

Study-phase mechanisms of memory organization in free recall

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## Abstract

Memories are organized by meaning. For example, when recalling favorite restaurants, one might organize responses by the type of food served. Experimentally, this organization of associated experiences is captured by the free recall paradigm, in which participants have the tendency to consecutively recall stimuli that share meaning – a phenomenon termed semantic clustering. Intuitively, it would seem that semantic clustering is the result of processes during test – that is, a single retrieval cue may trigger the recall of multiple associated experiences. However, previous work has shown that study-phase neural signals predict subsequent semantic clustering, suggesting that semantic organization is at least partly driven by study-phase processes, although it remains unclear what processes underlie these signals. Here, we hypothesized that semantic organization is supported by differential processing of associated study items, whereby processing of later study list items is influenced by the presentation of semantically associated items earlier in the study list. To test this hypothesis, we recorded scalp electroencephalographic (EEG) activity while participants performed a free recall task. Each study list was comprised of “pairs” of individually presented words, half of which were strongly semantically associated (e.g. “dog” and “cat”) and half of which were weakly semantically associated (e.g. “road” and “shore”). We separately assessed memory performance for first (“dog,” “road”) and second associates (“cat,” “shore”) and find that probability of recall is greater for strong second associates (“cat”) compared to weak second associates (“shore”). We find that second strong associates are more likely to be semantically clustered than first strong associates. We replicate the finding that semantic clustering is characterized by power increases over frontal and parietal/occipital brain regions. Critically, we show that the neural subsequent semantic clustering effect differs across pairs of semantic associates, with increased high frequency activity and decreased low frequency activity for second compared to first associates. Collectively, these results suggest that semantic organization of memories arises from differential processing of associated study items.

## Introduction

Memories are organized by meaning (Bousfield, 1953). For example, if you were asked to name your favorite artists, you might organize your responses by their art style. You might say “Monet and Degas are my favorite Impressionists, but my favorite Abstract Expressionists are Pollock and Rothko.” Intuitively, it may seem that this tendency to organize arises from processes active during test, i.e. that a single retrieval cue triggers the recall of multiple associated experiences. However, previous work has demonstrated that neural signals during memory formation predict subsequent organization (Long & Kahana, 2017), suggesting that the tendency to organize is at least partly driven by processes active during study. However, it remains unclear what process or processes underlie these signals. The aim of the current study is to elucidate the mechanisms during study that lead to memory organization.

Retrieved context theory offers insight into memory organization. Retrieved context theory posits that items and their spatiotemporal context – a combination of internal states and external stimuli – are bound together when memories are formed (Howard & Kahana, 2002; Sederberg, Howard, & Kahana, 2008) and that context is used as a cue to guide retrieval at test. The tendency to consecutively remember items that share meaning – a phenomenon termed ‘semantic clustering’ – may be the result of the same semantic features being part of multiple context representations. For example, encountering the item ‘dog’ is likely to activate semantic features such as ‘fur’, ‘pet’, and ‘tail’ (Collins & Loftus, 1975; Anderson, 1983). These semantic features constitute part of the context representation that is bound to the item ‘dog.’ Encountering the item ‘cat’ is likely to activate the same features, which, via item-context binding are bound to the item ‘cat’. To the extent that context guides retrieval, similar context representations will lead ‘dog’ and ‘cat’ to be clustered during recall.

There is evidence that the brain supports item-context binding. First, it is well established that the hippocampus supports associative memory (Ranganath et al., 2004; Farovik, Dupont, & Eichenbaum, 2010; Eichenbaum, 2017), as the ability to form and retrieve associations is impaired following hippocampal lesions (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua,

2002). Second, hippocampal activity patterns differentiate items based on spatiotemporal context (Wang & Diana, 2017; Long & Kahana, 2019; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019). Finally, increased activity in both the hippocampus and lateral prefrontal cortex predicts subsequent organization (Blumenfeld & Ranganath, 2006; Long, Öztekin, & Badre, 2010; Long & Kahana, 2015). The neural evidence also extends beyond the hippocampus. By comparing electroencephalographic (EEG) activity recorded during the study of subsequently semantically clustered words, previous work has identified a neural signature of semantic clustering characterized by power increases across anterior brain regions (Long & Kahana, 2017).

Although the process of item-context binding may support subsequent semantic clustering, prior work has failed to consider that multiple items contribute to the phenomenon of semantic clustering. Whereas the likelihood of recall can be assessed for individual study items, at least two associated study items must be recalled, and must be recalled consecutively, to constitute 'semantic clustering.' By collapsing over all subsequently semantically clustered study items, prior work has made the assumption that these items are processed in the same way; however, this may not be the case.

