Oscillatory correlates of free-recall dynamics due to perceptual shifts

By

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CHAPTER I

INTRODUCTION

The human experience is comprised of an ongoing stream of experiences that make up our everyday lives. Contextual theories of memory propose that information pertaining to this ongoing stream is integrated into a slowly-updating contextual representation that allows us to create a mental timeline of these experiences. While this contextual representation is ever-changing, there are moments of discontinuity or greater contextual change, allowing the cognitive system to organize and distinguish these experiences into meaningful events or episodes. These contextual changes have observable behavioral and neural consequences.

The free-recall paradigm has been used by memory researchers in order to simulate events as discrete lists of words with a defined beginning and end. In many cases, participants are asked to target the most recent list out of many. By contextual theories, this slowly-changing contextual representation provides temporal structure that allows the participant to focus retrieval mostly on the most recent list.

Sederberg et al. (2006) examined the relationship between oscillations in scalp EEG and individual list learning. They found that individual list items at the start of the list evoked a more pronounced decrease in oscillatory power in the alpha band (10–14 Hz) than mid-list items. Likewise, they observed a boost in stimulus-induced gamma power for start-of-list items that ebbed as the list progressed. Power in these bands related to the effectiveness with which individual list items were encoded. These effects reset at the beginning of each list, suggesting some mechanism that resets attentional and encoding processes between each list.

These findings are consistent with work by Pastötter et al. (2011) that implicated the end-of-list recall task in a reset of encoding processes. Specifically, a lack of intervening recall period between successive lists resulted in (1) impaired memorability for later lists, and (2) increased proactive interference from prior studied lists. These behavioral phenomena were accompanied by a buildup in evoked alpha power across successive lists, similar to that observed by Sederberg et al. (2006) within lists. Intervening recall tasks between lists then led to a reduction of proactive interference and improved memorability for material studied after the recall task, as well as prevented a buildup of stimulus-evoked alpha power. Similar behavioral phenomena were observed by Sahakyan and Kelley (2002) by simply using a mental imagery task between lists, indicating that a shift in mental context was sufficient to create mental distance between lists, allowing for reduced proactive interference of material studied prior to the shift and enhanced memorability for information following it. These shifts in mental context were also associated with a reduction in stimulus-evoked alpha power (Pastötter et al., 2008), suggesting that these between-list behavioral phenomena may be driven by a change in internal context that resets encoding processes.

Consistent with this theory, Murdock and Walker (1969) found that a mid-list shift in perceptual stimulus properties—specifically presentation modality (auditory or visual)—was accompanied by a boost in memorability for items immediately following the shifts. Such increased memory performance has been observed following shifts in a color associated with list items (Geiselman, 1975), encoding task (Polyn et al., 2009b), as well as taxonomic category of stimuli and perceptual background during presentation (Davelaar, 2013). These behavioral effects have been proposed to relate to start-of-list primacy processes through shifts in mental context (Brown et al., 2007; Davelaar, 2013), but little neural work has been conducted to compare the underlying processes.

Our goal in this study was to characterize the oscillatory response of items following a shift in perceptual features, and to compare these patterns of oscillations to those observed in start-of-list items by Sederberg et al. (2006). To accomplish this, we recorded scalp EEG while participants studied lists of items to be later recalled in a free-recall task while shifting the perceptual features of those items during encoding.

CHAPTER II

METHODS

Participants

Twenty-two (12 female) volunteers were recruited via fliers posted around the Vanderbilt University campus. All participants were native English speakers between 18 and 35 years of age. Consent was obtained in accordance with procedures approved by the Vanderbilt University Institutional Review Board. Participants were paid $15/hour for their participation, with up to an additional $10 earned per session dependent upon performance in the task. Data from two participants were removed from the analysis for the following reasons, respectively: one for purposely ignoring visual stimuli, and one for not completing their second session.

Stimulus characteristics

The stimuli were drawn from a pool of 421 items. This pool is a subset of words from the Auditory Toronto Word Pool, restricted to include only words whose semantic meanings were characterized by the Word Association Spaces (WAS) project (Steyvers et al. 2004, this resulted in the removal of 55 words from the original pool). Further inspection of the pool revealed eight pairs of words with nearly identical pronunciation; one of each pair was removed from the pool. The WAS project provided a value for each pair of words in the pool, characterizing the semantic similarity of those words to one another. These values were used to ensure that highly semantically similar items were not presented in the same list: If a pair of items in a potential study list had a WAS-derived similarity score greater than 0.625 (using a cosine-based similarity metric), the list was discarded and re-created.

List construction

Participants were run in a variant of the free-recall paradigm. Stimuli were either presented in the auditory (over headphones) or in the visual (text on-screen) modality using PyEPL (Geller et al., 2007).

