Differential Time Frequency Dynamics in Memory and Prioritization of Value -Directed Stimuli

by

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ABSTRACT

The ability to preferentially encode and later retrieve valuable information amidst a plethora of miscellaneous information is an essential aspect of human memory. Several hypotheses have been suggested to explain the enhanced ability to successfully encode high value items. These include the hypothesis that the prefrontal executive control processes are engaged for valuable information, producing elaborative rehearsal strategy. Another hypothesis is that greater attentional resources are allocated to higher value items via the reward driven mid-brain dopamine systems interacting with hippocampal and cortical areas to produce enhanced memory. To further understand the neural mechanisms of value on memory, electroencephalogram data under a value-directed remembering paradigm (VDR) was analyzed for oscillatory activity. During the task, participants encoded words assigned a different point value with the instruction to maximize the point value of recognized words during test. To analyze frequency activity during encoding, conditions of subsequent memory as subjective responses of either recollection (i.e., "remember") and familiarity (i.e., "know") were assessed. A possible way to observe the allocation of attention resources in the brain are alpha oscillations (8-15 Hz) which are thought to underlie this process. Participants demonstrated superior memory for high versus low value point items. Following the hypothesis that there is a greater recruitment of attentional resources for high value information, alpha oscillatory power in the occipital/temporal cortex displayed significantly more desynchronization for high value compared to low value conditions during encoding. As well, successful retrieval compared with unsuccessful retrieval and subsequent "remember" or "know" conditions resulted in a qualitatively different, more sustained desynchronization of alpha and other unanticipated frequency band oscillations during encoding that are discussed. Taken together, these findings support previous research for alpha-band desynchronization during encoding items of value into memory and potentially open paths to decouple value and memory driven processes.

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CHAPTER 1

INTRODUCTION

An important aspect of human memory is the ability to prioritize certain information over a range of miscellaneous or unimportant information. While some of what is encountered is valuable to remember, much of the other information encountered is non-essential and can be forgotten. For example, remembering the names of important people in life but forgetting the names of many others encountered is a favorable ability to a more broad, general encoding of all names for all people. While remembering your new boss's name is most likely important, the ability to remember every person's name you encounter at a shopping mall is less important. Given that the central nervous system is limited in its capacity to engage with and remember information, it is therefore crucial that to adaptively optimize memory, humans can preferentially encode valuable information over other less important information (Broadbent, 1958). If all information were to be encoded the same, additional interference from these inputs would make the memory of important information difficult (Broadbent, 1958, Cowan, 2000; Knowlton et al., 2022). This experience of information from the past that is rewarding or seen as important, can then motivate behaviors in the future guiding choices for "adaptive memory" (Shohamyet al., 2010).

Numerous studies have shown that rewarding or important information is remembered better than non-rewarding or unimportant information (Heyeret al., 2010; Kahnemanet al., 1969; Loftus et al., 1970; Weiner et al., 1966). These studies provide robust evidence that humans have an implicit ability to encode and retrieve valuable or rewarding information over less rewarding information. A common method to study the selective effect of value on memory is the value directed remembering (VDR) paradigm. Generally, in this paradigm participants are presented with word lists assigned varied point values for future tests. It is common that the words are presented through pairing of a number value next to a word (i.e., SHOE 4; Watkins and Bloom, 1999), but value can also be represented through other contextual elements (Forner-Phillips, 2020). Before the study list begins, participants are instructed that for each correct word remembered during test they will earn the corresponding value assigned during the study phase. The important goal being to maximize their total point score. As expected, this VDR paradigm has demonstrated that participants recall more words assigned high values than low values (Castel et al., 2002; Castel, 2008; Elliott, 2020).

