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Common and differential electrophysiological mechanisms underlying semantic object memory retrieval probed by features presented in different stimulus types

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ABSTRACT

How the brain combines the neural representations of features that comprise an object in order to activate a coherent object memory is poorly understood, especially when the features are presented in different modalities (visual vs. auditory) and domains (verbal vs. nonverbal). We examined this question using three versions of a modified Semantic Object Retrieval Test, where object memory was probed by a feature presented as a written word, a spoken word, or a picture, followed by a second feature always presented as a visual word. Participants indicated whether each feature pair elicited retrieval of the memory of a particular object. Sixteen subjects completed one of the three versions (N = 48 in total) while their EEG were recorded simultaneously. We analyzed EEG data in four separate frequency bands (delta: 1–4 Hz, theta: 4–7 Hz; alpha: 8–12 Hz; beta: 13–19 Hz) using a multivariate data-driven approach. We found that alpha power time-locked to response was modulated by both cross-modality (visual vs. auditory) and cross-domain (verbal vs. nonverbal) probing of semantic object memory. In addition, retrieval trials showed greater changes in all frequency bands compared to non-retrieval trials across all stimulus types in both response-locked and stimulus-locked analyses, suggesting dissociable neural subcomponents involved in binding object features to retrieve a memory. We conclude that these findings support both modality/domain-dependent and modality/domain-independent mechanisms during semantic object memory retrieval.

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1. Introduction

Object knowledge, as a specific form of semantic memory that is essential for interacting with our environments, is represented in multiple sensory, motor, and cognitive semantic subsystems (Allport, 1985; Martin, 2007; Hart et al., 2007). Probing various properties/features of objects has been found to elicit activations in their corresponding modality-specific brain regions, including visual form (shape), visual attribute (color), sound, smell, taste, manipulability, touch, motion, etc. (Martin, 2007; Martin and Chao, 2001; Goldberg et al., 2006; Kellenbach et al., 2001, 2003; Beauchamp et al., 2002, 2003; Noppeney and Price, 2002; Kraut et al., 2002a, 2006). How different properties of an object (for instance, a cat being an animal, having four legs and fur, and purring) are recalled and integrated to cohere as a single concept remains poorly understood.

A mechanistic account of the processes involved in integrating these multiple representations into a whole, the Neural Hybrid model, has been proposed by Hart and Kraut (2007). Under this model, an object concept is stored on the basis of distinct neural encodings for category-based and/or feature-based semantic knowledge representations that exist in separate subsystems, including various sensory, motor, lexical-semantic, and limbic systems. Activity in these distributed systems is coordinated through interactions between the medial superior frontal cortex (medial BA-6 in the pre-supplementary motor area, pre-SMA), caudate, and thalamus (Hart et al., 2013). We have probed the interactions between these brain regions by using the Semantic Object Retrieval Test (SORT), in which subjects have to decide whether two features result in retrieval of a particular object (Kraut et al., 2002b). The term "feature" here is used to refer to many aspects of object knowledge (e.g., cat), including attributes (tail), action (meow), function (pet), etc. In each trial of the SORT, two features are given, for example,

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"humps" and "desert", for subjects to produce an answer; in this case, "camel". There are also pairs of features that do not typically result in any object memory retrieval, for example, "humps" and "monitor". The former is called a retrieval trial and the latter a non-retrieval trial. The majority of experimental paradigms targeting semantic memory have used either verification or priming in the context of word associations and semantic relations (Martin, 2007; Kutas and Federmeier, 2000). Most of these tasks do not mandate retrieval of a specific concept (e.g., objects) but are related to processing of meaning in general, reporting on category or semantic relatedness between stimuli (probed as individual words/pictures or in the context of a sentence). The SORT task differs in that participants are required to directly evaluate whether the features result in retrieval of an object memory or not by making an explicit response.

Given that there is a strong emphasis on synchronization of neural activity in the Neural Hybrid model, further clarification of neural mechanisms underlying the retrieval processes requires techniques with sufficient temporal resolution. Scalp EEG, with millisecond resolution, is a non-invasive technique that primarily records the summation of postsynaptic excitatory and inhibitory potentials predominantly from the cortical structures immediately subjacent to the recording electrode. EEG data can be processed to extract event-related spectral perturbation (ERSP) and event-related potentials (ERPs). ERSP examines the spectral decomposition of EEG data, which can dissociate differential effects across multiple frequency bands, each of which may be associated with a particular set of cognitive processes (Cohen, 2014; Delorme and Makeig, 2004). ERP derive from averaging of EEG epochs to capture consistent changes in phase-locked neural activity as reflected in the timing and shape of ERP waveforms (Luck, 2005). To date, several neurophysiological studies using either technique have been performed to examine semantic object memory retrieval during SORT (Ferree et al., 2009; Brier et al., 2008; Chiang et al., 2014, 2015).

