



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 post-synaptic 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 dissociate 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; Kiehl 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

sensory or perceptual differences in the stimuli. Alternatively, if some underlying mechanisms are unitary and do not vary with the format of input information, we would expect common effects among different stimulus types, independent of input format. These retrieval mechanisms may not be mutually exclusive, and examining these questions is important to understanding how different types of information are channeled via multiple semantic subsystems to activate a coherent object memory representation.

2. Methods

2.1. Subjects

Forty-eight young adult human subjects participated, with 16 subjects in each version of the SORT (auditory word: 12 F, $M_{age} = 21.4$ years, $SD = 2.7$; visual word: 10 F, $M_{age} = 21.4$ years, $SD = 2.9$; picture: 13 F, $M_{age} = 23.6$ years, $SD = 5.1$). All were right-handed (Edinburgh Handedness Inventory >40), native English speakers. Exclusion criteria included a history of neurological or psychiatric disorders, current treatment with psychotropic medications, traumatic brain injury, learning disabilities and communication disorders, and uncorrected visual or hearing impairments. Informed consent was obtained from all participants in accordance with the protocols approved by the Institutional Review Board of The University of Texas at Dallas.

2.2. Stimuli

The stimuli in the auditory-word [AW]/visual-word [VW] SORT include 112 words. These words represent features of objects, and in these experimental paradigms are paired with another word related to the same object to constitute 56 retrieval word pairs in total. An equal number of 56 non-retrieval word pairs were created by randomly re-pairing the words from the retrieval pairs so that they are not linked to any objects. For example, the word pair 'banana' and 'jungle' would facilitate memory retrieval of 'monkey' (retrieval pair). In contrast, 'banana' and 'monitor' should not facilitate memory retrieval of any object (non-retrieval pair). For the AW version, all 112 auditory word stimuli that match the visual words were recorded by a male native English speaker (sampling rate 22,050 Hz, 16 bits, sound duration controlled for 0.5 s per word). For the picture [Pic] version of the SORT, the picture stimuli were created or collected from clip art databases or the Internet, based on the meanings of the word stimuli. These stimuli are line drawings that represent 56 features (one in each of the 56 retrieval pairs). For example, a picture-word pair would be a picture of a banana and the written word "jungle". Non-retrieval pairs were created by randomly pairing the pictures with words that would not typically lead to any retrieval of an object. In all these tasks, if one pair of stimuli (such as retrieval pair, e.g., humps-desert) was always presented before the other pair (such as non-retrieval pair, e.g., cat-desert), there would be concerns for repetition or (in)compatibility effect. The former results from recalling the same stimulus (desert) and the latter results from recalling an inconsistent relationship between the first pair and the second pair. The presentation order of the stimulus pairs was counterbalanced across participants, which also minimized the contribution of these effects. To test our pictorial stimuli for recognizability and consistency of naming, we showed the 56 pictures to a separate sample of undergraduate students ($N = 77$, 67 F, $M_{age} = 23.4$ years, $SD = 4.4$) and asked them to write down the first three things/concepts they thought of when seeing each picture. Even though the participants were not explicitly asked to provide names of the pictures, on average the pictures were correctly named by 62% ($SD = 30.91$) of the subjects. Another group of subjects ($N = 11$, $M_{age} = 23.6$ years, $SD = 2.9$) were asked explicitly to provide the names of the picture stimuli (only one answer for each picture) and the agreement of picture naming was 79.9% ($SD = 29.23$). The naming agreement could have been underestimated also since we did not include those names that did not match exactly to

the corresponding words used for the AW and VW versions. For instance, a picture of fangs may be named as teeth, which would still properly represent the feature, but was not included for analysis. These results validated using these pictorial features as proper probes for the intended features and retrieval targets.

2.3. Experimental paradigm and procedures

Each subject performed one version of the SORT (Fig. 1). The first stimulus (a visual word or a picture) was presented for 500 ms, followed by a white blank background for 1000 ms and subsequently the second stimulus for 3000 ms. When the first stimulus was an auditory word (duration of 500 ms), a fixation point ("+") remained on the screen for the entire time (1500 ms) to fixate eye gaze until the second stimulus was presented. Between trials, there was an interval during which a visual fixation target (i.e., a "+" sign) stayed on the screen (jittered in length between 2500 and 3500 ms; mean = 3000 ms). Upon seeing the second stimulus (Fig. 1), subjects had to indicate if the two sequentially presented features elicited the memory of any particular object by pressing the button under right index and middle fingers for "yes" and "no" answers, respectively, using a button box. Subjects had to respond by the end of the 3 s interval during which the second stimulus remained on the screen. Any response made after 3 s or before 300 ms was labeled as an incorrect trial. Reaction time (RT) and accuracy were recorded for each trial. There were 6 different sequences with pseudorandomized orders of the stimuli for all three versions of the SORT (AW, VW, Pic). The entire task lasted about 15 min, and halfway through the task, there was a rest period for 1 min.

The instructions were, "You will first see a plus sign. Then you will see a word (VW)/hear a spoken word (AW)/see a picture (Pic), followed by a written word. These words represent features that are related to objects. If the two words (VW and AW)/the picture and word (Pic) combine to make you think of a particular object, press the number 2 button with your index finger. If the two words do not combine to make you think of a particular object, press the number 3 button with your middle finger. Press the buttons firmly. Be as quick and accurate as possible. *Keep your eyes open (AW).*" Here we have used *italicized text* to delineate differences in instructions for each task version.