A different variation to the VDR paradigm involves recognition memory tests as opposed to free recall. This allows for more precise investigation of the effect of value on memory recollection and familiarity. Dual-process models have proposed that recollection and familiarity are distinct processes allowing to observe differential effects on memory. (Mandler et al., 1980; Wixted et al., 2007; Yonelinas, 2002). In this model recollection is conscious retrieval of associative information presented during the study phase and judgments of familiarity are a more automatic appraisal of stimulus familiarity (Yonelinas, 2002). Results from studies utilizing these various VDR paradigms have led to theories about the underlying processes.

Throughout the research on value-directed remembering, two main hypotheses have been considered to explain value-driven gains in memory. The first hypothesis is that the ability to preferentially encode high value items relies on a strategic recruitment of encoding strategies leading to a deeper semantic processing of valuable information

(Cohen et al. 2017). While evidence exists for this theory, another central hypothesis has emerged to explain the value-based memory phenomena. An alternative theory is that value drives an implicit reward-driven allocation of attentional resources through mid-brain dopaminergic reward systems (Adcock, 2006; Elliott, 2020). In this view a more automatic reward driven allocation of attention affords greater memory capabilities for high value information. Research has now begun to try to parse these somewhat contrasting theories.

Alpha-band oscillations observed through electroencephalography data have been thought to underlie the allocation of resources for attention and performance. (Bonnefond et al., 2017; Fries, 2005; Hanslmayr et al., 2016, 2012; Jensen et al., 2010; Klimesch et al., 2012; 1996). During task engagement, alpha activity is seen to be elevated in brain regions contributing toward successful performance while areas that are unnecessary or task irrelevant display higher alpha power (Bacigalupo & Luck, 2019; Doesburg et al., 2016; Foxe & Snyder, 2011; Handel et al., 2011; Ikkai et al., 2016; Klimesch et al., 1996; Minarik et al., 2018; Poch et al., 2017). Further, this alpha activity increase associated with task engagement is seen during the processes of successful encoding and retrieval of information (Clarke et al., 2018; Hanslmayr et al., 2009, 2012, 2016; Khader & Rösler, 2011; Klimesch et al., 1996). Considering these observed dynamics in frequency activity, if high value items are receiving greater allocation of attention resources it could be that alpha oscillations underlie the value-driven effects (Forner-Phillips, 2021). This makes observations of alpha activity a potential way to observe the deployment of greater attentional resources toward high value items. The present study uses electroencephalography (EEG) to investigate the time frequency dynamics of value and memory during encoding of rewarding information in a value-based recognition memory task to assess the neural underpinnings of value-driven effects.

CHAPTER 2

REVIEW

Recognition vs. Familiarity

The dissemination of recognition and familiarity into separate processes has been displayed throughout the literature. While recollection is often closely associated with high recognition and confidence for memory, it is also known that participants make accurate memory judgments for items that are not confidently recognized (Yonelinas, 2002). A common way to evaluate the differential mechanisms of recognition and familiarity processes is the “remember/know” paradigm (Tulving, 1985). Several studies have characterized recognition and familiarity as distinct processes with evidence from various methodology including fMRI and EEG studies (Adante et al., 2012, Adcock et al., 2006). These studies show evidence for a dual-process model where these processes are functionally dissociable and to a degree rely on separate regions of the brain (Adante, 2012; Rugg et al., 2007). While recollection encompasses conscious retrieval of associative information from during the study phase, familiarity-based judgments are a more automatic appraisal of familiarity to the present stimulus. With this dual process model, certain variations in memory tasks can therefore elicit differential effects on either recollection or familiarity, a potentially useful way to gain insight on value-driven memory effects (Yonelinas, 2002).

Previous research has examined the effects of value on memory in recognition tasks. In a VDR recognition task by Adcock et al. (2006), value-based effects on memory were found be exclusive to remember and high confidence responses, with no specific effects on familiarity. These results were replicated by the previous ERP study showing value-driven gains in remember responses with no effect on familiarity (Elliott, 2020). Taken together, these results indicate that value has specific effects to high confidence remember responses with no effect on familiarity. Interestingly, both studies also revealed evidence for dopaminergic-reward process driven gain in value driven memory.