There is reason to suspect that items may be processed differentially depending on the presentation of prior associates during study. First, it is known that associated items can prime one another (Foss, 1982; Balota & Lorch, 1986; McNamara & Altarriba, 1988). Specifically, the way that a word is processed can change based on its association with previously encountered words. For example, words in a sentence are processed more quickly if they are preceded by a semantically associated word (Blank & Foss, 1978). Second, repetition of the same stimulus can act as a "reminder," triggering retrieval without conscious effort (Hintzman, 2011). For example, hearing a familiar song on the radio might remind a person of where they were when they first heard it. There is behavioral evidence that this 'reminding' effect may extend to semantically associated stimuli (Greene, 1989). For example, if one encounters 'dog', and then later encounters 'cat', they may be reminded of 'dog' while viewing 'cat' because of the shared meaning between the two items. More generally, retrieval of prior knowledge impacts memory encoding. Presentation of information that is congruent with prior knowledge is linked to stronger retrieval-related

activity and better memory compared to information that is incongruent with prior knowledge (van Kesteren, Rijpkema, Ruiterm, & Fernandez, 2010), suggesting that semantically-mediated retrieval during study may support subsequent semantic clustering.

Together, these findings led us to form the hypothesis that semantic organization is supported by differential processing of associated study items. The alternative hypothesis is that semantic organization is supported by a single item-context binding mechanism applied to all subsequently semantically clustered items. To test our hypothesis, we conducted a human scalp EEG study in which subjects performed a free recall task. We manipulated the strength of semantic associations between “pairs” of individually presented study words, such that half of the “pairs” were strongly semantically associated (e.g. ‘dog’ and ‘cat’) and half were weakly semantically associated (e.g. ‘road’ and ‘shore’). We separately measured behavioral performance and neural signals for the first (dog, road) and second (cat, shore) associates in each pair. To the extent that later study items (e.g. cat) are influenced by the prior presentation of associated study items (e.g. dog), we would expect to find differential memory behavior and neural activity patterns for those items.

## **Materials and Methods**

### **Subjects**

Forty (22 female; mean age 20.625 years) native English speakers from the University of Virginia community participated. All subjects had normal or corrected-to-normal vision. Informed consent was obtained in accordance with the University of Virginia Institutional Review Board for Social and Behavioral Research and subjects were compensated for their participation. Two subjects were excluded from the final dataset: one whose EEG recording was not started until the third run, and one whose free recalls were not recorded. Thus, free recall data are reported for the remaining 38 subjects.

## Experimental Design and Statistical Analysis

### Free Recall Task

Stimuli consisted of 1602 words, drawn from the Toronto Noun Pool (Friendly, Franklin, Hoffman, & Rubin, 1982). From this set, 192 words were randomly selected for each subject.

*Study phase.* During each trial, subjects viewed a single word presented for 2000 ms followed by a 1000 ms inter-stimulus interval (ISI; Figure 1). Subjects were instructed to study the presented word in anticipation of a later memory test but did not make any behavioral responses. Each list was comprised of 16 words. Each list was split evenly into two parts (“first associates” and “second associates,” respectively) containing 8 words and separated by a brief 2000 ms delay. The critical manipulation was the strength of semantic association between first and second associates. Each first associate was “paired” with a second associate, separated by seven intervening items (a lag of eight). Semantic association strength was determined using Word Association Space values (WAS; Nelson, Zhang, & McKinney, 2001) where pairs having a WAS value of 0.4 or greater (Long & Kahana, 2017) were coded as ‘strong’ semantic associates and pairs having a WAS value less than 0.4 were coded as ‘weak’ semantic associates. As an example, in Figure 1, the pair dog-cat are strong semantic associates (WAS = 0.86), where dog is the first associate and cat is the second associate. In comparison, shore-road are weak semantic associates (WAS = 0.017), where shore is the first associate and road is the second associate. Both strong and weak semantic associates were weakly semantically associated to all other study words.

*Math distractor phase.* On each trial, subjects saw a three digit math problem with a solution (of the form, “ $X + Y - Z = A$ ”). Subjects had 4 seconds to verify whether the solution shown was correct. Each math problem was followed by a minimum 1000 ms ISI. If a response was made under 4 seconds the ISI was 1000 ms plus the remaining time. Subjects saw a total of four math problems, randomly generated, such that the distractor interval was always 20 seconds in duration.

*Free recall phase.* Following the math distractor, an auditory beep cued the subject to recall, or say out loud, any words that they could remember from the immediately preceding study phase. Subjects were given 45 seconds to recall as many words as possible in any order. Subjects were encouraged to continue trying to recall throughout the interval.

Subjects completed 12 runs for a total of 192 study trials. Words did not repeat within or across runs.