Each participant performed in two experimental sessions. In each session they performed 16 trials. Each trial consisted of a study period, in which a list of 24 words was presented serially, followed by a recall period, in which the participant vocally reported items from the study list. These vocal responses were recorded using a Audio-Technica AT2020 USB microphone, and were scored offline using *Penn TotalRecall*.[1]

Each study list was composed of 12 words from the auditory and 12 words from the visual modality, organized into four sets of six like-modality items each (e.g., six auditory items followed by six visual items, and so forth). We refer to each set of 6 items as a train; each list consisted of 4 trains. This list structure mimics a condition of a study performed by Murdock and Walker (1969).

The recall period was composed of two recall-by-category periods (here, we use category in a general sense, to refer to the two modalities, and not, e.g., to taxonomic categories). In a given recall period, a participant was asked to recall the studied words that were presented in a particular modality, in whatever order the words came to mind. After the end of that sub-period, recall of items from the other presentation modality were then prompted, such that all items from the list were given the opportunity to be recalled. If, for example, on a given trial the first recall-by-category period asked the participant to remember the auditory items, then the second period would probe the visual items. The order in which the modalities was probed was counterbalanced across lists.

There were two additional practice trials in the first session to familiarize participants with the recall-by-category structure. Data from these trials were not included in the analyses reported here. The list conditions were pseudo-randomly ordered across the full experiment. Particular words were not repeated within a session, but could appear in another study list in the other session.

Experimental procedure

The participant pressed a key to initiate the study list. Each visual stimulus was presented on-screen for 600 msec. This value was chosen to match the average duration of the auditory items (596 msec, SD=91 msec). For visual stimuli, the study interval for an individual item lasted 1750

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[1] This software package is available at http://memory.psych.upenn.edu/TotalRecall

msec, plus a short, variable interval described below. This 1750 msec period included the 600 msec word presentation, followed by a blank screen (save for a fixation cross) which lasted for 1150 msec. For auditory stimuli, the study interval for an individual item also lasted 1750 msec. The auditory file was played at the beginning of this period; participants were instructed to look at the fixation cross (+) which appeared in the middle of the screen. The duration of the variable post-stimulus interval ranged from 0 to 500 msec (uniformly distributed), regardless of modality.

After the final study item on a given list, the screen went blank for 1200 msec, then a written prompt (lasting 300 msec) indicated which modality should be recalled ("***WRITTEN'***" or "***SPOKEN***"). A 500 msec tone signaled the start and end of each recall period. The second recall-by-category period was preceded by a blank screen for 1400±200 msec. At the end of each session, there was a final free recall (FFR) period lasting 360 sec. During this period the participant was asked to freely recall all of the words from that session in any order, regardless of presentation modality.

Electrophysiological recordings and data processing

EEG activity was recorded using commercially available equipment (Net Amps 300 Amplifier, Net Station 4.3.1 acquisition environment, from Electrical Geodesics, Inc.). EEG was acquired using 129-channel HydroCel Geodesic Sensor Nets. A 0.1 Hz highpass filter was applied to the recorded voltage, which was then digitized at 500 Hz. Recordings were initially referenced to Cz, and were later converted to an average reference. Line noise was removed using a digital notch filter around 60 Hz.

A modified version of the eye motion correction procedure described by Gratton et al. (1983) was used to remove eye-related (movements and blinks) activity. In order to distinguish between blinks and eye movements, we characterized blinks by applying a threshold to the difference between a fast and slow running average of the difference between the electrodes above and below the eyes. In the beginning of each session of the experiment, participants were instructed to make 10 voluntary blinks and 60 eye movements (10 each of up, down, left, right, open, and close saccades) while recording EEG in the horizontal (HEOG) and vertical (VEOG) electrode pairs. A blink detector was applied to each participant's eye movements and voluntary blinks, where a threshold was adjusted to correctly identify at least 80% of the blinks while minimizing the number of eye movements incorrectly identified. This optimized blink detector was then applied to that participant's experimental data to identify time periods that contained blinks. In order to identify the slow changes missed by the blink detector, we added a buffer of 150 ms before and 500 ms after each time sample that contained a blink. Multiple linear regression was used to predict the signal at each electrode using (1) HEOG not containing blinks, (2) HEOG containing blinks, (3) VEOG not containing blinks, (4) VEOG containing blinks, and an intercept as predictors. The residuals from this regression were then used as corrected EEG.

Oscillatory analysis

Changes in oscillatory power over time were examined by using a Morlet wavelet transform with a wave-number of 6. Oscillatory power was then calculated at 34 logarithmically spaced frequencies from 2 to 100 Hz. These power values were then log-transformed and down-sampled to 25 Hz. Power was z-transformed relative to the mean and standard deviation of a baseline period, separately for each frequency, electrode, and session. The resulting power patterns were split into six distinct frequency bands – 2 to 4 Hz (delta), 4 to 8 Hz (theta), 10 to 14 Hz (alpha), 16 to 26 (beta), 28 to 42 Hz (low gamma), and 44 to 100 Hz (high gamma) – by taking the mean of the z-transformed power in each frequency band.