Word and picture stimuli were presented using Stim software (Compumedics Neuroscan, USA) on an LCD screen placed about 46 in. from the participant. Word and picture stimuli spanned about 5° of the horizontal visual angle, varying slightly by the word length and the picture size. All words and pictures were presented in black, with words in lower case *Times New Roman* font, against a white background. Auditory words were presented through two speakers placed at the same height above the ground (1.3 m), facing horizontally toward the subject's ear on each side (1.2 m). The volume of sound was controlled at 66 dB.

2.4. EEG data acquisition and processing

Continuous EEG was recorded using a 64-electrode elastic cap (Neuroscan Quickcap) through a Neuroscan SynAmps2 amplifier and using Scan 4.5 software (Compumedics Neuroscan, USA; sampling rate: 1 kHz, DC–200 Hz). Electrode impedances were typically below 10 k Ω . The reference electrode was located at midline between Cz and CPz, and vertical electrooculogram (VEOG) was recorded at sites above and below the left eye. Data were processed off-line using Neuroscan Edit software (Compumedics Neuroscan). Poorly functioning electrodes were identified by visual inspection of data and were excluded. Electrodes that had impedance over 20 k Ω were also excluded from analysis (both online and offline). Exclusion rate was no more than 5% of the total number of electrodes (averages of 1.69%, 1.13%, and 1.5% in the VW, AW, and Pic, respectively) to record technically adequate signals in any subject (following guidelines by Picton et al., 2000). The continuous EEG data were high-pass filtered at 0.15 Hz

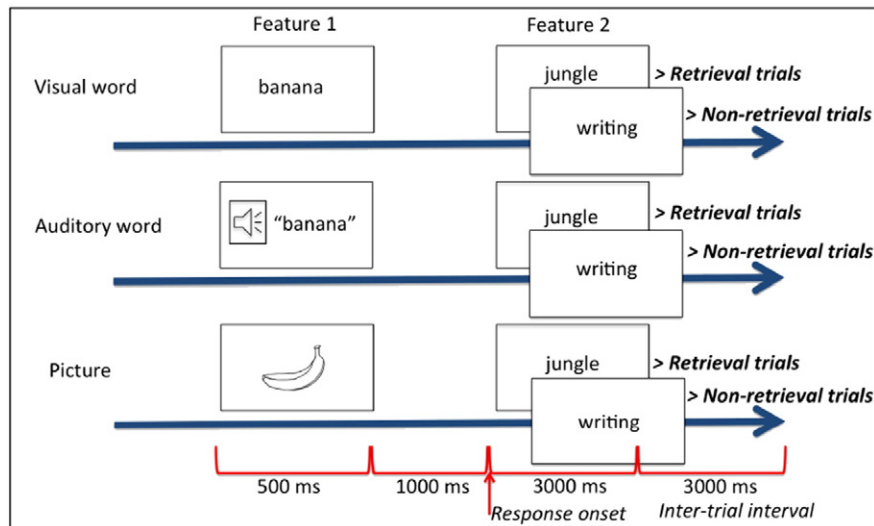


Fig. 1. Schematic view of the experimental design. Feature 1 is presented, followed by feature 2 as in all three versions of the SORT. The first feature varies with the version, so that it is a visual word, an auditory word, or a picture. The second feature is always a visual word regardless of the version. Retrieval trials bring to mind an object memory (e.g., “banana” and “jungle”) while non-retrieval trials do not (e.g., “banana” and “writing”). Parameters of stimulus timing are noted at bottom.

and corrected for eye blinks using the spatial filtering function in the Scan 4.5 software (Semlitsch et al., 1986; Compumedics Neuroscan, USA).

EEG data were then processed using an in-house processing schema based on EEGLAB functions (Delorme and Makeig, 2004) in MATLAB (MathWorks Inc.). For stimulus-locked analysis, EEG data were first segmented into multiple trial-by-trial epochs (−1000 to 2000 ms, time-locked to the second stimulus, a written word). Only correct trials were included for analysis. Outlier epochs (with data ± 5 SD from the mean for the epoch using EEGLAB functions) were excluded from analysis. Overall, 82.4% (39.9 trials) of the total correct retrieval trials and 80.9% (43.5 trials) of the total correct non-retrieval trials were retained in the AW-SORT, 82.1% (39 retrieval trials) and 80.5% (43.7 non-retrieval trials) in the Pic-SORT, 76.4% (38.5 retrieval trials) and 74.9% (39.6 non-retrieval trials) in the VW-SORT. Factorial analyses showed no significant statistical difference in data loss among the tasks and conditions, and no significant interactions ($p > 0.05$). For response-locked analysis, same criteria were applied but EEG epochs encompassed −1700 ms to 1200 ms. An algorithm computing the average based on spherical splines fitted to the data was then applied to interpolate EEG data (both stimulus-locked and response-locked analyses) to the sites of the bad electrodes (Ferree et al., 2009). Interpolation was used only when the number of bad electrodes was $<5\%$ of all 62 electrodes, and the bad electrodes were not contiguous (as previously applied in Ferree et al., 2009; Spence et al., 2013). After artifact/epoch rejection was performed and data from the missing electrodes were interpolated, we used Fast Fourier Transformation (FFT) to extract power data for frequencies from 1 to 40 Hz (with 1 Hz intervals), using Hanning window tapering that segmented the entire epoch into 60 and 80 time windows for stimulus-locked and response-locked analyses, respectively. The length of the sliding time windows were 500 ms in both analyses, resulting in temporal gaps (between two successive windows) of about 40 ms and 30 ms in stimulus-locked and response-locked analyses, respectively. We used a padding ratio of 2 which doubled the window length by adding zero padding resulting in frequency resolution of 1 Hz. In the stimulus-locked analyses, baseline correction within each frequency interval (1 Hz resolution from 1 to 40 Hz) was performed for each trial by subtracting the average power between −600 and −100 ms pre-stimulus onset from each time point post-stimulus onset. In the response-locked analyses, frequency-band-specific baseline correction was performed for each trial by subtracting the average power between 300 and 800 ms post-response onset from each time

point before the response. The power data were then converted to power spectral density (PSD, V^2/Hz) and logarithmically transformed for further statistical analysis.

