectives

The aim of this doctoral thesis was to understand the spatio-temporal neuronal dynamics supporting memory recall. Specifically, the first goal was to explore how the neural representations of episodic events unfold in the brain while an event is reconstructed from memory. The second aim was to study how these representations change with repeated retrieval.

Regarding the first research aim, we hypothesized that retrieval follows a feedback, abstract and modality-independent to detailed and sensory-specific processing stream. We therefore conducted two experiments aimed at deconstructing episodic memories into their constituent components. In the first study (Chapter 2), we investigated if modality-independent or cross-modal representations would be reactivated before sensory-specific ones. To answer this research question, we studied memory recall in different modalities, based on simultaneously acquired EEG-fMRI data. Participants were asked to perform a simple memory task in which they had to associate a dynamic video or audio clip with a random word. In a later retrieval phase, participants had to recall the dynamic clip after being cued with the related word. Using both spatially and temporally resolved multivariate analyses, we explored the representational structures across different brain regions, and how they unfold over time. We were particularly interested in examining such reactivations in sensory-specific visual and auditory cortices, as opposed to multisensory regions including parietal lobe and temporal pole.

A second experiment was aimed at unravelling the reconstructive process of memory recall within the visual modality, where we zoomed in on the ventral visual stream and specifically explored how visual object memories are reconstructed. We hypothesized a reversed reactivation along the ventral visual stream reconstructing features along a conceptual-to-perceptual gradient. To test this hypothesis, participants were scanned while they associated randomly allocated verb-object pairings, and while they later recalled the associated object upon the presentation of the verb. To examine the representational information flow during memory recall in a spatially and temporally resolved fashion, we fused our data with an existing EEG dataset acquired using the same paradigm. Using multivariate analyses, we decomposed the episodic memories into their constituent perceptual and conceptual features, which were explicitly manipulated in this experiment, and then unravelled the reconstructive neural information processing stream.

Regarding the second research aim, we wanted to investigate the representational changes of episodic memories that go along with repeated retrieval and the long-term stabilisation of a newly acquired memory. We hypothesized that when being repeatedly reactivated, memories undergo a transformation that favours conceptual features over perceptual ones. To test this, we used a behavioural paradigm using reaction times as a measure of the speed with which participants can access perceptual and conceptual features of a visual memory. Previous work established that such perceptual and conceptual reaction time measures reflect both a forward processing stream during visual perception, and a backward stream during memory reconstruction (Linde-Domingo et al., 2019). In the work reported in Chapter 4, we used this method to look deeper into representational changes within this backward stream. Participants repeatedly recalled a previously learned object when prompted with an associated cue word, and were asked to answer a perceptual or conceptual question about the retrieved object as fast as possible. Comparing their reaction time performance immediately after learning with the performance after a two-day delay, we investigated if the prioritised access to conceptual over perceptual features would be further enhanced after the delay. To investigate if this conceptual prioritisation was particularly enhanced by repeated retrieval beyond the effects of time-dependent consolidation, we finally compared the delayed performance of the repeated retrieval group with another group that instead underwent repeated study.

Principal findings

The present findings shed light onto the spatio-temporal representational information flow of episodic memory retrieval. Three major findings emerged from this line of research. First, we found that retrieval elicits a backwards information stream, presumably starting in the hippocampus and progressing backwards along the sensory processing pathways towards primary sensory cortices and additional cross-modal regions (Chapters 2 and 3). Second, the reversed processing stream follows a hierarchically descending gradient from modality-generic to individual episode coding, and from conceptual to perceptual representations (Chapters 2, 3 and 4). And finally, prioritised conceptual processing during retrieval facilitates a semanticisation of the reactivated memories in the long term (Chapter 4).

Reversed retrieval reconstruction

Comparison of findings in Chapter 2 and 3

In the introduction, I recapped established theories suggesting that to re-live previously experienced events, sensory patterns pertaining to these events need to be reinstated, providing the functional foundations for mental representations of recalled memories (Damasio, 1989; Marr, 1971; Tulving & Thomson, 1973). As previous research has suggested that the retrieval process starts in the hippocampus (Teyler & DiScenna, 1986; Teyler & Rudy, 2007), I argued that retrieval follows a backwards stream from the hippocampus, via late sensory and cross-modal regions, before reaching reinstatement in early sensory areas. Such a backwards propagation during retrieval was demonstrated through multidimensional similarity analyses (Chapters 2 and 3). On the one hand, decoding EEG and fMRI activation patterns separately provided us with information on when in the brain and where in time different features of episodic memories are represented. The data fusion of the two recording modalities then helped us to map the temporally dynamic processes onto specific brain loci, and thereby unravel the spatio-temporal trajectories that memories take during their reconstruction. These analyses resulted in several new insights, as described in the following.