Sets of study events were compared using a Wilcoxon rank sum test based on the mean of the z-transformed wavelet power during the encoding period (the 1400 msec interval beginning with presentation onset). This comparison was made separately for each electrode and frequency band. Correction for multiple comparisons was performed using a permutation procedure to generate an unbiased empirical estimate of Type I error rate (Sederberg et al., 2003, 2006). The rank sum test was performed on 1000 random shuffles of the experimental data for all electrodes and frequency bins, creating a distribution of p-values. Both the observed p-value and the distribution of shuffled

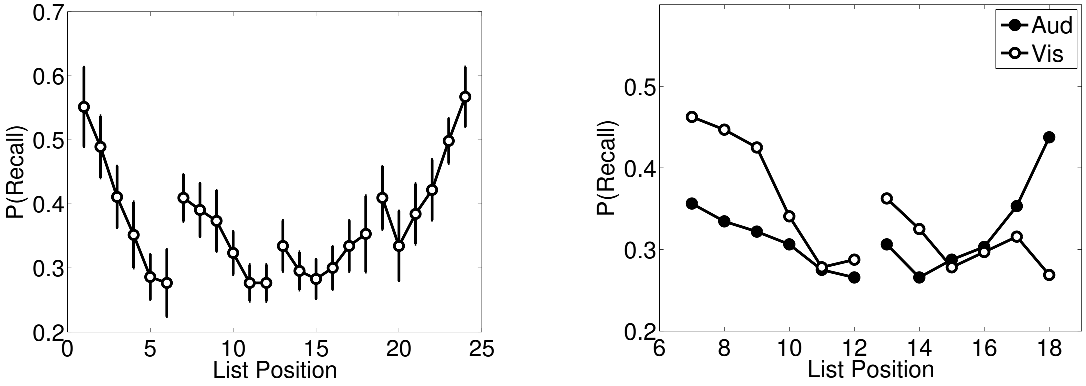
p-values were z-scored in order to sum across subjects. By then combining the resulting empirical distributions into a single distribution, we obtained a distribution of z-values that would give rise to a significant electrode by chance from each tail of the distribution. Significance thresholds were set to maintain a familywise Type I error rate of 0.05. We then applied these thresholds to the observed summed z-values to determine if an individual electrode was significant.

CHAPTER III

RESULTS

Behavioral performance

Participants recalled an average of 37.2% (SEM 3.1%) of the items on each study lists (visual items, 37.7%, SEM 3.4%; auditory items, 36.7%, SEM 2.9%). Fig. 1 shows the probability of recalling an item as a function of its position in the list, collapsed across presentation modality. Performance exhibited the standard primacy and recency effects in early and late list positions, respectively. The start-of-list primacy effect was confirmed using a matched t-test between recall for list position 1 and list positions 3–4 ($t(19) = 5.80, p < 0.001$). As encoding processes following shifts in modality were the primary focus of this study, subsequent analyses focus on the middle trains of list items (trains 2 and 3).



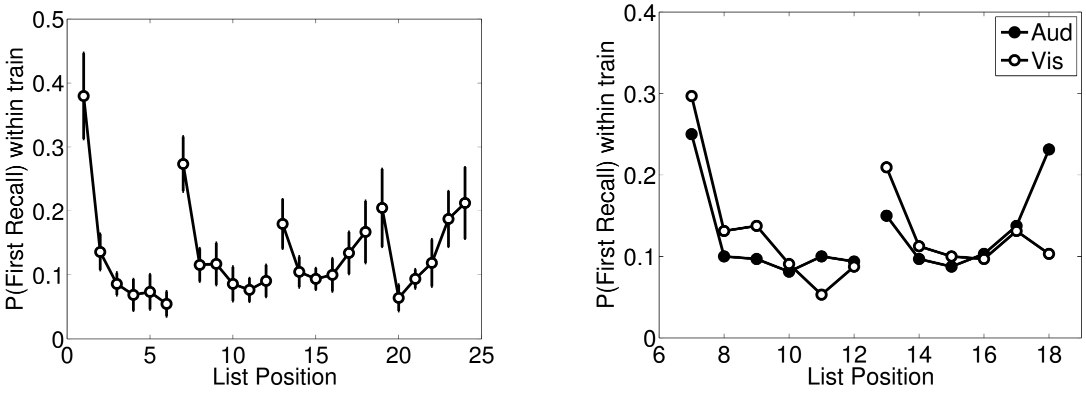
(a)

(b)

Figure 1. (a) Recall probability as a function of serial position, collapsed across presentation modality. Error bars represent Loftus and Masson (1994) corrected ±1 standard error of the mean. (b) Recall probability by list position for middle trains.