2.5. Behavioral analysis

Omnibus analyses were performed over all stimulus types. RT and accuracy were analyzed using mixed-model ANOVAs with a between-subject factor [stimulus type: AW, VW, and Pic] and a within-subject factor [condition: retrieval vs. non-retrieval].

2.6. EEG power and STAT-PCA analysis

The EEG power data were averaged across multiple frequency bands and separated by delta (1–4 Hz), theta (4–7 Hz), alpha (8–12 Hz), and lower beta (13–19 Hz). The EEG power data over different frequencies were analyzed separately using STAT-PCA (Spence et al., 2013). For each frequency range in the stimulus-locked analysis, the spatial units are electrodes (62 electrodes) and the temporal units are 40-ms time windows within an epoch (0 to 1200 ms post-stimulus). We thus had $62 \times 30 = 1860$ combinations of space and time (62 electrodes and 30 time windows in an epoch). In the response-locked analysis, the spatial units are electrodes (62 electrodes) and the temporal units are 30-ms time windows within an epoch (−1000 to 0 ms prior to response). We thus had $62 \times 34 = 2108$ combinations of space and time (62 electrodes and 40 time windows in an epoch).

To examine the overall effect of stimulus type on EEG power during object memory retrieval, we implemented a linear mixed model for each one of the 1860 (stimulus-locked)/2108 (response-locked) spatial/temporal units in the SORT EEG epochs (separately performed for each frequency range):

$$Y_{ijkl} = \mu + \lambda_i + b_{j(i)} + T_k + (\lambda T)_{ik} + \varepsilon_{ijkl},$$

to examine the effects of stimulus type (λ_i), condition (T_k) and the interaction between modality and condition (λT)_{ik}, on the scalp potential Y_{ijkl} , where each subscript indexes modality, subject, condition, and trial, respectively. Stimulus type ($i = 3$) had three levels including AW, Pic, and VW; condition ($k = 2$) included retrieval and non-retrieval trials; subjects were embedded in each stimulus type (between-subject design, $j = 16$); every trial was included in the analysis (therefore l varied across individuals) (see more detailed descriptions of this method in

Chiang et al., 2015). These statistical analyses were performed in the SAS software 9.4 using Proc Mixed, and the variances associated with subject variability, $b_{j(i)}$, and trial variability, ε_{ijkl} , were also estimated by restricted maximum likelihood. The F values of each of these three effects of interest (modality, condition and their interaction) per electrode per time-window were retained if the corresponding test was below the threshold of $FDR = 0.01$. Otherwise, the F values were set to zero for better isolation of the experimental task-related effects. We applied principal component analysis (PCA) to the temporal dimension of the 3 matrices of thresholded average potentials, each containing 62 spatial units (electrode) by 30/40 temporal units (time window in stimulus-locked/response-locked), and the main spatial components (PCA loadings) were retained using parallel analysis (Horn, 1965). Varimax rotation was applied to improve interpretation of the loadings. For each retained temporal component, the spatial components were the resulting PCA scores. The retained temporal/spatial components were visualized by plotting temporal PCA loadings as a time-series and spatial PCA scores in topographical distribution across scalp.

3. Results

3.1. Behavioral results

Group average RT and accuracy were presented in Table 1. For RT, the omnibus 2-way ANOVA revealed a significant main effect of condition, $F(1,45) = 41.8, p < 0.001$, overall, with retrieval trials (1015 ms) responded to more quickly than non-retrieval trials (1186 ms); the main effect of stimulus type was not significant ($p = 0.079$). A significant main effect of stimulus type (using 1-way ANOVAs) was found only for non-retrieval trials, $F(2,45) = 3.2, p = 0.048$, but not for retrieval trials ($p = 0.122$), which contributed to a significant condition/stimulus-type interaction in the omnibus analysis, $F(2,45) = 4.4, p = 0.018$. Among non-retrieval trials, RT was significantly longer in VW compared to Pic, $t(30) = 2.3, p = 0.028$, and was marginally longer in AW compared to Pic, $t(30) = 2, p = 0.06$.

For accuracy, the omnibus 2-way ANOVA revealed a significant main effect of condition, $F(1,45) = 37.8, p < 0.001$, with non-retrieval trials (90%) more accurate than retrieval trials (81.8%), but neither the main effect of stimulus type ($p = 0.89$) nor the condition/stimulus type interaction ($p = 0.11$) was significant.

3.2. EEG power results

In the stimulus-locked analysis, there was a main effect of condition for all frequency ranges. In delta (1–4 Hz), the temporal component (55.6% of the variance) peaked around 500 ms post-stimulus onset. It was maximal in amplitude at a central electrode (C1, Fig. 2a & b). This effect mostly reflected increased delta synchronization (compared to baseline) in retrieval compared to non-retrieval trials (Fig. 2c). There was a second PCA component for delta with the temporal component (27.6% of the variance) that peaked around 500 ms post-stimulus onset. It was maximal at CP3 and showed the same pattern between retrieval and non-retrieval trials. It seems that regardless of this minor discrepancy in space, these two components related to the same

underlying process. As such we would discuss only the first component to minimize redundancy. In theta (4–7 Hz), the temporal component (54% of the variance) onset around 700 ms post-stimulus onset, and was maximal in amplitude at bilateral central and parietal electrodes (Fig. 2a & b). This effect was due to increased theta desynchronization in retrieval compared to non-retrieval trials (Fig. 2c & d). In alpha (8–12 Hz), the temporal component (75.7% of the variance) onset around 700 ms post-stimulus onset, and was focused in midline and right central and parietal electrodes (Fig. 2a & b). This effect was contributed to by increased alpha desynchronization in retrieval compared to non-retrieval trials (Fig. 2c & d). In low beta (13–19 Hz), the temporal component (78.3% of the variance) arose around 700 ms post-stimulus onset and was focused in left central and parietal electrodes (Fig. 2a & b). Here, increased low beta desynchronization in retrieval compared to non-retrieval trials (Fig. 2c & d) drove this result. Topographical representation of the condition effect for each frequency band over time was reported in Supplemental Fig. a. No other effects survived at the level of $FDR = 0.01$.