In the previous version of SORT, two features were always presented in the visual word form. Neural mechanisms invoked by previous SORT-based studies may reflect activation of object retrieval through only one stimulus type (i.e., the visual word system) and may not generalize to other presentation modalities (auditory stimuli) or domains (nonverbal stimuli). In our daily lives we receive information from a great variety of formats, and are able to integrate information and extract meanings or identify common objects. For example, even though seeing a picture of a tiger can be very different from reading the word "tiger", they may both activate overlapping neural representation of the concept. Still, it is far from settled as to whether semantic object representations and their retrieval are subserved by a unitary system or by multiple semantic subsystems (Binder and Desai, 2011; Damasio, 1990; Hart and Gordon, 1992; Patterson et al., 2007). Separate lines of research have supported the existence of a unitary system (Simanova et al., 2014; Lambon Ralph, 2013; Binder et al., 2009) as well as multiple semantic subsystems (Martin, 2007; Martin and Chao, 2001). It may be that both exist, but the degree to which these systems are involved or interact is still debated (Simmons and Martin, 2009; Bonner and Price, 2013; Tsapkini et al., 2011). Multiple semantic subsystems may operate differently as a function of object features (visual color, visual form, touch, Goldberg et al., 2006; Kellenbach et al., 2001, 2003) or the modality in which object features are presented (verbal vs. nonverbal stimuli, visual versus auditory stimuli, Chao and Martin, 1999; Beauchamp et al., 1999). Studies have found that multi-modality input, compared to uni-modality input, results in increased activation in multi-modal processing brain regions or even in primary sensory regions (Senkowski et al., 2008). This multimodal nature of information integration could also occur in semantic integration between multiple semantic subsystems, but neither this integration nor how it affects object memory retrieval has been extensively investigated.

To begin to address these questions, we modified the previous SORT to include two main distinctions in stimulus types: stimulus modality (e.g., visual vs. auditory) and stimulus domain (e.g., verbal vs. nonverbal). In the new SORT paradigm, instead of presenting two visual words simultaneously, features were presented sequentially, one at a time. The first feature was presented in one of the three different stimulus formats: written (visual) words, spoken (auditory) words, or pictures. This was followed by the second feature always presented as a visual word. The effect of how object memory is probed, first by stimulus modality (visual vs. auditory), could then be examined by comparing the visual word to auditory word task, while the effect of stimulus domain (verbal vs. nonverbal) could be examined by comparing the visual word to picture task. In order to examine the neural mechanisms time-locked to both stimulus onset and response, we evaluated EEG responses time-locked to the second stimulus (always a visual word) and to the response on a trial-by-trial basis. Stimulus-locked analysis can dissociate processes involved in attentional and memory integration, while response-locked analysis can dissociated processes involved in accumulation and integration of memory information that will lead to a decision (Werkle-Bergner et al., 2014).

Since electrophysiological responses may contain both evoked (phase-locked) and induced (oscillatory but not phase-locked) neural activity, we used trial-based power spectral analysis, which can report on both types of neural responses (Cohen, 2014; Roach and Mathalon, 2008). This time-frequency power analysis allowed us to detect and evaluate EEG synchronization (increase in power compared to baseline) and desynchronization (decrease in power compared to baseline), that represents coupling and uncoupling, respectively, of multiple neuronal populations that are involved in retrieval of object memory (Pfurtscheller and Lopes, 1999). One prior study using EEG power analysis during the original visual word-only version of SORT (Ferree et al., 2009) showed an early onset long-duration delta synchronization (~1 Hz) maximal at both the midline frontal and occipital sites, in retrieval trials compared to non-retrieval trials, suggesting a prolonged search and selection process that leads to successful retrieval (Hart et al., 2013). In addition, later high-beta synchronization (20–35 Hz, after 1 s post-stimulus) was found at frontal midline and left frontal sites, implicating the end of object retrieval. The latter finding corresponds closely to the temporal pattern and spectral characteristics observed via intrathalamic electrical recordings in Slotnick et al. (2002).

We focused on four EEG frequency bands, based on the results from prior studies that have suggested that EEG signals in these bands reflect processes important in lexical and semantic processing. These frequency bands are delta (1–4 Hz), theta (4–7 Hz), alpha (8–12 Hz) and low beta (13–19 Hz). Overall, alpha and low beta desynchronization have been shown to be associated with retrieval of lexical and semantic information (Bakker et al., 2015; Bastiaansen et al., 2008; Berger et al., 2014; He et al., 2015; Kielar et al., 2014; Li and Yang, 2013; Shahin et al., 2009; Strauß et al., 2014; Willems et al., 2008). Theta synchronization is linked to memory processes involved in lexical and semantic processing as well as in working memory and executive functions during memory retrieval (Bastiaansen et al., 2008; Bakker et al., 2015; Ketz et al., 2014; Li and Yang, 2013; Maguire et al., 2010; Shahin et al., 2009; Strauß et al., 2014). Delta synchronization indexes inhibition of irrelevant processes or attention allocation during cognitive operations, including working memory and semantic tasks (Harmony, 2013; Brunetti et al., 2013; Güntekin and Başar, 2016). We used these measures to detect stimulus-type (modality and domain) dependent similarities and differences in neural responses during semantic memory retrieval.

We hypothesized that if the mechanisms underlying semantic object memory retrieval are supported by multiple subsystems and thus vary with input format, we will observe effects modulated by stimulus type (modality or domain) at the behavioral and/or neural level. Since alpha and beta desynchronization have been linked to semantic memory retrieval processes, we predicted that modality- or domain-dependent effects would be found in these frequency ranges, either in the stimulus-locked or the response-locked analysis. Since the second stimulus was always a visual word, any differential effects between stimulus types would not be readily explained by

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