We performed a three-factor repeated measures analysis of variance on percent recall by list position for items presented in the mid-list trains, with train number, within-train position, and presentation modality as factors. This analysis revealed a main effect of train position ($F(5,95) = 3.35, p < 0.01$), with no significant main effect of train number ($F(1,19) = 2.02, p = 0.17$) or modality ($F(1,19) = 1.98, p = 0.18$). A follow-up contrast of train position 1 vs. train positions

3–4 showed increased recall performance at the start of the train (i.e., following a modality shift) as compared with mid-train items ($t(19) = 2.64, p < 0.01$). The analysis also revealed interactions between train number and train position ($F(5,95) = 13.95, p < 0.001$), train number and modality ($F(1,19) = 12.17, p < 0.005$), train position and modality ($F(5,95) = 8.12, p < 0.001$), as well as between all three factors ($F(5,95) = 2.43, p < 0.05$).



(a)

(b)

Figure 2. (a) Probability of first recall within a given train as a function of serial position, collapsed across presentation modality. Error bars represent Loftus and Masson (1994) corrected ±1 standard error of the mean. (b) Within-train probability of first recall by list position for middle trains.

Another behavioral marker of primacy effects is exhibited by which item within each specific train is most likely to be recalled first. We refer to this as the within-train probability of first recall, which is shown in Fig. 2. The start-of-list primacy was again examined using a matched t-test between performance for list position 1 and positions 3–4 ($t(19) = 8.38, p < 0.001$). A similar three-factor repeated measures analysis of variance on this measure—using train number, train position, and modality as factors—also revealed a main effect of train position ($F(5,95) = 14.23, p < 0.001$), but no significant main effect of train number ($F(1,19) = 1$) or modality ($F(1,19) < 1$). Again, a follow-up contrast of train positions 1 vs. train positions 3-4 showed increased probability of first recall for items presented at the start of the train (i.e., post-shift in modality) as compared with mid-train items ($t(19) = 5.72, p < 0.001$). Significant interactions were found between train number and train position ($F(5,95) = 10.02, p < 0.001$), train number and modality ($F(1,19) = 9.03, p < 0.01$), and train position and modality ($F(5,95) = 4.46, p < 0.005$).

Oscillatory list position effects

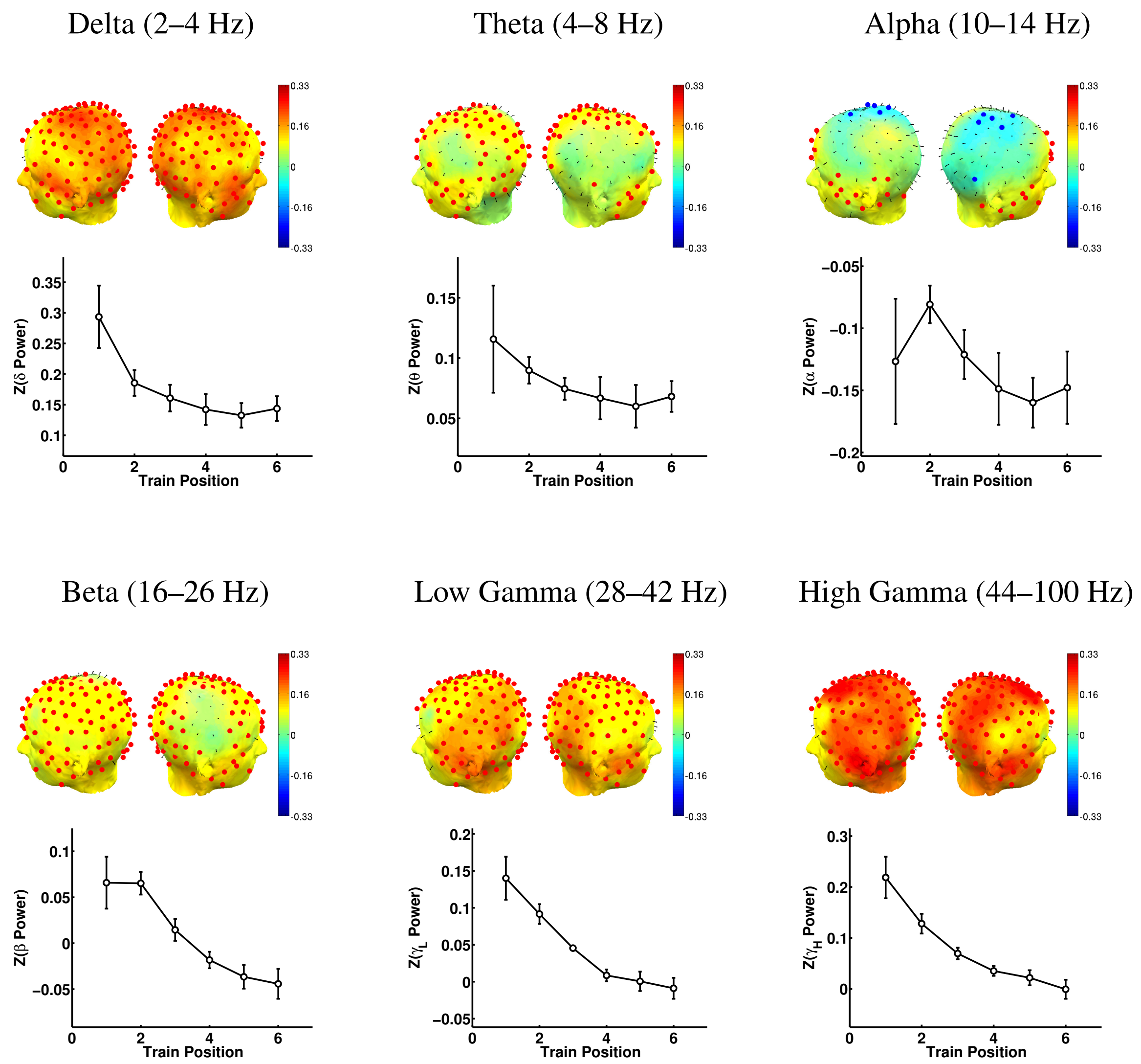
Start-of-list oscillatory list position effects