## **EEG data acquisition and preprocessing**

EEG recordings were collected using a BrainAmp system (Brain Products, Inc.) and an ActiCap equipped with 64 Ag-AgCl active electrodes positioned according to the extended 10-20 system. All electrodes were digitized at a sampling rate of 1000 Hz and were referenced to electrode FCz. Offline, electrodes were later converted to an average reference. Impedances of all electrodes were kept below  $50\text{k}\Omega$ . Electrodes that demonstrated high impedance or poor contact with the scalp were excluded from the average reference. Bad electrodes were determined by voltage thresholding (see below).

Custom Python codes were used to process the EEG data. We applied a high pass filter at 0.1 Hz, followed by a notch filter at 60 Hz and harmonics of 60 Hz to each subject's raw EEG data. We then performed three preprocessing steps (Nolan, Whelan, & Reilly, 2010) to identify and correct electrodes with severe artifacts separately for each subject. First, we calculated the mean correlation between each electrode and all other electrodes as electrodes should be moderately correlated with other electrodes due to volume conduction. We z-scored these means across electrodes and rejected electrodes with z-scores less than -3. Second, we calculated the variance for each electrode as electrodes with very high or low variance across a session are likely dominated by noise or have poor contact with the scalp. We then z-scored variance across electrodes and rejected electrodes with a  $|z| \geq 3$ . Finally, we expect many electrical signals to be autocorrelated, but signals generated by the brain versus noise likely have different forms of autocorrelation. Therefore, we calculated the Hurst exponent, a measure of long-range

autocorrelation, for each electrode and rejected electrodes with a  $|z| \geq 3$ . Rejected electrodes were excluded from the average re-reference. We found the average voltage across all of the remaining electrodes for each time sample and re-referenced the data by subtracting the average voltage from the filtered EEG data. We used wavelet-enhanced independent component analysis (Castellanos & Makarov, 2006) to remove artifacts from eyeblinks and saccades.

## **EEG data analysis**

In order to perform spectral decomposition, we applied a family of Morlet wavelet transforms (wave number = 6) to all electrode EEG signals across 46 logarithmically-spaced frequencies (2-100 Hz; Long and Kahana, 2015). After log-transforming the power, we downsampled the data by taking a moving average across 100 ms time intervals from -4000 to 4000 ms relative to stimulus onset and sliding the window every 25 ms, resulting in 317 time intervals (80 non-overlapping). Power values were then z-transformed by subtracting the mean and dividing by the standard deviation power. Mean and standard deviation power were calculated across all trials and across time points for each frequency.

## **Regions of Interest**

We selected two regions of interest (ROIs), left frontal and left parietal/occipital, based on a previous scalp EEG study (Long & Kahana, 2017). We focused on the left hemisphere as there is evidence that subsequent memory effects are typically left lateralized (Kim, 2011; Burke et al., 2014). The left frontal ROI includes electrodes Fp1, F3, F7, AF7, AF3, F1 and F5. The left parietal/occipital ROI includes electrodes P3, P7, O1, P1, P5, PO7 and PO3.

## **Behavioral data analysis**

Study items were assessed based on three factors: associate (first or second), semantic association strength (strong or weak), and subsequent clustering status. Strong semantic associates could be subsequently recalled and semantically clustered (SClust), whereby the study item was recalled preceding or following its semantic associate. By definition weak semantic associates



could not be semantically clustered. Any study item (strong or weak) could be subsequently recalled and temporally clustered (TClust), whereby the study item was recalled preceding or following its study neighbor. Any study item could be subsequently recalled and not clustered (NClust), whereby the study item was recalled, but not consecutively with either a study neighbor or a semantic associate.

## **Statistical analyses**

We used repeated measures ANOVAs and paired-sample *t*-tests to assess the effects of semantic association strength and associate on probability of recall. We used paired-sample *t*-tests to assess the proportion of first and second associates recalled in the different clustering conditions.

We used repeated measures ANOVAs to assess the effects of clustering condition and frequency on zPower. We used repeated measures ANOVAs to assess the effects of associate and frequency on the difference in zPower between subsequently semantically clustered items and subsequently recalled but not clustered items.

