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Material-specific long-term memory representations of faces and spatial positions: Evidence from slow event-related brain potentials

Patrick Khader[a,*], Martin Heil[b], Frank Rösler[a]

[a] *Experimental and Biological Psychology Department, Philipps-University Marburg, Germany*
[b] *Experimental Psychology Department, Heinrich-Heine-University Düsseldorf, Germany*

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Abstract

Motivated by models that propose material-specific cortical long-term memory representations we expected different topographies of event-related slow waves of the EEG during cued retrieval of two distinct types of information (faces and spatial positions), which are assumed to be processed and stored in topographically distinct cortical areas, i.e., in either the ventral or the dorsal visual pathway. Seventeen participants learned associations either between words and spatial positions or between words and faces. Each word was associated with either one or two positions or faces. In a cued recall test, one day later, participants saw two words and had to decide whether these were linked to each other via an associated spatial position or a face. Slow event-related potentials (ERPs) of the EEG were recorded from 61 scalp electrodes during both acquisition and recall. Response times increased monotonically with the number of faces and positions to be reactivated. Negative slow ERPs showed a comparable topography during anticipation learning and cued recall, but dissociated topographically for positions and faces. The maximum of the negativity increased when items were presented repetitively (compared to the first presentation) during learning, and also with the number of the to-be-reactivated associations during retrieval. These results are consistent with an information-processing model that assumes material-specific cortical representations of episodic memory contents, which are established as localized cortical cell assemblies during encoding, and which are being reactivated during recall.

Keywords: EEG; Slow waves; Episodic memory; Long-term representations; Object memory; Spatial memory

1. Introduction

A key topic in memory research is whether distinct long-term memory storage sites exist for different kinds of information. On a physiological, neuroanatomical level the question has been posed as whether distinct brain areas are specialized for representing different stimulus types, and in particular, brain imaging studies have been used recently to find an answer (e.g., Cabeza & Nyberg, 2000). Much of this evidence supports the claim that stored information is reactivated in multiple, anatomically distinct brain areas. For example, clearly distinct activation patterns were observed by contrasting spatial versus verbal working memory tasks (e.g., Jonides et al., 2003). In other studies even more specific category distinctions could be related to anatomically distinct activation patterns as, for example, for faces, houses, tools, chairs, etc. (Haxby et al., 2001). Due to these kinds of imaging results and further findings, including single-cell recordings and lesion studies, permanent long-term memory engrams are assumed to be consolidated and reactivated in the very same neocortical cell assemblies in which information is also processed on-line during perception (Damasio, 1989; Greenberg & Rubin, 2003; McClelland, McNaughton, & O'Reilly, 1995; Mesulam, 1998; Paller, 1997; Rösler & Heil, 2003; Squire, 1992).

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[*] Corresponding author. Tel.: +49 6421 2823838 (O); fax: +49 6421 2828948.
E-mail address: Khader@staff.uni-marburg.de (P. Khader).
URL: http://staff-www.uni-marburg.de/~cablab.

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Consistent with this hypothesis, neuroimaging studies have demonstrated that domain-specific perceptual cortices that were engaged during encoding of a specific stimulus are reactivated when this stimulus is retrieved from memory. For example, Nyberg, Habib, McIntosh, and Tulving (2000) found in a PET study that remembering that visual words had been paired with sounds at encoding activated some of the auditory brain regions which were active during encoding. Furthermore, Nyberg et al. (2001) found that verbal retrieval of action phrases was associated with reactivation of motor brain regions if the actions were performed overtly or covertly during encoding. In an fMRI study, Wheeler and Buckner (2003) presented word–sound (e.g., train–*sound of a train*) or word–picture pairs (e.g., apple–*picture of an apple*) during encoding, but only the words at retrieval, and found stronger brain responses for words that had been associated with pictures in late object-sensitive regions of the inferior temporal cortex. Furthermore, Wheeler, Petersen, and Buckner (2000), using a similar paradigm, found that remembering pictures and sounds reactivated subsets of those regions of the auditory and visual cortex that were found to be active during their perception (see Vaidya, Zhao, Desmond, & Gabrieli, 2002, for related results with pictures using a recognition memory test). Evidence for such recapitulation processes that reactivate stimulus-specific representations was also found by Kahn, Davachi, and Wagner (2004) in a recognition memory experiment where the bilateral parahippocampal cortex was found to be differentially engaged during accurate recollection of having engaged in scene imagery at encoding, whereas the left prefrontal cortex was differentially engaged during recollection after having performed a reading task at encoding.