We next sought to characterize change in oscillatory power as a function of list position. Based on the oscillatory serial position effects observed by Sederberg et al. (2006), we expected to see widespread oscillatory patterns of increased delta and gamma activity, as well as decreased alpha activity, for start-of-list items. Fig. 3 shows the topography of electrodes exhibiting significant power differences between start-of-list items (serial position 1) and relatively later items (serial positions 3–4) for each frequency band. To visualize the changes in power, we show the mean power for each frequency band as a function of list position based on data averaged over all electrodes. Nearly all frequency bands (except alpha) exhibited widespread decreases in power across the first several list positions (i.e., power was increased for list position 1). These topographies did not vary widely across modality and are thus combined in the figure.

Mid-list oscillatory list position effects following modality shifts

Having characterized start-of-list position effects we then sought to determine the oscillatory correlates of mid-list shifts in perceptual properties of the stimuli to be remembered. Fig. 4 displays the topography of electrodes exhibiting significant power differences between items at the start of a new train (i.e., immediately following a shift in presentation modality, train position 1) and mid-train items (train positions 3–4) for the second and third trains in each list. Again, average power is plotted over all electrodes as a function of within-train position for illustration of the direction of these effects over the course of the list.

If post-shift oscillatory patterns are related to the processes of encoding primacy items, then we would expect a similar pattern of results to the start-of-list items. We do observe increased delta activity for post-shift items, but we also observe widespread decreases in alpha and beta power for



Delta (2–4 Hz)

Theta (4–8 Hz)

Alpha (10–14 Hz)

Beta (16–26 Hz)

Low Gamma (28–42 Hz)

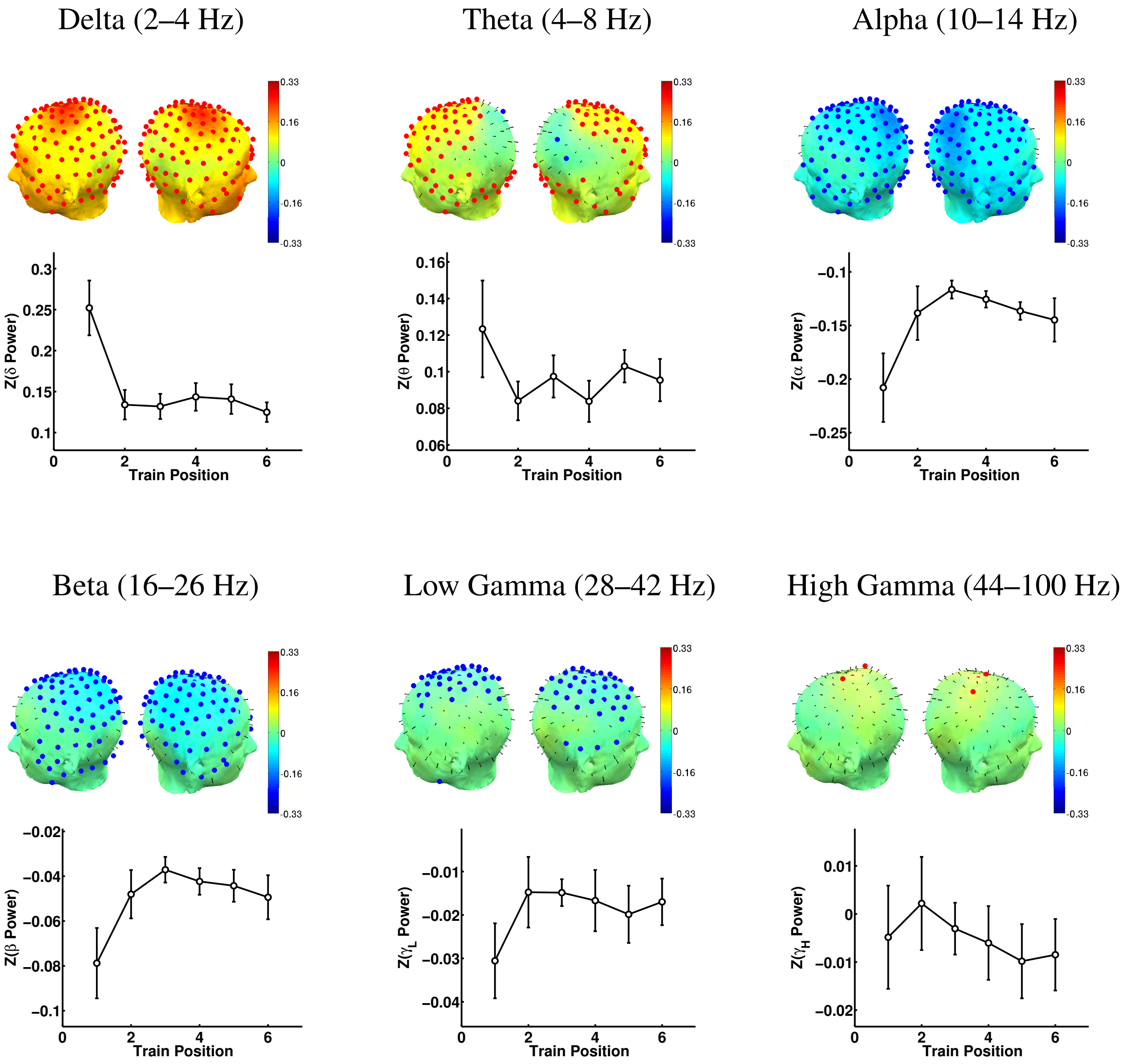
High Gamma (44–100 Hz)