## **Results**

### **Behavioral Results**

According to our hypothesis, semantic organization is supported by differential processing of associated study items. Thus, our first goal was to test whether first and second associates are differentially remembered by virtue of their semantic association strength. We ran a two-way, repeated measures ANOVA to evaluate the effects of semantic association strength (strong, weak) and associate (first, second) on probability of recall (Figure 2A). We found a main effect of semantic association strength ( $F_{1,37} = 29.16, p < 0.0001$ ) driven by greater probability of recall for strong than weak semantic associates. We found a main effect of associate ( $F_{1,37} = 8.461, p = 0.0061$ ) driven by greater probability of recall for the first associate compared to the second

associate. We found a significant interaction of semantic association strength and associate ( $F_{1,37} = 8.483, p = 0.0061$ ). For first associates, probability of recall was greater for strong ( $M = 0.4972, SD = 0.1665$ ) than weak ( $M = 0.4561, SD = 0.1674$ ) associates ( $t_{37} = 2.7677, p = 0.0088$ ). For second associates, probability of recall was greater for strong ( $M = 0.4764, SD = 0.1742$ ) than weak ( $M = 0.3794, SD = 0.1332$ ) associates ( $t_{37} = 5.6889, p < 0.0001$ ). Thus, the difference in probability of recall between strong and weak items is greater for second compared to first associates.

Because the experimental design allowed for the possibility that participants could rely on either episodic and semantic associations to guide their recall, we next sought to determine participants' relative tendencies to engage in temporal versus semantic clustering of strong semantic associates. In other words, were participants organizing items either by their position in the study list (temporal clustering) or by meaning (semantic clustering)? To investigate the degree to which participants clustered their recalls of strong semantic associates, we assessed the proportion of first and second strong semantic items recalled and either semantically clustered (SClust), temporally clustered (TClust), or neither semantically nor temporally clustered (NClust; Figure 2B).

We ran a  $2 \times 3$  repeated measures ANOVA with factors of associate (first, second) and clustering condition (SClust, TClust, NClust). The dependent variable was the proportion of items recalled. There was a main effect of associate ( $F_{1,37} = 4.245, p = 0.0464$ ) and a main effect of clustering condition ( $F_{2,74} = 5.515, p = 0.0059$ ). There was a significant interaction between associate and clustering condition ( $F_{2,74} = 4.837, p = 0.0106$ ). The proportion of semantically clustered items was greater for second ( $M = 0.2924, SD = 0.1470$ ) compared to first associates ( $M = 0.2558, SD = 0.1383, t_{37} = 2.0573, p = 0.0468$ ). The proportion of temporally clustered items was greater for first ( $M = 0.3368, SD = 0.1513$ ) compared to second associates ( $M = 0.2640, SD = 0.1454, t_{37} = 2.3893, p = 0.0221$ ). The proportion of not clustered items did not significantly differ between first ( $M = 0.3540, SD = 0.1270$ ) and second associates ( $M = 0.4113, SD = 0.1531, t_{37} = 2.0106, p = 0.0517$ ). Taken together with the dissociations in probability of recall, these clustering proportions suggest that first and second associates are processed differently.

## Subsequent semantic clustering effects

In order to identify the study-phase neural mechanisms that underlie semantic clustering, we first sought to replicate previous findings, in which subsequent semantic clustering elicited power increases across anterior regions of the brain (Long & Kahana, 2017). We analyzed the subsequent semantic clustering effect (SCEs) by comparing spectral power during study of subsequently semantically clustered items and subsequently recalled but not clustered items, excluding any items that were temporally clustered or weakly semantically associated (Long & Kahana, 2017). We calculated spectral power across six frequency bands: low theta (3-4 Hz), high theta (6-8 Hz), alpha (10-14 Hz), beta (16-26 Hz), low gamma (26-44 Hz), and high gamma (44-100 Hz) and two regions of interest (ROIs): left frontal (LF), and left parietal/occipital electrodes (LP, Figure 3 A-Bs, top panel). For each ROI, we ran a  $2 \times 6$  repeated measures ANOVA to evaluate the effects of clustering condition (SClust, NClust) and frequency on zPower. In LF, there was a main effect of clustering condition ( $F_{1,37} = 4.944$ ,  $p = 0.0324$ ) whereby there was greater zPower for SClust than NClust items. There was no main effect of frequency ( $F_{5,185} = 1.477$ ,  $p = 0.199$ ). The interaction between clustering condition and frequency was not significant ( $F_{5,185} = 0.896$ ,  $p = 0.485$ ). In LP, there was a trending main effect of clustering condition ( $F_{1,37} = 2.873$ ,  $p = 0.0985$ ) whereby there was greater zPower for SClust than NClust items. There was a main effect of frequency ( $F_{5,185} = 14.02$ ,  $p < 0.0001$ ). The interaction between clustering condition and frequency was not significant ( $F_{5,185} = 1.14$ ,  $p = 0.341$ ). This replicates previous results (Long & Kahana, 2017) and suggests that subsequent semantic clustering is supported by increased spectral power over frontal and parietal/occipital regions.