VDR Mechanisms

Ariel and Castel (2014) proposed two models to explain the enhancement of memory toward high value items. These included the information reduction hypothesis and the resource allocation hypothesis. For information reduction hypothesis, participants completely ignore low value items during encoding. In the resource allocation hypothesis participants engage encoding with both high and low value items; however, they allocate more attentional resources to high value items. To test these hypotheses, eye tracking software to measure pupil diameter and fixation duration while studying lists of words assigned different point values was assessed. The primary findings were as such: Participants' pupils dilated more during the encoding of high point value words which was associated with subsequently better memory for these high value items. Additionally, it was found that participants fixated on all words irrespective of their value. Together these eye tracking results support the resource allocation hypothesis. As subjects were presented with words of differing value, there was a degree of engagement regardless of value but dynamic changes in pupillary dilation to value were associated with high valued items and later memory (Ariel and Castel, 2014).

Further supporting the resource allocation hypothesis, Stefinidi et al. (2018) used an adapted VDR paradigm to investigate the influence of value on free recall dynamics. This study consisted of three experiments. In the first experiment value and control conditions were compared for free recall dynamics. Following the initial experiment, the order of values presented were manipulated in descending and ascending order conditions where values were presented in either a congruent or incongruent fashion as the study progressed. Interestingly, during the descending condition participants recalled more low value items than the other two conditions following theories on primacy effects (Rundus, 1971; Wixted & Ebbesen, 1991). The authors concluded from these findings that for both high and low value items participants engaged attentional resources but allocated more so for high valued items. These free recall and eye-tracking experiments together indicate that while all information is attended to, high value items recruit more resources (Stefinidi, 2018). Since these results show a certain allocation of resources are utilized in the process of value-directed effects, the underpinnings of neural mechanisms contributing to this process are of interest.

VDR Neural Mechanism

Throughout the research on value-directed remembering, two main hypotheses have been considered to explain the neural drivers of value-based effects. The first hypothesis is that the ability to preferentially encode high value items relies on a top-down, strategic recruitment of encoding strategies leading to a deeper semantic processing of valuable information (Cohen et al. 2014). Following this line of thinking, the ability to engage deeply with item context and optimal rehearsal strategies are needed for value-driven gains (Cohen et al. 2017). For example, if one learns of an area that has proven to be fruitful for fishing, you might actively engage this memory by picturing the location or forming an association with some sort of other contextual element in one's knowledge. In order not to lose this memory, you might also actively recall on it following its presentation or discovery in detail. Prior research has provided evidence to support this view.

In a study by Cohen et al. (2014), differences in brain activity were examined at encoding using a subsequent free recall design. Brain regions such as the left inferior frontal gyrus and left posterior lateral temporal cortex exhibited differences in activation that correlated with individual differences in selectivity index (SI), a measurement used to examine how strongly value effects memory (Castel et al, 2002). These brain regions are associated with semantic processing and the authors conclude these frontotemporal semantic processing hubs that support elaborate rehearsal may be a crucial driver for value-based encoding effects. In another fMRI study Cohen et al. (2016) evaluated older adults and younger adults for functional activation in semantic processing areas during a VDR task before and at encoding. While differences were seen between younger and older adults, activation patterns were consistently observed to be engaging the pre-frontal cortex mediated control mechanisms, supporting the elaborative rehearsal hypothesis.

Studies using EEG have attempted to replicate these functional imaging results. In EEG research the frontal slow wave FSW component is thought to underlie frontal semantic processing reflecting deep encoding. In studies where elaborative associative strategies are explicitly implemented, the FSW component amplitude is observed to be greater (Fabiani et al., 1990; Mangels et al., 2001). Considering the previous fMRI work, one could expect to see the FSW component affected during encoding of value-based stimuli as a process to prioritize and encode information. In the ERP work by Elliott et al. (2020) no evidence was found for contributing effects of value on this FSW component. In contrast, the early P3 component was observed to be significantly different for high and low value conditions, a component associated with allocation of attention, reward, and valuation of stimulus (Pfabigan et al., 2014; Polich, 2007; Sato et al., 2005; Walsh and Anderson, 2012). More specifically, evidence has been proposed to show that the P3 component may be at least partly driven by dopamine interaction (Pfabigan et al., 2014; Polich, 2007). Considering these seemingly opposing results, it is important to consider the alternative theory that dopaminergic midbrain hippocampal projections are underlying drivers of value-based effects.