Figure 3. Significant differences in oscillatory power for start-of-list items. The scalp topographies depict the electrodes that exhibited significant differences in mean power during the 0 to 1400 ms encoding interval between list position 1 and list positions 3–4, for six frequency bands. Red electrodes denote more power for primacy items, whereas blue electrodes denote more power for later positions. The line graph plots the mean *z*-transformed power across subjects over all electrodes. Error bars represent Loftus and Masson (1994) corrected ±1 standard error of the mean.

these items. Notably, there is no large significant difference in high gamma power as was observed at the start of the list. We noted that auditory items experience a larger increase in delta power in central regions after a shift in modality, while visual items exhibit a stronger decrease in alpha activity in posterior regions following such shifts.

Subsequent memory effects

We additionally observed how evoked oscillatory patterns related to whether an item would be later recalled or forgotten during the retrieval period. Increases in evoked gamma power for posterior electrode sites predicted successful relative to unsuccessful encoding for start-of-list items (train 1), while increases in stimulus-induced delta power and decreases in theta and alpha power predicted subsequent memory status for mid-list items (trains 2 and 3). The topographies of these effects are shown in Fig. 5. Univariate tests did not show reliable interactions between list/train position oscillatory effects and subsequent memory effects.



Delta (2–4 Hz)

Theta (4–8 Hz)

Alpha (10–14 Hz)

Beta (16–26 Hz)

Low Gamma (28–42 Hz)

High Gamma (44–100 Hz)

Figure 4. Significant differences in oscillatory power for items following a modality shift. The scalp topographies depict the electrodes that exhibited significant differences in mean power during the 0 to 1400 ms encoding interval between train positions 1 and train positions 3–4, for mid-list trains (i.e., trains 2 and 3), for six frequency bands. Red electrodes denote more power for post-shift items, whereas blue electrodes denote more power for items later in the train. The line graph plots the mean *z*-transformed power across subjects over all electrodes. Error bars represent Loftus and Masson (1994) corrected ±1 standard error of the mean.