Given our hypothesis that semantic organization is supported by differential processing of associated study items, and our behavioral findings above, we predicted that there would be differences in the SCEs for first and second associates. We calculated the SCEs separately for first and second associates (Figure 3 A-Bs, bottom panel). We ran a  $2 \times 6$  repeated measures ANOVA to evaluate the effects of associate (first, second) and frequency on the difference in zPower between subsequently semantically clustered items and subsequently recalled but not clustered items. In LF, there was no main effect of frequency ( $F_{5,185} = 0.951$ ,  $p = 0.449$ ) or asso-

ciate ( $F_{1,37} = 0$ ,  $p = 0.995$ ). We found a significant interaction between associate and frequency ( $F_{5,185} = 3.154$ ,  $p = 0.0093$ ). In LP, there was no main effect of frequency ( $F_{5,185} = 0.79$ ,  $p = 0.558$ ) or associate ( $F_{1,37} = 2.55$ ,  $p = 0.119$ ). We found a significant interaction of associate and frequency ( $F_{5,185} = 2.327$ ,  $p = 0.0444$ ). In both ROIs, the SCEs for second associates is characterized by increased high frequency activity and decreased low frequency activity relative to first associates, providing a neural basis for the dissociation between first and second associates at study.

## Discussion

The goal of the current study was to identify the study-phase mechanisms that lead to memory organization in free recall. We recorded scalp EEG while participants performed a free recall task in which each study list was comprised of strongly and weakly semantically associated items. This study shows four key findings. First, we found that semantic association with a prior list item improved memory for items presented later in the study list. Second, we found that later study list items are more likely to be semantically clustered than early study list items. Third, we replicated previous findings by demonstrating that semantic clustering is characterized by increased power over left frontal and parietal/occipital regions (Long & Kahana, 2017). Finally, we showed that the neural subsequent semantic clustering effect (SCEs) differs across pairs of semantically clustered items, with increased high frequency activity and decreased low frequency activity for later list items. Taken together, these results suggest that semantic organization arises from differential processing of associated study items, and more generally, that study-phase mechanisms are influenced by prior study items.

We found that later study list items are more likely to be recalled if they are semantically associated to prior study list items. In delayed free recall tasks in which no words are semantically associated, recall performance decreases over serial position, which may be due to interference (Oberauer, 2003). In our delayed free recall task, probability of recall for weak items decreased across the study list, consistent with prior findings. However, probability of recall for strong items was comparable across early and late list items. One interpretation is that a semantically associ-

ated prior study list item protects later items from the natural build up of interference that occurs as the study list progresses. Alternatively, the neural fatigue hypothesis (Tulving & Rosenbaum, 2006; Lohnas, Davachi, & Kahana, 2020) posits that effective encoding mechanisms cannot be engaged at a high level across all study items. Potentially, association to a prior list item may combat the neural fatigue that occurs as the study list progresses, boosting memory formation for the strong associates.

We find that the tendency to semantically vs. temporally cluster study items differs depending on when in the study list an item is presented. Early list items are more likely to be temporally clustered and less likely to be semantically clustered than later list items. Previous work has shown that participants naturally tend to engage in temporal clustering (Healey, Crutchley, & Kahana, 2014), but when there is a semantically oriented task, participants will engage in semantic clustering (Becker, Moscovitch, Behrmann, & Joordens, 1997; Long & Kahana, 2017). Although in our paradigm there is no explicit semantic orienting task, participants are aware of the semantic associations between study items (as indicated by post-task questionnaires) and therefore may use this to guide how they process the study items. However, participants cannot know which of the early study items will be “paired” with a semantic associate later in the list. Therefore, during the early list items, participants may default to processing that supports subsequent temporal clustering as they have not yet been oriented toward semantics. Upon encountering the associated later list item, subjects may engage in semantic-directed processing, leading to subsequent semantic clustering.

We replicated the finding that subsequent semantic clustering is characterized by spectral power increases over left frontal and parietal/occipital regions (Long & Kahana, 2017). Despite the absence of an explicit semantic orienting task – as in prior work – we still find evidence that study-phase processing supports subsequent semantic clustering. Given that participants were aware of the semantic associations across study items, our interpretation is that engagement in semantic processing occurs in response to top-down demands guiding attention toward the semantic features of items. The extent to which study-phase mechanisms support semantic clustering when awareness of these associations is minimized or eliminated is an important question

for future research.