An alternative theory posits that a more automatic reward-driven allocation of attentional resources through mid-brain dopamine-hippocampal interactions contributes to the effects of value on memory. Several fMRI studies have reported evidence that supports this view. In the subsequent remember/know VDR paradigm study by Adcock et al. (2006), the value-based enhancement of recollection was accompanied by activation in reward processing regions including the ventral tegmental area and nucleus accumbens along with the hippocampus, an important structure for memory encoding. Several other neuroimaging studies have revealed similar evidence. In a study by Wittman et al. (2005), pictures of objects that predicted monetary reward were associated with increased activity in reward-related mid brain dopaminergic areas such as the substantia nigra. This has also been extended to intentional encoding value paradigms where mid-brain dopaminergic structures and hippocampus displayed increased connectivity associated with magnitude of behavioral reward modulation (Wolosin et al., 2012). Similarly, when value and punishment are given for recognition, midbrain dopaminergic structures and hippocampus activation are found associated with reward (Shigemune et al., 2014).

Given these contrasting theories for value-based gains, further research into event related time-frequency dynamics has been employed in attempt to further understand.

Time Frequency Characteristics of VDR

One technique utilized in the analysis of EEG data is event-related spectral perturbations (ERSPs). These provide time-resolved information of phase-locked and non-phase locked spectral activity from the EEG signal. While many of the previous studies used fMRI to examine neural substrates of value-based memory, EEG provides superior temporal resolution for finer assessment of time-sensitive processes. This makes it an optimal technique to observe the temporal unfolding of value-directed effects (Makeig et al, 2004).

Oscillations in the alpha frequency band (8-13 Hz) are thought to underlie the processes of attention and the channeling of neural resources ((Bonnefond et al., 2017; Fries, 2005; Hanslmayr et al., 2016, 2012; Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 1996). As previously discussed, two hypotheses are often considered as mechanistic drivers of VDR effects. These include the elaborate rehearsal theory and automatic allocation of attentional resources (Knowlton et al., 2022). Because oscillations in the alpha band are associated with attentional resource channeling, allocation of attentional resources toward high value items associated with enhanced memory performance can be assessed.

Confirming the presence of alpha desynchronization activity increases for valuable information, Forner-Phillips et al. (2021), completed an experiment using EEG and a value-directed source recognition task designed to determine alpha desynchronization consistent with deployment of greater attentional resources are for high versus low value information was present. Participants were presented with 200 nameable color images (i.e., a picture of an apple) presented an equal number of times on two colored backgrounds corresponding to either high or low values. Participants were oriented during a practice phase before EEG acquisition to which backgrounds were high and low point values and that high value items would lead to more payment. At test, participants were again shown the original 200 objects with an additional 100 new objects one at a time and asked to judge whether each item was new or old and if old, which of the corresponding value backgrounds was it presented on. Unsurprisingly, participants exhibited better memory for items displayed on a high value background. Of theoretical interest, EEG analysis showed that participants exhibited greater alpha desynchronization in the high versus the low value background conditions during encoding. Based off these results, the authors suggest that participants engage strategic encoding strategies, and given the literature about alpha- desynchronization that this process underlies attentional resource allocation. This work is supported by the findings of Nguyen et al. (2019). In this study a free recall VDR paradigm was utilized, and participants exhibited greater alpha desynchronization for high vs low value items. The observation of alpha desynchronization postulated to be engagement of selective attention.