First, the fusion attempts in both neuroimaging datasets showed that once a memory cue is provided to participants, retrieval-related information travels from medial temporal to sensory cortices. This was shown in Chapter 2 (Fig. 1.10, 1.11), where the fusion over both video and audio trials showed an information propagation from medial temporal to visual, ventrolateral temporal and parietal areas. It was also observed in Chapter 3 (Fig. 2.9, 2.12), where retrieval specifically of visual information followed the ventral visual stream in the reversed direction relative to encoding. The results therefore speak for the previously suggested reversed memory retrieval stream (Damasio, 1989; Marr, 1971; Estefan et al., 2019; Staresina et al., 2013), that builds up to the eventual reinstatement of previous sensory representations (Bosch et al., 2014; Wheeler et al., 2000).

Further, the resulting reactivation of sensory pathways for both auditory (Chapter 2) and visual (Chapter 3) information was accompanied by stepwise information processing. First, the work in Chapter 2 showed that retrieval initiates generic modality processing before individual stimulus processing. Then, Chapter 3 demonstrated that retrieval within the visual modality also follows a conceptual-to-perceptual gradient. Both findings speak for a processing cascade that follows a decreasing hierarchy and stands opposed to perception (T. Carlson et al., 2013; Martin et al., 2018).

Concerning the timing of reactivation, the earliest activity of medial temporal and other cortical regions was detected just 500-600 ms after a memory cue was provided (Fig. 1.10, 1.11). This is the first time point that comes into consideration as a starting point of memory reactivation in line with previous findings on reactivation timings (for a review, see Staresina & Wimber, 2019). However, to detect the beginning of memory-related reactivation processes and clearly separate these from still ongoing cue-related processes, the neural representation of recalled item features needs to be revealed for instance by content-specific classifiers. At 500-600 ms, we were not able to decode any retrieved clip-specific features except for the generic modality. However, the generic modality could be deducted even without recalling the item, because it was set constant within a block. This makes it questionable whether the retrieval reconstruction started at this point in time. About 600-800 ms later, audio-specific information was reinstated in neocortical temporal regions (Fig. 1.6, 1.8). At this point in time, the recalled auditory clip could be decoded from the EEG. Therefore, the data suggests that this temporal information hub was related to the mnemonic reconstruction of item features. If we do assume that the recall started with our first temporal information hub around 550-600 ms, as suggested by previously (Staresina & Wimber, 2019), then the relay towards neocortical regions would have taken approximately 600-800 ms, as found in other studies (Estefan et al., 2019). Considering the visual representation transformation (Chapter 3), the relay from medial temporal (-2.2 s before button press) to more sensory visual areas (- 1.9 s before button press) took approximately 300-400 ms (Fig. 2.9). The fact that the ROI correlation peaks are close in time to the conceptual and perceptual decoding peaks respectively, as seen in Linde-Domingo et. al (2019), suggests that these ROI peaks are related to reconstructive memory processes. The duration of the representational transformation from high to lower level cortical regions is therefore comparable with the findings from Chapter 2 and previous research, which also indicated first reinstatement around 500 ms in medial temporal, and specifically hippocampal regions, followed by item-specific reinstatement in the temporal neocortex about 500 ms later (Estefan et al., 2019; Staresina & Wimber, 2019). Together, our results suggest the reconstruction of specific items succeeds about a second after cue onset. Further, we can deduct that within the reconstruction time frame, conceptual information should reactive around 300-400 ms before sensory information.

One finding, however, seems contradictory between the two studies. While the experiment in Chapter 3 demonstrates the reversed reactivation of regions along the ventral visual stream, including a late reactivation of early visual areas, Chapter 2 shows fast reactivation of primary sensory areas very shortly after presentation of a reminder (Chapter 2). Since there are currently no known direct anatomical backward connections from hippocampus to early visual cortex in the human brain, it is unlikely that a serial reconstruction stream originating from the hippocampus would reach early sensory cortices at this fast timescale (for a review: Insausti & Amaral, 2003). Further, the fact that we only find significant modality decoding but no specific audio/video clip decoding (Chapter 2) within the time frame of early sensory reactivation speaks against an early item-specific pattern reinstatement of those sensory visual regions. There is at least one possible alternative reason explaining this discrepancy between the two studies. Due to the blocked study design, participants of the study in Chapter 2 were constantly aware of the modality of the to-be-recalled stimuli. This means that participants were prepared to recall sensory-specific representations even before the onset of the cue word. Such presumed sensory-specific attention can be a major source for differential brain activations between modality conditions, for example due to enhanced sensory activations for attended and supressed activations for unattended modalities (Mozolic et al., 2008). Similarly, and specifically, task-specific neural processing activity has been found when participants prepared for memory retrieval, referred to as retrieval orientation (Rugg & Wilding, 2000; Herron & Wilding, 2004). For example, a previous study has shown that retrieval orientation towards a visual versus auditory recognition task enhanced activity in visual and auditory brain regions respectively (Hornberger et al., 2006). Similar to this study (Hornberger et al., 2006), the study of Chapter 2 was designed with alternating visual and auditory task blocks, making a retrieval orientation effect plausible. Previous research thus suggests that the fast, modality-generic neocortical reactivation during retrieval is likely to be related to a task-related preparatory processing state instead of a reconstruction related reinstatement. Together, the reasons explain why a seemingly instant re-activation of primary sensory cortices during retrieval was found in Chapter 2 but is not evident in the study of Chapter 3.