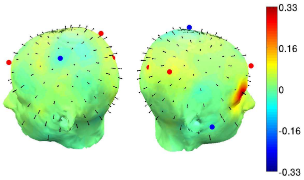
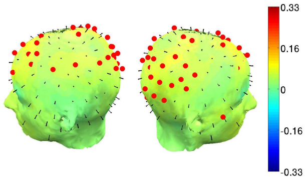
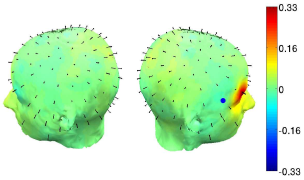
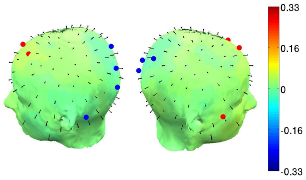
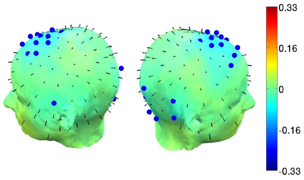
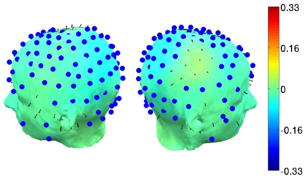
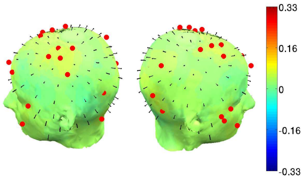
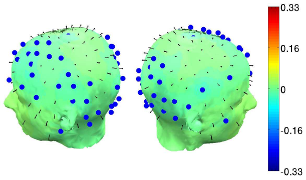
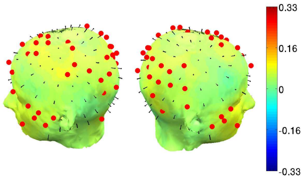
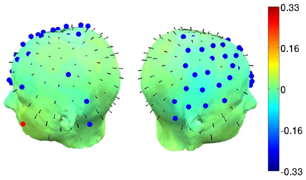
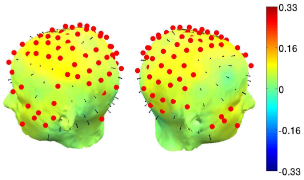
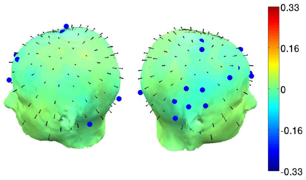
Frequency band	Start-of-list SME	Mid-list SME
Delta (2–4 Hz)		
Theta (4–8 Hz)		
Alpha (10–14 Hz)		
Beta (16–26 Hz)		
Low Gamma (28–42 Hz)		
High Gamma (44–100 Hz)		

Figure 5. Topography of significant subsequent memory effects (later recalled – later forgotten) for items from both early (Train 1) and middle (Trains 2 and 3) serial positions. Each pair of scalp topographies illustrates the electrodes exhibiting significant increases (red) or decreases (blue) in power during encoding that predicted successful retrieval for six distinct frequency bands.

CHAPTER IV

DISCUSSION

This study explored how patterns of oscillatory activity change with shifts in perceptual stimulus properties. In examining the topographies of these responses, we aimed to relate them to both start-of-list primacy effects as well as boosts in memorability following novelty-induced shifts. Our results may provide a basis for teasing apart aspects of these specific primacy effects.

Behavioral effects

Our results reproduce the boost in memorability previously observed following shifts in stimulus properties (Murdock and Walker, 1969; Geiselman, 1975; Polyn et al., 2009b; Davelaar, 2013), both in overall recall performance as a function of list position, as well as in terms of which items are targeted first by the memory system within experimentally-controlled subgroups. This boost to post-shift memorability supports the theory that these perceptual shifts are sufficient to induce a shift in mental context (Brown et al., 2007; Davelaar, 2013). This was observed regardless of modality. Analyses of variance, however, also revealed a number of interactions between factors of train number, train position, and modality on recall performance. These interactions are most likely due to recency effects for auditory items extending to the end of the third train. Auditory items have been shown to exhibit increased recall performance for recency positions (Murdock and Walker, 1969; Watkins, 1972), and these recency effects can be observed for auditory items in the behavioral measures examined in Figs. 1 and 2. The specific causes of this modality-specific boost to recency items has still been largely unexplored in the literature.

While modality-specific effects are beyond the scope of this study, there appear to be differential boosts to memorability between visual and auditory items. It is unclear from the data as of yet whether this supports classic dual-store theories of auditory and visual memory processes (e.g., Murdock and Walker 1969; Hintzman et al. 1972), or perhaps the modalities disrupt each other in the memory system to varying degrees. The vocal nature of the recall task may require more phonological processing for visual items, perhaps leading to enhanced encoding due to task demands. Efforts applying statistical modeling frameworks may be used to further elucidate the role of these specific perceptual features in novelty-induced shifts.

Oscillatory list position effects

Having characterized the behavioral effects of these modality shifts, we sought to examine their related oscillatory responses to better understand the processes underlying these effects. Previous research by Sederberg et al. (2006) observed widespread increases in gamma power and decreases in alpha power for start-of-list positions, as well as increased delta power for start-of-list items. The comparison of these results with the current study are summarized in Table 1.

Frequency band	Sederberg et al. (2006)	Start-of-list	Post-shift
Delta (2–4 Hz)	↑	↑	↑
Alpha (10–14 Hz)	↓	—	↓
High gamma (44–100 Hz)	↑	↑	—

Table 1. Noted changes in oscillatory power with list position (compared with mid-train positions) examined by Sederberg et al. (2006) as compared with the current study.