Since EEG changes in the delta, alpha, and beta frequency bands all seemed to arise/onset around the same time and remained significant within similar time window (600–1200 ms), the boundaries between these frequency bands would seem to be artificial. In other words, oscillations at these frequencies might indeed correlate with one another, and separating these frequencies could not be justified. In order to test this possibility, we modified the STAT-PCA analysis to focus only within the time window between 600 and 1200 ms but included the entire frequency domain (from 1 to 40 Hz). Using the same approach as described in the Methods section, we constructed a data matrix with 40 spectral units and 62 spatial units ($40 \times 62 = 2480$) and then applied the same general linear model-based analyses to the matrix. Last we did sequential spectral-spatial PCA (first on frequency, secondly on electrode) on the statistical output thresholded at $FDR = 0.01$. Using this data-driven approach, we found that theta, alpha, and beta were dissociated as separate PCA components, each of which showed frequency ranges similar to the predetermined ones (Supplemental Fig. 2), validating our approach of segmenting frequency bands in the first place.

Response-locked analyses were performed in order to exclude the possibility that the EEG effects were significantly influenced by the RT differences between retrieval and non-retrieval conditions and also to examine pre-response neural mechanisms that lead to a decision during semantic object memory retrieval. There was a main effect of condition for all frequency ranges. In delta (1–4 Hz), the temporal component (65.9% of the variance) peaked around –200 ms pre-response onset. It was maximal in amplitude at a fronto-central electrode (FC1, Fig. 3a & b). This effect mostly reflected larger delta power in retrieval compared to non-retrieval trials (Fig. 3c). In theta (4–7 Hz), the temporal component (67.9% of the variance) started early and plateaued around 400 ms pre-response onset, and was maximal in amplitude at right temporal and midline parietal electrodes (Fig. 3a & b). This effect was due to larger theta power in retrieval compared to non-retrieval trials (Fig. 3c & d). In alpha (8–12 Hz), the temporal component (60.2% of the variance) sustained from early time frame till around 400 ms before response onset, and was focused in bilateral central and parietal

Table 1
Behavioral data (accuracy/RT).

	RT-R (ms)	RT-NR (ms)	p values	Acc-R (%)	Acc-NR (%)	p values
AW (N = 16)	1081 (179)	1214 (228)	0.007**	80.9 (5.7)	89.9 (8.6)	0.003**
Pic (N = 16)	946 (186)	1046 (255)	0.026*	80.6 (5.7)	91.8 (7)	<0.001**
VW (N = 16)	1018 (181)	1297 (353)	<0.001**	83.9 (5.8)	88.2 (7.1)	0.057

Each box represents mean (standard deviation). The p values represent the significance of paired t -tests between retrieval and non-retrieval trials within each task, for reaction time (RT) and accuracy (Acc), separately. R: retrieval trials; NR: non-retrieval trials.

** $p < 0.01$.

* $p < 0.05$.