Last but not least, our neuroimaging data also demonstrated the involvement of lateral and predominantly medial parietal regions (including precuneus and retrosplenial cortex) during retrieval, which have frequently been reported in previous studies (Ranganath & Ritchey, 2012; Ritchey et al., 2015; Rugg & Vilberg, 2013; Wagner et al., 2005). In fact, both lateral and medial parietal engagement has often been observed during the recognition of previously seen material (Konishi et al., 2000) and, more related to the current thesis, the detailed recollection of episodic memories (Dobbins et al., 2003). Univariate medial parietal recollection effects have been found for both picture and auditory recall (Buckner et al., 1996), which is relevant for our visual and auditory study designs (Chapter 2 and 3). Importantly, domain-general parietal engagement during recollection has been put in relation to the previously discussed retrieval orientation effect. Irrespective of task performance, some studies found both stronger lateral parietal and medial (precuneus) activation during domain-general recollection than during recency or novelty judgments (Dobbins et al., 2002, 2003; Dobbins & Wagner, 2005). The parietal engagement was therefore related to task orientation and control mechanisms specifically during memory retrieval. The above findings are important for both neuroimaging studies in this thesis (Chapter 2 and 3), as the used paradigms both used cued recall tasks, which are assumed to heavily rely on recollection (Yonelinas, 2002). Further, specifically in Chapter 2, and as previously described, a retrieval orientation effect is especially plausible due to the alternating visual and auditory block design and therefore a strong parietal engagement is not surprising.

The effects reported in this thesis, however, suggest a role for parietal regions beyond general task demands. Specifically, these regions not just showed a univariate increase in activation during retrieval, but also held decodable information about the retrieved memories. Previous work suggests that lateral (Favila et al., 2018) and ventral parietal regions (Long & Kuhl, 2021) do represent mnemonic information and that they represent both semantic and episodic information for retrieved items (Ferreira et al., 2019; Jonker et al., 2018). It should be noted that this observation is generally in conflict with most prominent neurocomputational theories of memory reinstatement, which all suggest that memory recall reinstates the same, or partly the same, patterns that were active during initial encoding (Alvarez & Squire, 1994; Damasio, 1989; McClelland et al., 1995; O'Reilly & Norman, 2002; Teyler & DiScenna, 1986). According to these computational theories, this pattern reactivation should thus be limited to sensory pathways, and not include additional regions like parietal lobe that were not involved in representing the original episode. However, several studies have observed such a spatial transformation of object representations between encoding and retrieval, from sensory to lateral, fronto-parietal regions as seen in the classification and searchlight fusion results in Chapter 3 (Favila et al., 2018; Xiao et al., 2017; Jeong & Xu, 2016; Favila et al., 2020). A recent review offers a number of explanations for the phenomenon and discusses the role of the parietal lobe in conceptual representations, enhanced internal processes, and unique retrieval-related control (Favila et al., 2020). While these processes can explain the enhanced engagement of parietal lobe in representing retrieved information, they do not yet offer a satisfying account for how the transformation from sensory to parietal cortex representations takes place. An fMRI study using the behavioural paradigm in Chapter 4 could be suited to further investigate the underlying spatial transfer processes within the brain: Comparing mnemonic perceptual and conceptual fMRI representations over repeated retrieval versus restudy could reveal the particular contribution of repeated retrieval to the spatial transfer of different memory features. Observing the representational changes over the course of two days (as in Chapter 4) could further show how repeated retrieval influences a representational transfer over time. Finally, it will be important to study unique contributions of different mediating factors (as named in Favila et al., 2020) in more detail, and more importantly, to come up with a unifying neurocomputational framework that can account for the memory transformations and their role in memory reactivation.

Concerning the timing, both EEG-fMRI studies showed that parietal regions reactivated at a time point close to the reactivation of sensory-specific regions such as auditory (Chapter 2) and visual cortex (Chapters 2 and 3). The most likely reason for the similar reactivation time could be the close anatomical proximity between parietal and sensory-specific visual and auditory areas. Direct and indirect anatomical connections from hippocampus to medial and lateral parietal cortex enable the reactivation of the parietal cortex (Insausti & Muñoz, 2001; Kobayashi & Amaral, 2003; Kondo et al., 2005; Lavenex et al., 2002; Muñoz & Insausti, 2005), and from there the information could be relayed to visual cortex relatively directly (Selemon & Goldman-Rakic, 1988). Alternatively, visual information could be reactivated by indirect connections from hippocampus over the ventral visual stream, and then directly project from visual to lateral parietal areas (Baizer et al., 1991). So, due to the direct projections from parietal to visual areas and vice versa, reactivations in those areas can happen closely in time. The comparatively late simultaneous activation of visual, parietal and also frontal areas just before subjective recollection (Chapter 3) additionally hints at memory and imagery buffer function as a preparation for the upcoming task (Baddeley, 1998; Christophel et al., 2012, 2017; Ganis et al., 2004; Levy, 2012; Wagner et al., 2005).