In addition to these neuroimaging studies an ERP study by Senkfor and Van Petten (1998) found posterior recording sites to be sensitive to the successful recovery of source information in a recognition task for spoken words where correct versus false recovery of the voice that spoke the word during encoding was compared. Other ERP studies, however, failed to find brain responses which differ according to the condition of encoding (i.e., shallow versus deep encoding and visual versus auditory presentation during encoding) (Allan, Doyle, & Rugg, 1996; Allan, Robb, & Rugg, 2000). However, robust differential topographies during long-term memory retrieval, which depended on the retrieved type of stimulus were found with event-related slow waves in previous studies of our group (e.g., Rösler, Heil, & Hennighausen, 1995), which are described in more detail below.

The aim of the present study is to investigate whether the recapitulation theory as described above also holds for the classical distinction between the dorsal and the ventral visual processing pathways, which was found during perceptual processing in delayed matching-to-sample tasks (Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). For example, Postle and D'Esposito (1999) used event-related fMRI to monitor shape and location memory in a delayed recognition task. Participants had to store either the location or the shape of visual objects. The location task activated the superior parietal cortex, whereas the object task activated the ventral posterior temporal cortex. These studies provided clear evidence for category-specific activations in anatomically distinct locations, but mostly working memory tasks were used, i.e., tasks in which specific stimuli had to be stored for only brief temporal intervals (e.g., *n*-back recognition tasks, Sternberg-like matching-to-sample tasks with brief delays, etc.). Accordingly, the found activation patterns can be functionally related to perceptual processes, priming and brief episodes of working memory storage, but not necessarily to encoding and retrieval of more permanent, long-term memory representations. In order to test this, a learning and retrieval paradigm is necessary, which separates the encoding and the test episode for at least several hours. Furthermore, in delayed recognition tasks – *n*-back or matching-to-sample – a stimulus is first stored and later the same stimulus is presented while the subject decides whether it is old or new. Thus, the perceptually presented stimuli are of the same type as the representations reactivated in memory. Therefore, it cannot be decided whether the activation patterns related to distinct categories are primarily caused by the perceptual analysis of the stimuli or by the reactivation of stored representations. To dissociate these processes it would be necessary to trigger distinct memory representations by presenting in both cases the very same type of perceptual stimulus. In that case, the perceptual process in the retrieval situation would be constant while distinct memory representations would be activated nevertheless.

The present study follows these lines of reasoning and investigates whether the distinction between the dorsal and ventral pathway holds not only for perceptual and working memory tasks, but also for long-term memory tasks, because a permanent encoding of spatial versus object knowledge should take place in the brain areas specialized for the one or the other type of information, i.e., in dorsal (parietal) areas for spatial and in ventral (temporal) areas for non-spatial information. In previous studies we developed a modified fan-paradigm (Anderson, 1974) in which long-term memory recall can be tested for different types of contents without confounding perceptual processing with the reactivation of stored representations (see Heil, Rösler, & Hennighausen, 1994). Moreover, the paradigm allows to study temporally separated activation patterns during acquisition and retrieval. In one study (Rösler et al., 1995), participants had to learn associations between line drawings of simple objects (cars, tools, etc.) on the one side, and either spatial positions, words, or color patches on the other. In a recall phase that took place one day later only the drawings were presented to trigger the recall of the associated positions, words, or colors. The topography of event-related EEG slow waves prevailing during recall showed a parietal maximum for positions, a left frontal maximum for words, and an occipital to right temporal maximum for colors. Thus, these data demonstrated that material-specific cell assemblies seem to be activated