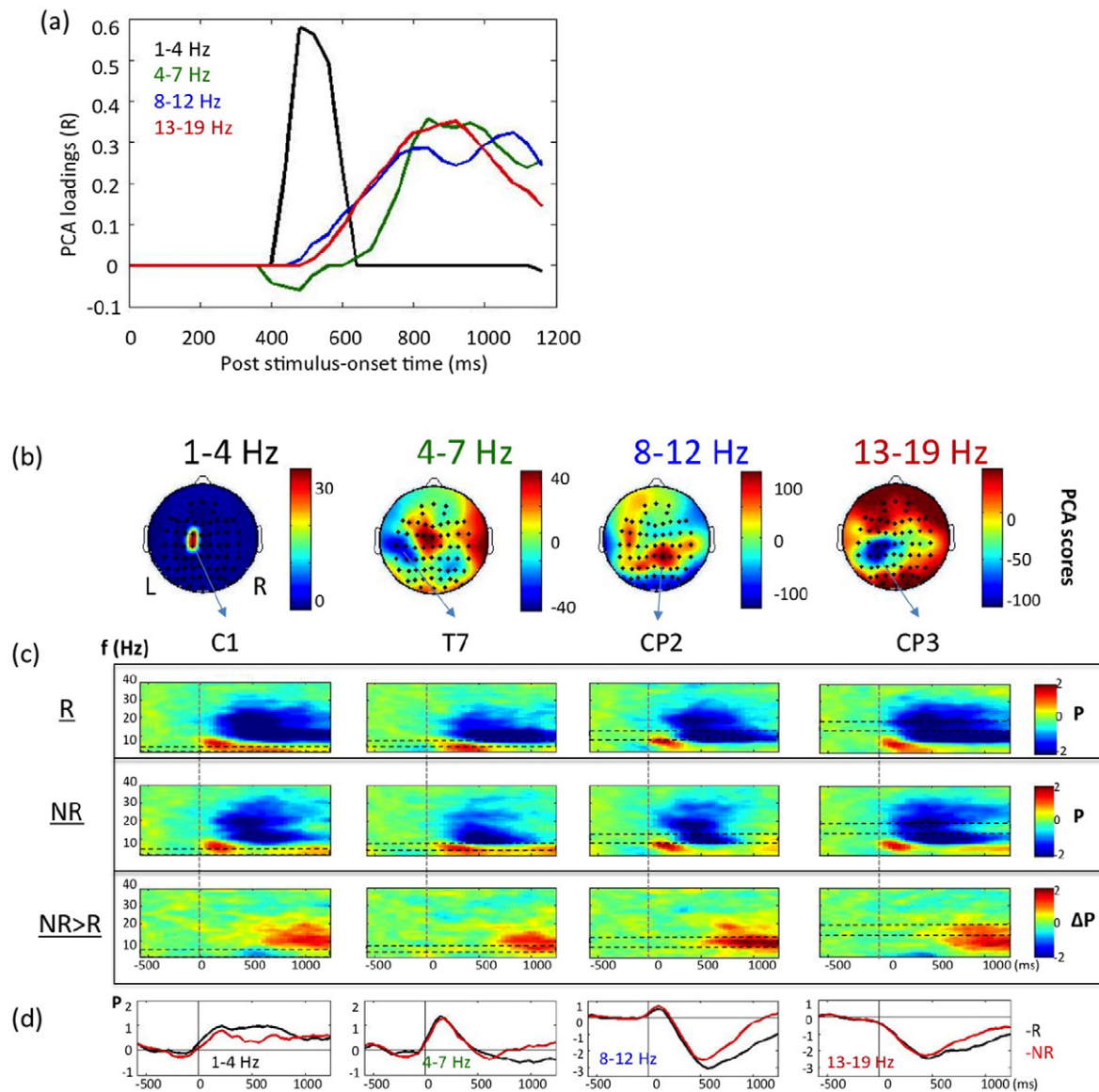


Fig. 2. Results of STAT-PCA analyses common to all tasks for stimulus-locked EEG epochs. The temporal factors are plotted starting from the stimulus onset (of the second stimulus) to 1200 ms post-stimulus onset (a). The spatial factors are plotted in separate columns for each frequency range (b). Electrodes that revealed the most prominent effects are plotted individually with spectrograms that represent the magnitude of P (-2 to 2 , color bars; unit = $\log_{10}(\text{PSD})$; PSD = power spectral density, V^2/Hz) for frequencies of 1–40 Hz (y-axis) and time points of -600 to 1200 ms (x-axis) (c). These spectrograms are plotted separated for retrieval (R) and non-retrieval (NR) trials, and their difference ($\text{NR} > \text{R}$). Power change over time for each frequency of interest is then plotted to accentuate the difference between conditions (d).

electrodes (Fig. 3a & b). This effect was contributed to by larger alpha power in retrieval compared to non-retrieval trials (Fig. 3c & d). In low beta (13–19 Hz), the temporal component (68.4% of the variance) arose around 300 ms pre-response onset and was focused in right central and parietal electrodes (Fig. 3a & b). Here, increased low beta desynchronization in retrieval compared to non-retrieval trials (Fig. 3c & d) drove this result. Topographical representation of the condition effect for each frequency band over time was reported in Supplemental Fig. 3.

Interactions between stimulus type and condition were significant for alpha power (no other effects survived at the level of $\text{FDR} = 0.01$). Three PCA components were found. The first component arose around 500 ms pre-response onset (53% of the variance) and was maximal at the anterior frontal and midline central sites (Fig. 4a & b). By extracting mean power from the chosen time window (-600 to -400 ms) and using 1-way ANOVA in the post-hoc tests to examine the effect of

stimulus type for retrieval and non-retrieval trials separately, we found that this later effect (relative to response time) was mainly contributed to by alpha power differences in non-retrieval trials, $F(2,45) = 4.29$, $p = 0.02$, but not in retrieval trials, $F(2,45) = 0.32$, $p = 0.729$, at anterior frontal sites (AF3; Fig. 4). Non-retrieval trials in AW had significantly more negative alpha power than did VW, $t(30) = 3.32$, $p = 0.002$, but no differences were found between AW/Pic and VW/Pic ($p > 0.1$) (Fig. 4c). In addition, alpha power differences modulated by stimulus type were significant in both retrieval, $F(2,45) = 4.55$, $p = 0.016$, and non-retrieval trials, $F(2,45) = 4.85$, $p = 0.012$, at midline central sites (C2; Fig. 4c). In retrieval trials, AW had larger (more positive) alpha power than did Pic, $t(30) = 3.22$, $p = 0.003$; no differences between AW/VW and Pic/VW were found ($p > 0.05$). In non-retrieval trials, both AW and Pic had larger (more negative) alpha power than did VW, $t(30) = 2.83$, $p = 0.008$ and $t(30) = 2.38$, $p = 0.024$, respectively (Fig. 4c). The second PCA component