Together, both neuroimaging studies suggest that during recall, retrieval related information spreads from medial temporal lobe along sensory pathways to primary sensory brain regions, which finally reinstate activity patterns that have previously represented sensory encoding patterns. Additionally, spatial transformations from encoding-related sensory to retrieval-related parietal regions were observed. The studies also suggest that during the retrieval process, representations follow a decreasing hierarchical gradient.

Comparison of methods in Chapter 2 and 3

I would now like to give a short recap on the observations made when comparing the two different designs of the neuroimaging studies. The two neuroimaging studies do not only differ with respect to their stimulus materials, but also general methodologies. The first difference is related to the general neuroimaging design. While the first neuroimaging study (Chapter 2) includes a simultaneously acquired EEG-fMRI dataset, the second study fuses the EEG and fMRI data of two separately acquired sessions (Chapter 3). Both bring along some advantages and disadvantages. While simultaneously acquired data is necessarily associated with a highly noisy EEG dataset and requires additional preprocessing methods (Allen et al., 1998), one advantage of the study design in Chapter 2 was the ability to map not only participant-specific, but also trial-specific recall process onto the brain in a time-resolved fashion. With very simple and computationally parsimonious correlation-based RSA, spatio-temporal neural processes can be unravelled. For instance, if a strong representational similarity is detected within electrode correlations between certain trials, the same trials should also yield a strong representational similarity somewhere in the brain when correlating the corresponding voxel patterns. As such, trial-by-trial based temporal representations can be related to locations in the brain (see also Debener et al., 2006). In contrast, a separately acquired dataset will provide the advantage of cleaner EEG data. However, representations in one set of participants will likely slightly differ from the representations in the other set of participants (see also Scrivener, 2021). In our special case, where stimuli were presented in different perceptual variations between participants (line drawings versus photographs), spatio-temporal mapping in the searchlight fusion has suffered specifically within the first 200 ms under the between-subjects design (Fig. 2.11). We believe that the design is one reason for the failure to show early perceptual components in the temporal domain. Equally, separate datasets do not allow to map temporal and spatial information on a trial-by-trial level, such that differences in the strength or timing of memory reactivation within a participant cannot be accounted for in the fusion analyses.

The second difference between the two studies (Chapter 2 and 3) lies within the analytical approaches that were implemented to suit the respective simultaneous or non-simultaneous neuroimaging acquisition and are thus closely related to the points above. Comparing the correlation- and classification-based RSA methods, as implemented in the respective studies, it is important to elaborate on subtle but important differences in the inferences that can be made based on these different data fusion approaches (see also Cichy & Oliva, 2020). The correlation-based method in Chapter 2 capitalises on the individual activation pattern differences between each pair of stimuli, within each participant. The representational dissimilarity matrices from this analysis thus reflect which stimuli are systematically represented as similar or dissimilar across the pool of object images within subjects. Therefore, there is no need for similar geometries across subjects (to give an illustrative example, one participant might represent a horse and a zebra as more similar, another one a horse and a donkey) in order to find a mapping between the EEG and fMRI patterns. Together, the correlation-based RSA approach thus offers a simple analytical implementation, a straight-forward interpretation of findings, and allows for representational variation across participants.

The classification approach in Chapter 3, on the other hand, generalizes over a whole set of participants including the same pair of stimuli. In order to reveal a match between the EEG-based structures of individual participants by means of classification, representational distances between objects need to be relatively consistent across participants (see also Cichy & Oliva, 2020). To use the example above, in order to achieve above-chance classification, the zebra needs to be represented as equally similar to a horse in all participants. Importantly, the method not only requires consistency in the spatial patterns based on the EEG topographies, but also the consistency in the time course of object-evoked patterns across participants. If a (re)activation is slow in one participant and fast in another, the classifier will not be able to decode representations between subjects. These factors create a set of conditions that need to be fulfilled to find a match between an individual's fMRI-based similarity structure and this subject-generalized EEG-based structure, and might further explain the limited ability to detect early perceptual representations in the temporal domain (Fig. 2.11, Chapter 3). On the other hand, to point out some advantages of the classification-based approach, it is generally more robust as it is based on a larger set of trials and validated through randomisation processes (also see Misaki et al., 2010). Hence, considering the inter-individual stimulus pool differences and the additional topography differences, the classification-based similarity approach still proved to be powerful enough to detect some meaningful similarities between the EEG-based representational geometries of one participant group and the fMRI-based geometries of another group (Fig. 2.8-2.10 & 2.12, Chapter 3).

Next, I would like to give a note on the choice of stimulus repetitions. Having said that classification-based RSAs are a more powerful tool to uncover representational structures within neuroimaging data sets, it is important to mention that this method requires a certain amount of repetitions of each given stimulus. Since the design of our neuroimaging study in Chapter 3 only included one repetition per stimulus, a cross-subject classification is a useful workaround (Poldrack et al., 2009; Shinkareva et al., 2008; Wang et al., 2020). However, a within-subject classification-based RSA would have been even more powerful (also see Shinkareva et al., 2008), as the results would have been more robust to inter-individual differences. Such inter-individual differences could include different temporal and spatial electrode pattern representations as described previously. Other important differences between individual measurements include anatomical, functional, performance - or electrode position related factors, which can additionally influence the signal and prevent successful decoding. Hence, even if classifications are a handy method to perform RSA in a between-subjects design, it would profit from more trial repetitions within subjects.