With numerous studies reporting on the separate neural mechanisms and underpinnings of value on memory, further examination of neural generators contributing to this process is warranted. The previous ERP results provide an interesting perspective with the lack of detection of a FSW component and a significant P3 interaction with value increases (Elliott, 2020). Observations of alpha-oscillations thought to underlie allocation of attentional resources are another way to observe the functional activation for value driven- effects (Foner-Phillips, 2020; Nguyuen, 2019). Further examination of the recent ERP data (Elliott, 2020) into the time-frequency domain may contribute a more complete picture of the neural processes leading to this effect.

PURPOSE

The primary intention of this research was to further understand the neural mechanisms that contribute to value-directed remembering through utilizing a VDR remember-know recognition paradigm expanding on the previous event-related potential work from Elliott et al. (2020). Analysis of electroencephalography data was employed with subsequent memory retrieval to take advantage of the high temporal resolution and investigate the time frequency dynamics of value and memory conditions. These conditions were compared using event related spectral perturbation maps with a specific interest in alpha-band desynchronization associated with allocation of attentional resources in the occipital/temporal cortex.

HYPOTHESIS

Given the previous literature, it was hypothesized participants would display greater desynchronization in alpha band frequencies for components clustered in the bilateral occipital/temporal cortex for high value item versus low value item conditions from 450 to 650 ms post onset of stimulus. The event-related spectral perturbation maps for memory in general will display similar alpha desynchronization. Lastly, for recognition and familiarity conditions, differences in ERSP were expected to be qualitatively different than value specific conditions.

CHAPTER 3

METHODS AND DESIGN

Participants

The remaining 28 participants previously recruited for an EEG study on memory by Elliott et al. (2020) through the Arizona State University research pool were used for the study analysis. This sample size was chosen based upon a previous experiment by Elliott and Brewer et al. (2019) which utilized the same paradigm. Adequate effect sizes were found in this previous study and a post-hoc sensitivity analysis confirmed sufficient power to detect a minimal effect size of $f = 0.202$, a medium effect size. For analyzing subsequent remember/know conditions at encoding, an additional two participants were dropped for an insufficient number of familiar or “know” responses to recognition or “remember” responses ($n=26$).

Materials and Design

The procedure was implemented and utilized by Elliott et al. (2020). EEG recording was taken during encoding and retrieval of 400 nouns selected from the Toronto noun pool were used (Friendly et al., 1982). Point values (1, 3, 7, or 9) were randomly assigned to 40 words in the study phase. Participants completed five study-test blocks. In the test phase participants were presented with 80 words (40 new words and 40 from the most recent list, randomly presented) one at a time, without point values. Participants then classified items as either old or new and judgments of their subjective state of recollection were recorded.

Procedure

The data was obtained from the study procedure used in the first ERP study (Elliott, 2020). All experiments followed a protocol approved by Arizona State University's Institutional Review Board. Written and informed consent was obtained from each participant prior to initiating the study. Instructions were as follows: Participants were told they would be completing multiple study-test blocks in a recognition memory task. They were instructed that their task was to remember as many words as possible, with the overall goal of maximizing their score on each recognition memory test. The study list consisted of 40 randomly selected nouns randomly paired with point values represented as integers (1, 3, 7, 9). A total of ten of each value was presented in each study block. These noun-value pairs were presented sequentially for 2 ms. The inter-stimulus interval was randomly jittered from 300 to 500 ms in 17 ms increments so that evoked activity did not interfere across stimulus presentation. Participants were instructed that the point value paired with the word would be earned if correctly recognized without considering confidence rating. Additionally, they would lose one point for incorrectly "recognizing" a new word as old.

To clarify the difference between remembering and knowing, participants were provided the following instruction adapted from Herzmann and Curran (2011): "Make a remember judgment if you not only remember the word, but also consciously remember the experience of studying the word. For example, perhaps you remember the specific value of the word, something else that happened in the room while you were studying it (like a cough or sneeze), an association that came to mind, or what came just before or after the word in the study phase. To give you a real-world example, imagine you are walking across campus and recognize someone, but cannot recall their name or where you have met them. You are certain you have seen this person before, but do not remember anything specifically about them or where you met them. This would be 'knowing.' If you recognize this person and remember that it is John whom you met in Biology class, this would be 'remembering.'"