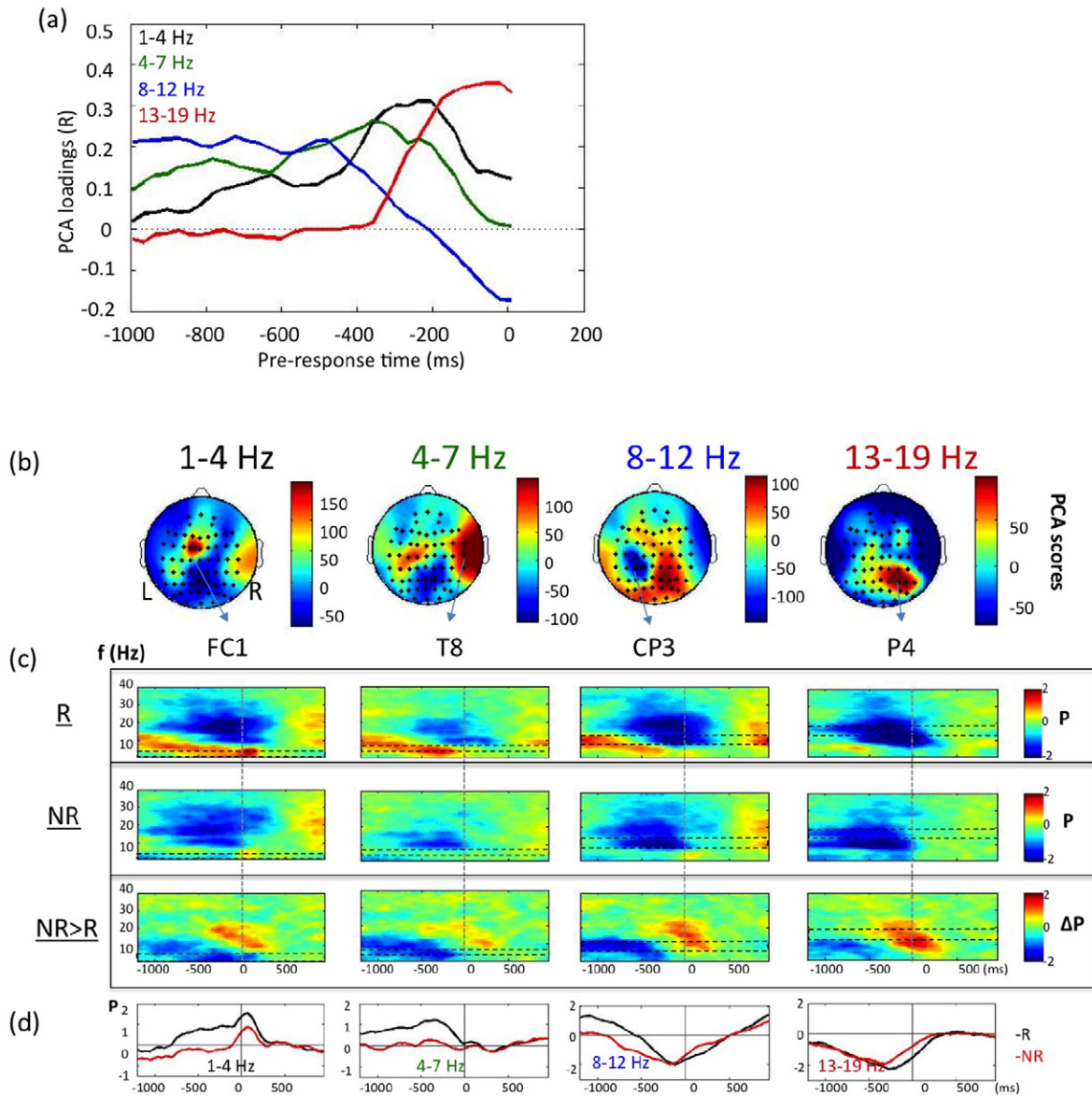


Fig. 3. Results of STAT-PCA analyses common to all tasks for response-locked EEG epochs. The temporal factors are plotted starting from 1000 ms prior to response to response onset (a). The spatial factors are plotted in separate columns for each frequency range (b). Electrodes that revealed the most prominent effects are plotted individually with spectrograms that represent the magnitude of P (-2 to 2 , color bars; unit = \log_{10} (PSD); PSD = power spectral density, V^2/Hz) for frequencies of 1–40 Hz (y-axis) and time points of -1200 to 950 ms (x-axis) (c). These spectrograms are plotted separated for retrieval (R) and non-retrieval (NR) trials, and their difference ($\text{NR} > \text{R}$). Power change over time for each frequency of interest is then plotted to accentuate the difference between conditions (d).

(14% of the variance) arose around 1000 ms prior to response and did not result in significant differences between stimulus types ($p > 0.05$). The third PCA component (9.7% of the variance) arose around 700 ms prior to response and was maximal at midline central and parietal sites (Fig. 4a & b). Post hoc tests (using mean power within the window between 800 and 600 ms before response) showed that this effects was mainly driven by differences in retrieval trials across stimulus types, $F(2,45) = 4.1$, $p = 0.023$, but no such effect was found in non-retrieval trials ($p > 0.1$) (Fig. 4c). Further tests showed AW had significantly larger (more positive) alpha power than Pic, $t(30) = 2.95$, $p = 0.006$, but no differences were found between AW/VW and VW/Pic ($p > 0.1$) (Fig. 4c).

Finally, we also examined the baseline condition based on analysis time-locked to the first stimulus. We found that baseline power distribution across frequencies did not differ significantly across different stimulus types and did not suggest that any interactions could be contributed simply by differences in baseline (details of this analysis can be found in the Supplemental methods/results.)