Comparatively, the first EEG-fMRI study (Chapter 2) included a large number of repetitions of each dynamic stimulus, but little inter-stimulus variability, since there were only four video and four audio clips overall. An important trade-off becomes evident here. On the one hand, using a large set of stimulus repetitions increases the classification power (compare Chan et al., 2011). On the other hand, the major downside of repeating trials is that we cannot assume that the neural representations remain stable across repetitions. Even in studies of visual object recognition, which typically use many repetitions to decode stimulus-specific patterns, neural repetition effects (e.g., priming, or repetition suppression (Henson, 2003; Henson & Rugg, 2003)) might be problematic though mostly ignored. In memory studies there are additional concerns when repeating stimuli across trials. For example, repeating the same stimulus but combining it each time with a new associate (like in Chapter 2) will likely lead to the build-up of memory interference over time (Anderson, 1983). Further, as shown in Chapter 4, repeated recall involves a transformation of memory representations. Even if our behavioural study of Chapter 4 only shows representational changes after a time delay, other studies suggest that neural changes can be detected immediately with repeated reactivation of memories (Brodt et al., 2018; Brodt et al., 2016). Finally, repeated encoding of the same stimulus or association is generally incompatible with studying a truly one-shot episodic memory mechanism, and thus brings theoretical concerns (Baddeley, 2013). These factors have to be considered when a) choosing the stimulus design of a study and b) interpreting the findings.

I would like to conclude the methods comparison with a note on stimulus manipulation with additional future suggestions. This thesis aimed at deconstructing episodic memories into their hierarchical feature components and track their retrieval-induced reconstruction. The first EEG-fMRI design (Chapter 2) included a stimulus manipulation on the level of modality, and we could trace the different auditory and visual processing streams. However, the chosen stimulus manipulation did not provide the opportunity to resolve hierarchical representational structures along the processing trajectories. In other words, it is impossible to disentangle from this design whether lower-level or higher-level features contributed most strongly to the classification (or similarity) of the two modalities, and more importantly, the individual video and audio clips. In contrast, the second EEG-fMRI study (Chapter 3) offered us more control over the different levels of feature representations, explicitly differentiating between low-level perceptual and high-level conceptual dimensions. Unfortunately, the failure of the planned fusion of simultaneously acquired EEG and fMRI data (Chapter 3) did create difficulties in tracking perceptual processing in the fusion approach, because perceptual format was not held constant for a given object across participants. In other studies, the same perceptual and conceptual feature manipulation has proved itself as useful to demonstrate memory representations in the temporal EEG domain (Linde-Domingo et al., 2019) and behaviour (Lifanov et al., 2021).

Together, the two neuroimaging studies provide two alternative methodological examples how to track spatio-temporal processes in the brain during perception and memory retrieval. This thesis provides some insight on the advantages and disadvantages of the two approaches, which should be considered in future data fusion studies.

Retrieval enhances semanticisation

Comparison of findings in Chapter 3 and 4

At the beginning of this thesis, I introduced the hypothesis that repeated retrieval enhances conceptual over perceptual access beyond the effects of time- and sleep-dependent consolidation. In the present work, we used feature-specific reaction times as a measure of access to mnemonic information at different levels of the presumed visual processing hierarchy. Both Chapter 3 and Chapter 4 speak for a faster access to conceptual than perceptual features of recalled episodic memories and replicate previous findings (Linde-Domingo et al., 2019). Specifically, a conceptual-to-perceptual access stream was shown in RTs in Chapter 4 and even Chapter 3 (due to premature retrieval button press, see discussion in Chapter 3). In addition, Chapter 4 demonstrates that with repeated retrieval practice, conceptual access is further facilitated over perceptual access, and this increasing gap in feature access can be observed after a delay of 2 days. It is noteworthy that both the verb cue and the object were meaningful stimuli and thus there could be a general tendency to process the conceptual meaning of the verb-object association over the perceptual details of the object during the encoding process. This is important as the levels-of-processing framework suggests that semantic processing at a very deep operational level leads to more elaborate and more memorable traces (Craik & Lockhart, 1972). Further, according to the transfer-appropriate-processing framework (Morris et al., 1977), memory is best when retrieval processes match those at encoding (also see Tulving & Thomson, 1973). Hence, one could argue that a general tendency to encode the meaning of an event over the perceptual detail will lead to the enhanced conceptual reactivation and consolidation within successful memory (Morris et al., 1977).

However, we argue that neither the level-of-processing effect nor transfer-appropriate-processing can solely describe the enhanced semanticisation of recalled memories, as our restudy control group underwent the same encoding conditions, however this group did show a significantly smaller (in fact, absent) conceptual-perceptual reaction time gap on the second day. For this reason, the advantage of conceptual over perceptual access cannot be a trivial effect of attending the meaning both during encoding (and re-encoding) but must be specifically enhanced with retrieval practice.