If a word was not recollected but participants were sure they had seen it previously on the study list, they were instructed to respond with "definitely know" and for instances where they thought they had studied the word but were less confident "maybe know". "Maybe new" responses were instructed to be used if they thought the word was new but not confident and "definitely new" responses if they felt certain the word was new.

Words were presented below a central fixation cross in the center of the computer screen with values appearing above concurrently. Following the study block, a test phase with an additional 40 new words randomly intermixed with the previous 40 words from the study phase were presented. Test words were displayed one at a time consecutively and participants determined whether they thought this word was old or new. Subjective judgments of memory were recorded using a standard keyboard with the designated response options: Z "Definitely New"—left pinky, X "Maybe New"—left ring finger, C "Maybe Know"—left middle finger, V "Definitely Know"—left index finger, and M "Remember"— right index finger. While the test was untimed, participants were encouraged to respond with their first instinct.

Behavioral Data & Analysis

Processing of behavioral data for this study was completed previously by Elliot et al. (2020). For all subjects' raw hits ("remember" or "know" responses) were calculated as a proportion of total responses in that category divided by the total number of items studied. “Maybe know” and “definitely know” responses were counted as “know” responses. False alarms were also corrected for by subtracting the false alarm rates from the hit rates in each category.

EEG Data Preprocessing

The raw data was previously recorded using a 32 channel EEG cap on a Neuroscan SynampsRT system by Elliott and colleagues (Elliott, 2020). The data was collected at 1000 Hz bandpass filtered from DC to 400 Hz. Data processing occurred offline. EEGLAB version v 2021.1 (Delorme & Makeig, 2004) in Matlab 2021b (Mathworks, Natick, MA) were used for EEG data processing and analysis. The data was down sampled to 250 Hz and band-pass filtered from 1 to 30 Hz. Reference was computed using the average of the left and right mastoid electrodes. Next, data was submitted to a GPU-optimized version of the independent component analysis infomax (ICA; Raimondo et al., 2012) algorithm. Ocular artifact components were identified through visual inspection of the data and removed from the unfiltered raw data via two independent researchers. A total of 1.1% of the data was subsumed through the ICA procedure. After removal of ocular artifacts, the raw data was filtered using an IRR Butterworth filter, .1 – 30 Hz. Data was time-locked to the onset of the word and was separated into epochs from -200 to 2000 ms relative to the onset of stimulus. -200 to 0 were set for the baseline correction of each epoch. During encoding, an average of 35 trials per subject with the highest trial count of 49 was recorded across all conditions. Excess noise in the electrical data was identified using a moving window 60 ms wide and moving in increments of 20 ms across the epoch. Differences in peak-to-peak voltage greater than 80 μV for all channels was used to establish the rejection criteria. If four or less electrodes exceeded this criterion for noise rejection, spherical interpolation of these electrodes occurred. If greater than four electrodes exceeded this threshold, the trial was removed. Overall, this led to the exclusion of 1.0% of the data ranging from 0 – 10.2% of correct trials across participants. EEGLAB STUDY feature was then used to construct the study format for cluster-based comparison. Independent components were source localized using DIPFIT2 (Oostenvald et al., 2011). A wavelet transformation was utilized to convert the data into the time-frequency domain using a modified Morlet wavelet transformation in 25 ms steps for 30 log-spaced frequencies between 4 hz and 40 Hz with 2 cycles at 4 Hz and 4 cycles at 40 Hz. Event-related spectral perturbation (ERSP) maps were calculated from the time frequency conversion for each condition within each component. Only components with less than 15% residual variance were included in the final analysis. Component clusters were created by running Principal Component Analysis producing a global distance matrix specifying distances between components for the clustering algorithm given an N-dimensional cluster position vector for each component. The distances of components' dipole models and activity measure from one another in the space of the joint PCA-reduced measures were selected. Clusters were formed based on dipole location and ERSP maps with 3 dimensions for dipoles and 7 dimensions for ERSP with the weighting 10 for dipoles, 1 for ERSP. Finally, a K-Means algorithm was used to cluster the components with all components more than 3 standard deviations away from a cluster centroid grouped into an outlier cluster. Re-clustering of the components was then inspected for robustness and consistency of the data as well as optimal inclusion of individual components contributing toward the cluster. This was done to ensure the interpretation of the event related spectral perturbations was for the general population at a subject level. Clustering of an average of 2 components per subject for the cluster of interest was used (Delorme & Makeig, 2004).