4. Discussion

Using a modified version of SORT where we varied the stimulus type of the first object feature followed by a second feature that was always a visual word, we found effects that are modulated by stimulus modality/domain in the first feature and those that are common to all stimulus types underlying semantic object memory retrieval. Behaviorally, non-retrieval trials had longer RT and better accuracy compared to retrieval trials. These effects have been consistently shown in all previous SORT studies using only visual words as stimuli (Brier et al., 2008; Chiang et al., 2014, 2015). As proposed before, this difference between conditions may indicate a longer and more exhaustive search in non-retrieval compared to retrieval trials that is required before making a decision (Chiang et al., 2014); this search seems to last even longer in the verbal domain (VW and AW) compared to the nonverbal domain (Pic) when non-retrieval RT was considered. In terms of EEG data, stimulus-locked and response-locked analyses rendered separate findings but will be

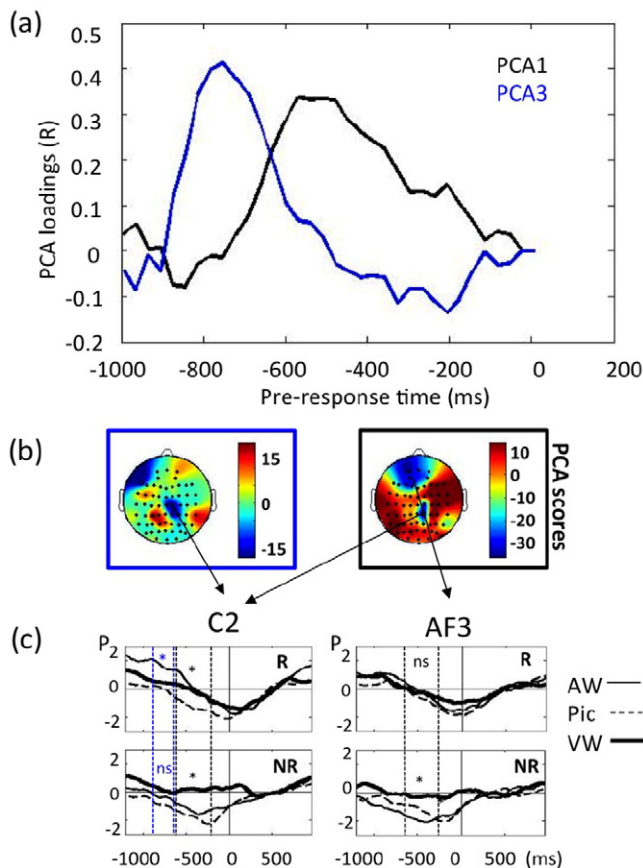


Fig. 4. PCA results on the interaction effect between condition and stimulus type based on response-locked analysis. Two main effects peaked around 500 ms and 700 ms prior to response represented in black and blue, respectively (a). The earlier effect is maximal at central sites and the later effect is maximal at anterior frontal and central sites (b). The interaction at the earlier time frame (at C2 within the blue dotted time window) indicates significant main effect of stimulus type found only in retrieval (R) ($p = 0.023$) but not in non-retrieval (NR) ($p = 0.146$) condition in the unit of P ($\log_{10}(\text{PSD})$; PSD = power spectral density, V^2/Hz) (c). The interaction at the later time frame (within the black dotted time windows) indicates significant main effect of stimulus type in R ($p = 0.016$) and NR ($p = 0.012$) conditions at C2 (c). At AF3, the effect is only significant in NR ($p = 0.02$) (c). Statistical tests were based on the mean power within the time windows (earlier: 800 to 600 ms prior to response; later: 600 to 400 ms prior to response) using 1-way ANOVA with stimulus type as the one factor. $p < 0.05$ (*); not significant (ns).

discussed together in the following sections, each of which addresses one frequency range.

4.1. Alpha power results

We found that prior to response alpha power was larger in retrieval than in non-retrieval trials. This effect lasted for a long period of time, until about 300 to 400 ms prior to response. Within this same time window (−1000 to −300 ms), two main interaction effects between stimulus type and condition were found in the alpha power. One effect that peaked around 500 ms prior to response distinguished different stimulus types for both retrieval (at the central sites) and non-retrieval trials (at the frontal and central sites). An earlier interaction effect that peaked around 700 ms prior to response was found mainly in the retrieval trials at the central sites. In other words, *modality-dependent changes* seemed to start earlier in retrieval trials (700 ms before response) than non-retrieval trials (500 ms before response), dissociating modality-dependent pre-response processes in retrieval trials from those in non-retrieval trials. These changes in alpha power prior to response plausibly reflect accumulation and integration of semantic

information that lead to final decision (Werkle-Bergner et al., 2014). Our findings suggest that this information integration process for cross-modality semantic binding (in AW, from auditory to visual) can elicit more neural recruitment than within-modality semantic binding (in Pic, from visual to visual) in retrieval trials. This integration process also seems to be modulated by both cross-domain (in Pic, from nonverbal to verbal) and cross-modality (in AW, from auditory to visual) semantic binding compared to within-domain/modality semantic binding (in VW, from verbal/visual to verbal/visual) in non-retrieval trials. In retrieval trials, these modality-dependent processes could be indicative of access to memory stores that are modality-dependent and can be distinguished from those in non-retrieval trials that may simply reflect information integration during search for memory, considering only retrieval trials elicit object memory. All these neural signatures of modality-dependent alpha power changes lead to a decision that is predicated upon the mnemonic content where information needs to be generated and integrated (Ratcliff, 1978). We also contend that these alpha changes signifying memory retrieval are not decision making per se, which adapts to a variety of tasks and may be more modality-independent and (cognitive) domain-general (Ho et al., 2009; Fellows, 2004).

We found main effects of condition in stimulus-locked analyses of alpha power. The accentuated alpha desynchronization (compared to pre-stimulus onset baseline) associated with retrieval compared to non-retrieval trials reflects neural mechanisms that are more prominent when an object memory is successfully retrieved. It arises between 700 and 800 ms post-stimulus onset. It has been suggested that alpha desynchronization reflects suppression of global processing that leads to task-based regional activation (Pfurtscheller and Lopes, 1999; Shahin et al., 2009; Li and Yang, 2013). Hence, in order for an object to be retrieved, global cortical activity has to be suppressed, so more specific activation of the regions associated with the targeted object driven by task-directed processes can be facilitated. As a proxy for this proposed mechanism, alpha-band EEG power change is frequently associated with mental operations not limited to semantic memory, but enhancement of attentional focus in general, that could be utilized by different cognitive processes (Klimesch, 2012; Wang and Bastiaansen, 2014). Alternatively, it also has been shown that after successful object activation in memory, there is later neural activation correlated with mental imagery and other later cognitive processes associated with the retrieved memory, particularly in the alpha frequency band (Michel et al., 1994; Bartsch et al., 2015).