These findings of increased conceptual access are plausible with respect to the backwards propagating reconstruction stream (Staresina & Wimber, 2019) that was shown during retrieval in Chapter 3. We demonstrated that late regions along the ventral visual stream, assumed to hold conceptual representations, get re-activated before earlier visual regions that are involved in lower-level perceptual representation. Due to this temporally prioritised reactivation, the connection between the hippocampus and ventral visual regions presumably likely benefits more from the retrieval process than the connection between the hippocampus and more distant posterior visual regions. The hippocampal-ventral cortical dialogue during repeated retrieval will in turn facilitate access to conceptual features (Dudai et al., 2015; Frankland & Bontempi, 2005; Winocur & Moscovitch, 2011), as shown in Chapter 4.

As discussed in Chapter 4, we thus suggest that the recall-induced memory reactivation causes retrieval-induced plasticity in the connections between the hippocampus and neocortex, as well as within the semantic network. The simultaneous activation of these different nodes is assumed to enable such a long-term plasticity (Hebb, 1949). The relay from hippocampal towards neocortical structures is in agreement with several previous computational theories and functional findings

(Antony et al., 2017; Brodt et al., 2016, 2018; Ferreira et al., 2019). The work in this thesis does not give any direct insight into the neural changes that occur beyond the first day of practice, as our imaging studies do not include a second testing day. However, the behavioural work in Chapter 4 suggests that retrieval-induced conceptual embedding of episodic memories is especially strengthened over time, suggesting that the semanticisation becomes specifically evident when hippocampal traces might decay (see discussion in Chapter 4 and Ferreira et al., 2019).

Comparing Chapter 3 and 4, both studies thus consistently show the priority of conceptual representations during retrieval in the temporal domain and speak for a gradually increasing conceptual-perceptual gap with repeated remembering. The dominance of conceptual features during retrieval was not only shown in the temporal domain, but also in the stronger spatial representation within fMRI patterns (Chapter 3), faster reaction times and higher accuracies for conceptual than perceptual questions (Chapters 3 and 4). Altogether, these results favour the view that the anatomy of the brain and its inherent connections dictate a) what features are most likely to be accessed and b) how likely these features are to become strengthened or weakened over time.

Summarized, we can conclude that memory access to certain features is accompanied by re-establishment of these feature representations, that is, reinstatement on a neural level. For instance, while conceptual features seem to be more strongly represented in the brain and prioritised in time, they are also more accurately recalled than perceptual features (Chapter 3 and 4). Our findings thus support the idea, introduced at the beginning of the thesis, that sensory brain representations during initial perception provide the scaffold for reactivated memory representations (Mitchell &

Johnson, 2009; Tulving & Thomson, 1973). Together, both studies show that retrieval is a non-exhaustive reconstructive process and stimulates the stabilisation as well as the transformation of newly acquired episodic-associative memories.

Comparison of methods

Chapter 3 and 4 both make inferences about neural processes during retrieval. Previously, reaction times have often been used in research on perception. For instance, in the field of vision research, reaction times were used to study the dynamics of natural and artificial object (VanRullen & Thorpe, 2001) or context (Joubert et al., 2007) processing. Importantly, it was found that behavioural measures of perception are highly related to brain representations and can thus be used to make inferences about the underlying neural processes (Contini et al., 2021). Only few studies have taken the next step and used reaction times as indicator of neural processes during memory retrieval. Some that did have shown that similarly to encoding, the categorization speed during recognition (e.g. familiar/non familiar, Barragan-Jason et al., 2015) and active memory recall tasks (e.g. drawing/picture or animate/inanimate Linde-Domingo et al., 2019) is closely related to temporal decoding peaks of the same categories and can thus be used to make inferences about neural processes. Our studies (Chapter 3 and 4) used a similar memory recall paradigm to deconstruct episodic memories into feature representations, and even went a step a further to see how these representations change with time and repeated testing. On the one hand, the RT patterns demonstrate differences in feature access during retrieval (Chapter 3) and showed a strong relation to the neural dynamics during feature reconstruction (Chapter 3). On the other hand, RTs showed how feature access and presumably related feature representations change with time and repeated testing (Chapter 4). Both studies confirmed that RT measurements can be a useful method to study retrieval and even consolidation processes.

While both studies used the same simple memory paradigm in which participants had to encode and recall pictures of objects, there was one difference in the sequential order of tasks, which is important with regard to the research objectives of the two studies. In Chapter 3, participants were asked to recall the object upon the presentation of a cue and push a button to indicate successful retrieval. Only after this button press, they were asked to answer a question about perceptual or conceptual features. Introducing a button press to mark successful retrieval was supposed to provide us with an indication of the time when the episodic memory was mentally reinstated. This timing was meant to provide a useful anchor to align the trials to, such that if there was a consistent reactivation cascade leading up to the subjective recollection, representations would be better aligned in time between trials and between subjects (see Linde-Domingo et al., 2019). This was supposed to facilitate signal detection within the EEG, especially in the case when some participants took more time to recall an object than others. In contrast to the design in Chapter 3, the retrieval task in Chapter 4, which was not accompanied by any neuroimaging methods, started with the presentation of the question and was immediately followed by the verb cue, skipping the subjective retrieval button press. Hence, in this case, reaction times were used to offer us direct insight into the speed of access to perceptual and conceptual memory features. The studies thus provide two alternative examples of how to use reaction times in retrieval paradigms a) to indicate subjectively completed retrieval and

b) to directly measure timing between different feature reconstructions, showing how beneficial the use of reaction times in retrieval studies can be.