Increased gamma power for early serial positions

Our findings reproduced the increased gamma band (44–100 Hz) responses for early list positions observed by Sederberg et al. (2006) (Fig. 3). This is consistent with the previous account that these topographies relate to increases in top-down attention or allocation of resources for early items (Engel et al., 2001), such that the participant is actively engaged in the task of learning a new list of items. Increases in evoked gamma power have also been observed when participants attend to task-relevant stimuli (Tiitinen et al., 1993; Debener et al., 2003). We observe that, even with a shift in presentation modality, there is a lack of change in high gamma power for mid-list positions (Fig. 4). These results may reflect that early list items are better remembered due to a change in task goals. The overall goal of encoding individual items for later memory retrieval does not change within the list. While item-level features may vary, all items are relevant for the impending recall task. Start-of-list items, however, may benefit from an initial shift from pre-list experiences to the mental demands of the primary encoding task. As the mid-list shifts in this study were restricted to item-specific perceptual novelty, future work may examine whether a shift in internally-directed processes would elicit the same pattern of responses. This may possibly be observed through a shift in encoding task (Polyn et al., 2009b), or shifts from a task-irrelevant distraction task (e.g., performing arithmetic).

Decreased alpha power for positions following mid-list shifts

We did not reproduce the widespread alpha band (10–14 Hz) power decreases previous observed by Sederberg et al. (2006). We did, however, observe much more widespread decreases in alpha power following mid-list shifts in modality (Fig. 4). Alpha power increases have been correlated with increased working memory load (Jensen et al., 2002), which Sederberg et al. (2006) interpret as a divided encoding process. The mid-list decreases in alpha may then relate to a release from proactive interference of earlier list items (Hanslmayr et al., 2012), allowing for focused encoding of post-shift items. This focused encoding may then boost the processing of post-shift items (Pastötter et al., 2008), allowing them to be more successfully encoded and thus remembered better at recall, accounting for correlations with subsequent memory status. This does not rule out the possibility that increases in alpha power relate to poor encoding processes due to inattention (Klimesch et al., 1997; Klimesch, 1999).

Increased delta power for both early and post-shift positions

Increases in delta power were observed at both early positions—replicating Sederberg et al. (2006)—and post-shift positions. Such increases have been found to correlate with increased processing and successful encoding for both visual and auditory items (Weiss and Rappelsberger, 2000). Sederberg and colleges also found increased delta responses to correlate with subsequent memory performance regardless of an item's position within the list. Increased delta power at these primacy and post-shift positions may indicate that both parts of the list benefit from increasing attentional encoding of stimuli. Alternatively, Hanslmayr et al. (2011) suggest that these oscillations may relate to the binding of stimulus representations to temporal context, especially when coupled with start-of-list increases in gamma power (Summerfield and Mangels, 2005; Hanslmayr and Staudigl, 2014).

Dissociated subsequent memory effects

The observed oscillatory subsequent memory effects reliably reproduce the topographies observed by Sederberg et al. (2006) for both start-of-list and mid-list items. Increases in gamma power relate to the subsequent memory status of start-of-list words, while decreases in alpha and theta power relate to the same difference for mid-list items. Sederberg et al. (2006) also observed a positive delta SME lower in magnitude than that of higher frequencies. While individual fluctuations in these frequencies may predict subsequent memory performance, it is notable that these effects did not interact with within-train position. It is possible that due to the conditional nature of these analyses (i.e., dependent upon the number of recalls made for a particular individual in a particular list position), this comparison lacked sufficient statistical power. It is also possible, however, that this potentially indicates differential encoding mechanisms for encoding and contextual maintenance.

CHAPTER V

CONCLUSIONS

This study explored the consequences of mid-list shifts in perception on memory performance and how these consequences relate to start-of-list primacy effects. We examined how electrophysiological responses may inform our understanding of memory encoding processes at list positions following these shifts. While both early and post-shift items show evidence of increased item processing and contextual binding through increased delta activity, they show differences in gamma and alpha responses potentially relating to processes of encoding and attention. Future work should be done to evaluate the proposed mechanisms implied by these neural effects.

While we reproduce the alpha and gamma responses observed by Sederberg et al. (2006) for subsequent memory status, we extend this dissociation to within-list position effects following shifts in perceptual properties. The lack of interaction between these effects may indicate different aspects of alpha power on list-learning processes. Klimesch et al. (1996) have suggested the possibility of sub-bands of alpha power corresponding to different cognitive processes of attention and semantic encoding. Similarly, alpha oscillations have been linked to both the forgetting of older information and the enhanced encoding of new information (Bäuml et al., 2008). Alternatively, it is possible that these neural oscillations may reflect processes not specifically related to memory formation, but rather to different perceptual and cognitive processes engaged by the encoding task (Hanslmayr and Staudigl, 2014).

As these neural signals have been linked to a number of proposed mechanisms, future work may rely on cognitive models to disentangle how these oscillatory markers relate to shifts in mental context. Potential mechanisms suggested by the literature include a shift-related disruption of contextual state (Brown et al., 2007; Davelaar, 2013), an enhancement to post-shift stimulus integration (similar to the influx of perceptual information proposed by Zacks et al. 2007), or increased contextual binding for post-shift items (Sederberg et al., 2008; Polyn et al., 2009a). These mechanisms have each been proposed to account for boosts in memorability for new episodes or events, thus a neurally informed model may be used as a statistical framework to evaluate their proposed relationship with alpha oscillations and recall behavior (Kragel et al., 2015).

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