4.2. Beta power results

We also found main effects of condition in beta power in both stimulus and response-locked analyses. Both analyses revealed increased beta desynchronization in retrieval compared to non-retrieval trials, with somewhat overlapping timing and spatial distribution. Low beta-band EEG power change may be linked to mechanisms more specifically involved in lexical or semantic retrieval as suggested by previous studies (Bakker et al., 2015; Lewis et al., 2015; Bastiaansen et al., 2008). This beta desynchronization is potentially mediated by the pre-SMA-caudate-thalamus circuit that has been proposed to underlie the retrieval process of object memory (Hart et al., 2013). This is supported by results from previous studies showing both scalp-recorded and intra-cranial beta frequency differences between retrieval and non-retrievals, hypothesized to represent integration of the features of an object into an integrated memory representation (Slotnick et al., 2002; Hart et al., 2013). Beta power changes found in prior studies (20–35 Hz) seem to differ from those in the current study (13–19 Hz). The main reason is likely to be the difference in simultaneous stimulus presentation (prior studies) and sequential stimulus presentation (current study), which warrants more focused investigation in the future.

4.3. Delta power results

Delta power also showed changes between conditions in both stimulus-locked and response-locked analyses. In stimulus-locked analysis, prior to the significant drop in alpha and low beta power for retrieval trials, around 500–600 ms post-stimulus onset, there is an increase in mid-line frontal and central delta synchronization for retrieval trials compared to non-retrieval trials. In response-locked analysis, there was an increased delta power in retrieval compared to non-retrieval trials about 200 ms prior to the response. These two analyses separately revealed an early delta effect (stimulus-locked) and a late delta effect (response-locked), suggesting two separate processes. However, judging from partly overlapping spatial distribution, we posit that these two effects reflect similar cognitive mechanisms. Delta synchronization has been associated with cortical inhibition that is posited to attenuate the activity of irrelevant networks to accomplish the current task, and has been associated with neural activation in the medial frontal cortical regions (Harmony, 2013), potentially including pre-SMA in the superior medial frontal area. It is thus plausible that this increased early delta activity (in stimulus-locked analysis) represents early pre-SMA involvement in supporting selection and goal-directed processes that would subsequently lead to later increases in alpha and low beta desynchronization to retrieve an object memory. In contrast, the increased late delta activity (in response-locked analysis) may represent a later pre-SMA involvement processes around making a decision, such as disengagement of cortical co-activation elicited by successful retrieval of object memory. These findings fit with our model hypothesizing pre-SMA may be involved in both initiating and terminating the memory retrieval process (Hart et al., 2013).

4.4. Theta power results

Theta power also showed main effects of condition in both stimulus-locked and response-locked analyses. In stimulus-locked analysis, around the same times that alpha and low beta band EEG power dropped more significantly for retrieval trials compared to non-retrieval trials, there is also an increase in theta desynchronization that is larger in retrieval compared to non-retrieval trials. Even though the frequencies showed similar timing of effects, we have shown that these frequencies did not cluster and were separable by data-driven approach (PCA) even without setting boundaries among frequency bands, supporting that these frequency bands reflect independent neural entities. Similarly, in response-locked analysis, retrieval trials showed greater theta change than non-retrieval trials. This theta synchronization is distributed among central and temporal regions, which has been suggested to be associated with cognitive control functions during memory retrieval (Bakker et al., 2015; Melleme et al., 2013; Shahin et al., 2009). We thus posit that these cognitive control related theta power changes may be associated with information accumulation and integration that occur prior to or around decision processes (Werkle-Bergner et al., 2014), which are needed in memory retrieval processes in general. This is also supported by the suggested distinction between alpha and theta, respectively, to correlate with semantic long-term memory performance and the ability to encode new information (Klimesch, 1999), in which case theta is associated with search processes during retrieval and updates newly activated information. Alternatively, a compatibility effect has also been observed as changes in theta power synchronization (Nigbur et al., 2011). However, since all sequences were thoroughly counterbalanced across participants, with one pair presented first in some but the other pair presented first in others, this effect has been minimized.

In conclusion, we have identified neural processes modulated by stimulus type in both retrieval and non-retrieval conditions during semantic object memory retrieval as measured by alpha-band EEG changes. Particularly in retrieval trials, the modality-dependent processes could indicate access to or activation of memory stores that requires accumulation and integration of information prior to making a decision.

Retrieval trials also showed increased magnitude of neural activity compared to non-retrieval trials in multiple frequency bands across all stimulus types. Alpha and beta desynchronization sustain over a longer time period, which indicate memory access and integration that is mediated by the pre-SMA-caudate-thalamus circuit to complete feature integration and object memory retrieval. Both early delta synchronization and later delta synchronization occur near pre-SMA, both assisting in access and decision in memory retrieval. Finally, theta synchronization is an indicator of cognitive control in retrieving object memory. These processes may need to be further dissociated into other cognitive sub-processes, which is beyond the scope of the current study. These oscillatory cortical phenomena, dependent upon or independent of the stimulus format in which object memory is probed, further enrich the Neural Hybrid model in explicating the mechanisms of how separate object features can be tied together to generate and decide upon a coherent object concept during memory retrieval.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ijpsycho.2016.06.011>.

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