Our central finding is the dissociation in neural SCEs across study list items. Whereas in the aggregate we find that elevated spectral power across all frequencies predicts subsequent semantic clustering, this broad spectral increase appears to separately be driven by low frequency activity (LFA) increases for early list items and high frequency activity (HFA) increases for later list items. The subsequent memory effect (SME; Paller, Kutas, & Mayes, 1987) – differences in study-phase activity between items that are later recalled compared to those that are not recalled – is typically characterized by increased HFA and decreased LFA ( $HFA_i/LFA_d$ ; Gruber, Tsivilis, Montaldi, & Muller, 2004; Osipova et al., 2006; Sederberg et al., 2007; Burke et al., 2013; Long, Burke, & Kahana, 2014). In our study, later list items that are subsequent semantically clustered perfectly mirror this  $HFA_i/LFA_d$  pattern. However, the  $HFA_i/LFA_d$  pattern has routinely been observed outside the domain of memory (Crone, Boatman, Gordon, & Hao, 2001; Bauer, Oostenveld, Peeters, & Fries, 2006; Lachaux et al., 2007; Dalal et al., 2009), suggesting that these signals do not reflect memory processing *per se*, but may instead reflect the extent to which participants are “on-task” or responding to task demands (Long & Kuhl, 2019). Although in our paradigm the experimentally imposed task demands were the same for all items – participants were instructed to study all items for a subsequent recall test – semantically associated prior list items may have effectively altered the putative ‘task’ performed on the later list items. We plan to investigate dissociations in the SCEs across time, as well as the neural signals underlying subsequent temporal clustering, to further elucidate the dissociations between early and late list items.

By demonstrating that the study-phase signals that predict subsequent semantic clustering differ across study list items, we provide evidence in support of our hypothesis that semantic organization is supported by differential processing of associated study items. Two potential mechanisms may account for this differential processing. First, it could be that when studying a later list item (e.g. ‘cat’), the participant is reminded of the semantically associated prior list item (e.g. ‘dog’). This ‘reminding’ triggers explicit retrieval of dog during the presentation of cat, allowing the participant to form an associative memory of both items, leading to subsequent semantic clustering.

There is evidence in support of this reminding mechanism in the literature as repeated occurrence of the same stimulus can act as a “reminder” (Hintzman, 2011) and reminding extends to semantically associated stimuli (Greene, 1989). Alternatively, the semantically associated prior list item could prime the participant for the later list item. In other words, by virtue of the previously presented semantic associate, participants may increase their attention toward a later list items’ semantic features, rather than explicitly retrieving the prior list item. Further investigations are needed to directly measure retrieval and adjudicate between these two mechanisms.

In summary, we show that semantic organization of memory arises from differential processing of associated study items. These findings provide insights into the study-phase mechanisms of semantic organization. More broadly, we contribute to a growing body of literature showing that study-phase mechanisms are not static, but instead that the processing of study items is influenced by prior experiences.

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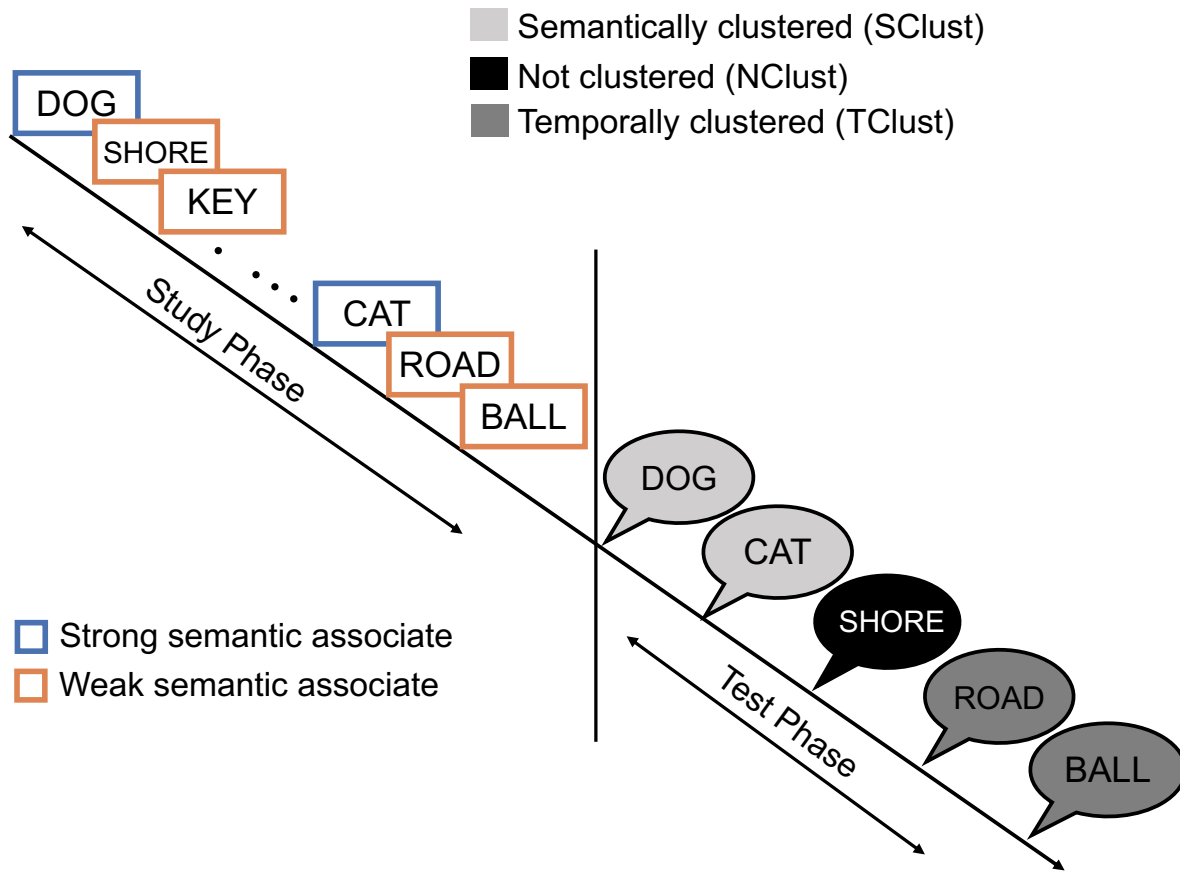