In conclusion, feature-specific reaction times proved themselves as useful indicators of the timeline of reconstructive retrieval processes. They can not only be used as indicator for completed reinstatement (Chapter 3) but also as indicator for partly reconstructed episodic memories, including their specific features at different processing stages (Chapter 4). Additionally, we showed that they can measure representational changes at retrieval between different time points (Chapter 4). Finally, the use of RTs in combination of neuroimaging offers a complementary and powerful method to draw conclusions about the speed of neural processes.

Future directions

The studies in this doctoral thesis have given us insight into the spatio-temporal dynamics of feature reactivation in episodic memory. Specifically, the work demonstrates a temporal gradient of the reconstructed representations, from modality-generic to sensory-specific representations within the auditory and visual domain, and from conceptual to perceptual representations within visual retrieval. Finally, it provides insight into how representations change over time and with repeated retrieval. Below I discuss a number of gaps in our understanding of episodic memory retrieval that should be addressed in future research.

One future research aim might lie in further backing up the evidence for a reversed reconstruction stream by means of methods that allow for causal rather than correlational conclusions. Throughout this thesis, our work is based on a the working hypothesis that the reconstruction stream is serial and backwards propagating (see also Staresina & Wimber, 2019). Evidence from this thesis speaks in favour of the latter assumption of a backwards propagating stream, with a reconstruction process following hierarchically decreasing processing stages along sensory pathways in a reversed order with relation to encoding. However, the directional information flow between the conceptual and perceptual hubs has not been considered within the projects of this thesis. Other studies do suggest directional information progression at earlier stages of memory activation, specifically between hippocampus and neocortex. For example, one study implemented a cross-correlation analysis on intracranial electrodes in the hippocampus and neocortex and demonstrated directional coupling from hippocampus to neocortex during retrieval, as reversed to encoding (Griffiths, Parish, et al., 2019). In a future project, it would be informative to additionally investigate directional coupling between high- and low-level neocortical regions along the ventral “what” streams and directly link the coupling to feature representations within these areas. This could, for example, be implemented by means of granger causality analyses on an MEG dataset (Michalareas et al., 2016) or dynamic causal modelling (Friston et al., 2019). Such a functional connectivity analysis between different cortical regions could potentially depict the serial trajectory and direction of information progression more clearly.

Regarding the assumption of a serial reactivation stream, neurostimulation such as transcranial magnetic stimulation could be used to further unravel the dependencies between the different stages of the retrieval related trajectories. Even if the directional flow between regions was established, it is well possible that some neocortical regions depend on the previous reactivation of a preceding region, while others are reactivated in parallel. The dependency analysis in Chapter 4 provides some indication that late perceptual stages of the reconstruction cascade depend on earlier conceptual stages. To fully establish such a temporal dependency, TMS or other invasive stimulation could be used to interfere with memory reactivation at a given stage of processing, and examine the knock-on effects on later reactivation stages (for example see Busan et al., 2009; Ellison & Cowey, 2007; Nyffeler et al., 2002). To give an example, Chapter 3 suggests that the information flow supporting retrieval of visual information progresses from the hippocampus over ventral temporal cortices to early visual cortices. As such, interrupting information flow from the ventral temporal cortices might prevent reinstatement in the visual cortex, which would prove that information reaches the visual cortex via feedback propagation from more ventral areas. Relating the neuroimaging findings to behaviour, we would further expect that perceptual but not conceptual recall would be interrupted. Such methods would lay down a strong foundation for the demonstration of a serial reverse stream and additionally establish causalities between neural representations and behavioural performance.

Another future research goal lies in completing the picture of what information is contained in a reconstructed episodic memory. As introduced in the beginning of this thesis, episodic memories have many more features and dimensions than those that have been addressed in this thesis. In particular, there is much room to explore various contextual features (Tomita et al., 2021). One typical feature, for example, is contextual information about the location in which an event occurred. In Chapter 2, I described that spatial information follows a different pathway than information about object identity while an experience is being encoded into memory. Moreover, there is some work suggesting that spatial context plays a special priority role for episodic memory, providing the scaffold on which episodic memories are built and reconstructed (Robin & Olsen, 2019). It would be interesting to investigate how feature reactivation proceeds along the dorsal pathway when spatial information is recalled from memory. Does spatial reconstruction also follow a reversed processing stream? And what is the temporal order in which contextual and item features are reconstructed? Do these two sources of information get reconstructed simultaneously, or consecutively? And does information about one source aid the reconstruction about the other? Our two EEG-fMRI studies show us the involvement of dorsal regions (such as the parietal lobe) in memory reconstruction, which may be related to the reconstruction of contextual spatial information about the previously encoded episodes (Ritchey & Cooper, 2020). However, our stimulus manipulations have not tapped into spatial representational structures and as such, we could not make any inferences on spatial-contextual processing. Since spatial-contextual information is one of the hallmark features of episodic memory, future studies should address this matter.

Similarly, emotional features are an important characteristics of episodic memories and strongly shape memory organization (Dunsmoor et al., 2015; Tomita et al., 2021). It has been shown that emotional context during the initial experience can enhance the retention of memories with the passage of time (Yonelinas & Ritchey, 2015). Many studies have pointed out the important role of the amygdala in the memory enhancement related to emotional context (Murty et al., 2010). For instance, it was proposed that the amygdala can boost perceptual processing and conceptual evaluation (Murty et al., 2010) and is responsible for emotional association (Yonelinas & Ritchey, 2015). While these ideas put focus on the engagement of the amygdala during encoding, it would be informative to see how the amygdala is involved in the reconstructive process of memory retrieval. Under the assumption of an (at least partly) serial reconstruction process, it would be specifically interesting to see at which stage the amygdala gets involved and whether its engagement speeds up or qualitatively improves the neocortical reinstatement. Finally, to improve our understanding of the role of the amygdala in memory reconstruction, we could study the interaction between amygdalar, MTL and neocortical processes over prolonged consolidation periods, and how their involvement in turn alters memory representations over time.

Spatio-temporal and emotional context are just two examples of contextual features that are likely to influence the retrieval process. In a natural everyday environment, more complex associations, such as social context, purpose or value play an additional role in memory formation (Paulus et al., 2021; Sonkusare et al., 2019; Tomita et al., 2021). In future attempts, a higher resolution of feature dimensions and contexts would thus be helpful to track the hierarchical development along the retrieval pathway, ultimately showing near-gradient like information transformation. The usage of naturalistic stimuli could further aid our understanding of memory formation and recall in a complex associative environment (Sonkusare et al., 2019).

Finally, further investigation needs to be done on the role of retrieval in the consolidation process. Chapter 4 showed that repeated retrieval in combination with extended retention periods enhances semanticisation, a process previously related to sleep-dependent memory consolidation (Antony et al., 2017). While online recall and offline consolidation during sleep are believed to share some common mechanisms, the difference in their respective functions, and the interaction between sleep and retrieval, have not yet been fully established. We know that both processes include a reactivation of memories: Retrieval is believed to actively reactivate memories via a hippocampal-neocortical dialogue (Antony et al., 2017), which ultimately leads to the reinstatement of perception-related cortical patterns. Sleep also involves memory reactivation as shown within neural replay of previous encoding representations in rats (Wilson & McNaughton, 1994), and memory circuit reactivation during slow-wave sleep in humans (Rasch et al., 2007), strongly related to improved memory performance (Ramadan et al., 2009). Consolidation theories propose that the cortical reactivation integrates newly learned information with schematic concepts, which ultimately stabilizes memories and leads to a semanticisation (Dudai et al., 2015; Frankland & Bontempi, 2005; Káli & Dayan, 2004; Winocur & Moscovitch, 2011). Although some studies have looked at interacting effects of sleep and retrieval (Bäuml et al., 2014), it would be informative to understand their overlapping and unique contributions to memory consolidation from a functional and mechanistic point of view. A fully balanced mixed study design comparing two performances before and after wake versus sleep periods while half of each condition is grouped into a restudy and the other half into a repeated retrieval task, could shed some more light on the specific contribution of retrieval and sleep dependent memory consolidation.

Summarized, I hope to have stimulated some future questions to investigate when studying memory retrieval processes. The last decades have seen a big leap in discovering the underlying neural processes and evolving representations, but there are many factors possibly mediating retrieval reconstruction and partly leading to enhancement or impairment of retrieval. Understanding retrieval and its interaction with the contextual environment (Mitchell & Johnson, 2009) may also lead to discoveries that can help us to treat pathological cases, when retrieval is not functioning.

Conclusions

Episodic memories are crucial parts of our identities as human beings. They mark our autobiographies and help us understand the world around us. It is truly fascinating how our minds and brains can capture the events in such richness and form retrievable representations of them. Previous research has shown that episodic memories start of as sensory experiences that carry multi-sensory, multi-layered and multi-dimensional features. The different features unfold as they progress along the sensory pathways before being encoded as memories. In this doctorate thesis, it was shown that retrieval follows a reversed processing stream with respect to perception and follows a hierarchically decreasing gradient. Further, it was shown that due to this retrieval gradient, high-level conceptual features of a memory are strengthened and therefore disproportionally enhanced over lower-level features with repeated retrieval. Contrary to the idea that retrieved episodic memories are instant photocopies of events, this thesis therefore rather confirms the view that memory recall is a reconstructive process that is subject to transformation (Mitchell & Johnson, 2009). Together, the current findings give insight into the spatio-temporal feature representations of reactivated episodic memories and hopefully stimulate a lot of further investigation on the reconstruction of episodic memories.

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