Figure 1. **Free recall task experimental design.** During the study phase, subjects studied a series of words one at a time (e.g. “dog,” “shore,” etc) in anticipation of a later memory test. Each word list was split into “first associates” (e.g. “dog,” “shore,” “key”) and “second associates” (e.g. “cat,” “road,” “ball”) which were paired with one another. Half of the associate pairs were strongly semantically associated (e.g. “key” and “door”) and the other half were weakly semantically associated (e.g. “shore” and “road”). Strong semantic associates are shown here in blue and weak semantic associates are shown in orange for demonstration purposes only; participants were not given any indication of semantic association strength. During the test phase, subjects verbally recalled any words that they could remember from the immediately preceding study phase, in any order. We defined our conditions of interest as items subsequently recalled and semantically clustered (SClust), items subsequently recalled and not clustered (NClust), and items subsequently recalled and temporally clustered (TClust).

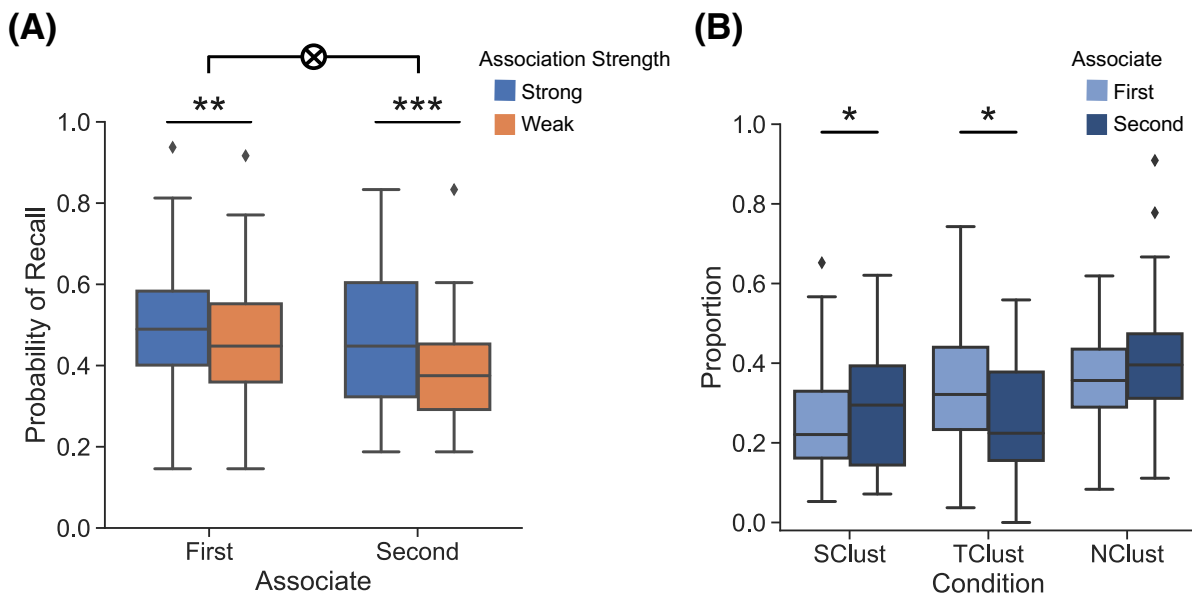


Figure 2. **Recall performance and memory organization.** **(A)** Probability of recall is greater for strong (blue) compared to weak (orange) semantic associates and is greater for first compared to second associates. There is a significant interaction between associate and semantic association strength ( $p = 0.0045$ ). **(B)** There is a greater proportion of semantically clustered second associates than first associates ( $p = 0.0468$ ). There is a greater proportion of temporally clustered first associates than second associates ( $p = 0.0221$ ). \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ .

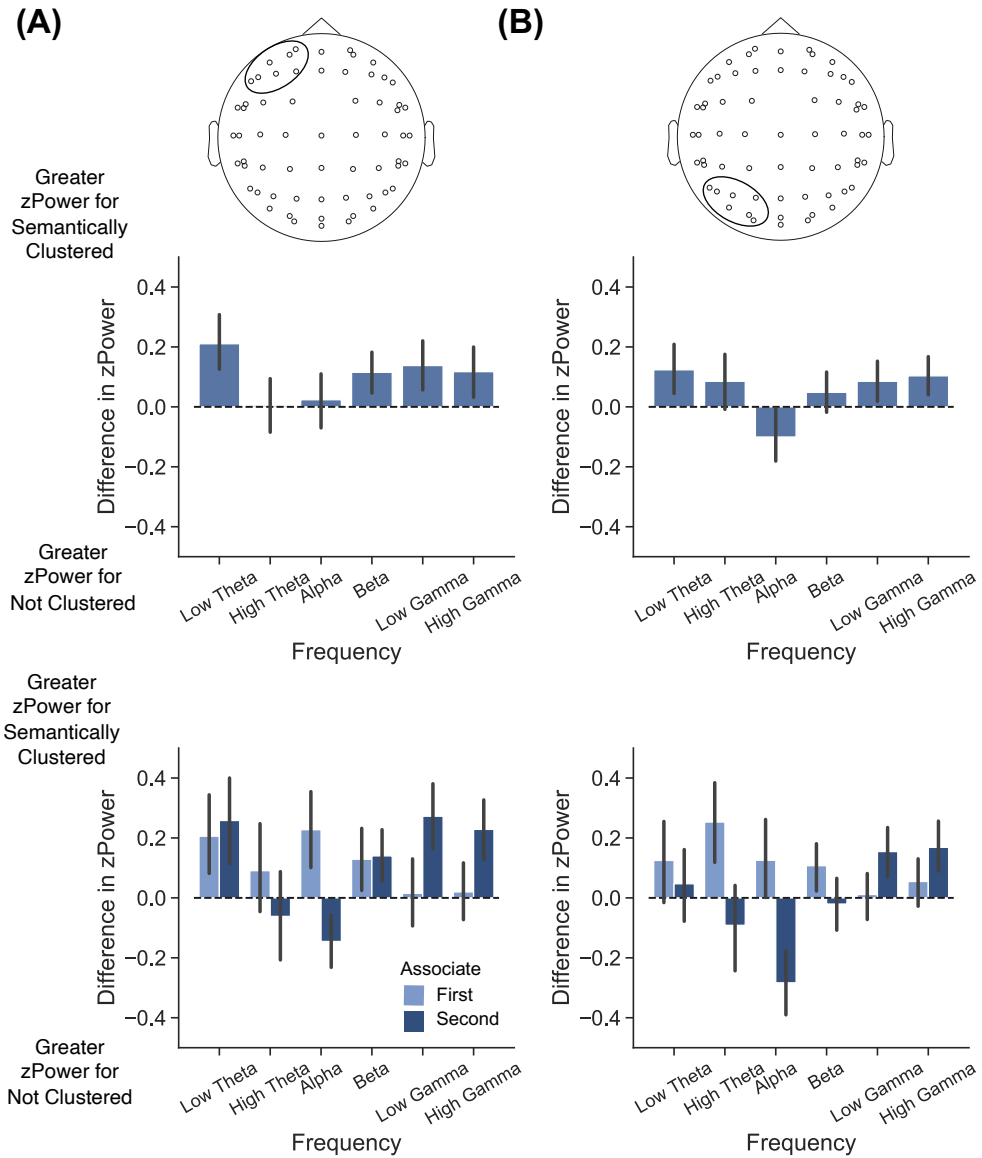


Figure 3. **Subsequent semantic clustering effects.** The top panel shows the difference in zPower between subsequently semantically clustered and subsequently recalled, but not clustered, items. The bottom panel shows the difference in zPower between subsequently clustered and subsequently recalled, but not clustered, items, for first (light blue) and second associates (dark blue). zPower is shown for six frequency bands (low theta: 3-4 Hz, high theta: 6-8 Hz, alpha: 10-14 Hz, beta: 16-26 Hz, low gamma: 28-42 Hz, high gamma: 44-100 Hz). zPower is averaged across the entire stimulus interval (2000 ms). Error bars denote standard error of the mean. **(A)** Left frontal electrodes. **(B)** Left parietal/occipital electrodes.