Encoding

ERSP maps were generated for High Value Hit and Low Value Hit conditions utilizing subsequent recollection sorting for “hit” (“remember” or “know”) responses at retrieval during encoding. This study design allows for the comparison of dynamic oscillatory activity between successful encoding of High value items with successful encoding of low value items. Additionally, the subsequent memory design allowed for several further analyses. To examine the value driven effect, High Value Miss and Low Value Miss conditions were compared to examine the effect of value at encoding regardless of the subsequent memory effect. Successful subsequent memory conditions across all value conditions were compared using High and Low value hit versus High and Low value miss conditions.

To examine the differential time frequency dynamics of recognition and familiarity, subsequent “remember” and “know” responses across all value conditions were sorted during encoding and compared. Due to limited familiarity “know” responses three additional subjects were dropped for the recognition and familiarity analysis (n=25). For all analyses, permutation-based statistics with 5000 iterations and a p-value of .05 were used. Correction for the issue of multiple comparison was implemented in EEGLAB using Fieldtrip (Oostenvald et al., 2011) with triangulation defining clusters and maxsum as the cluster statistic (Maris and Oostenvald, 2007)

CHAPTER 4

RESULTS

EEG Encoding Results

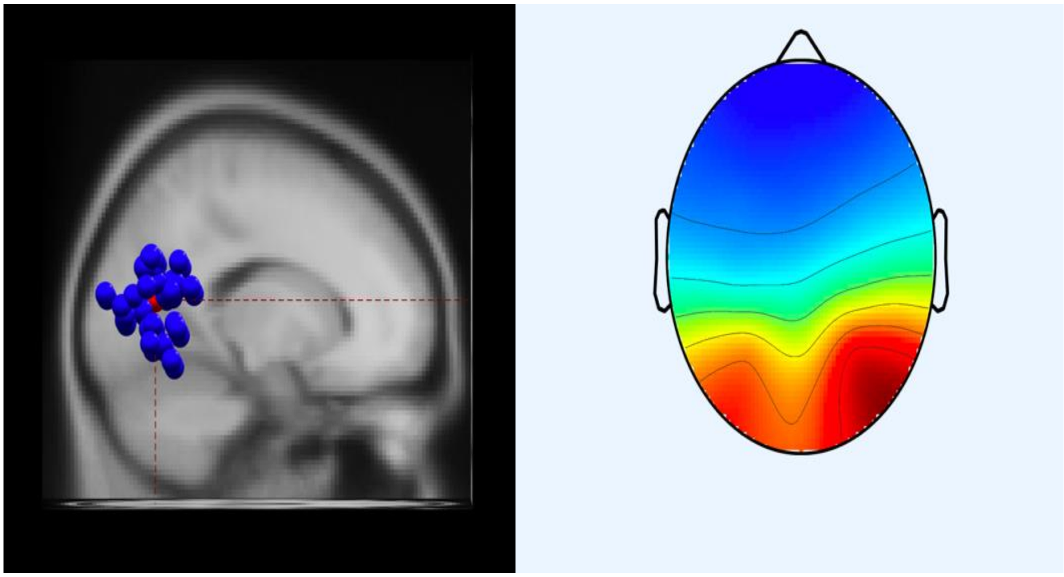
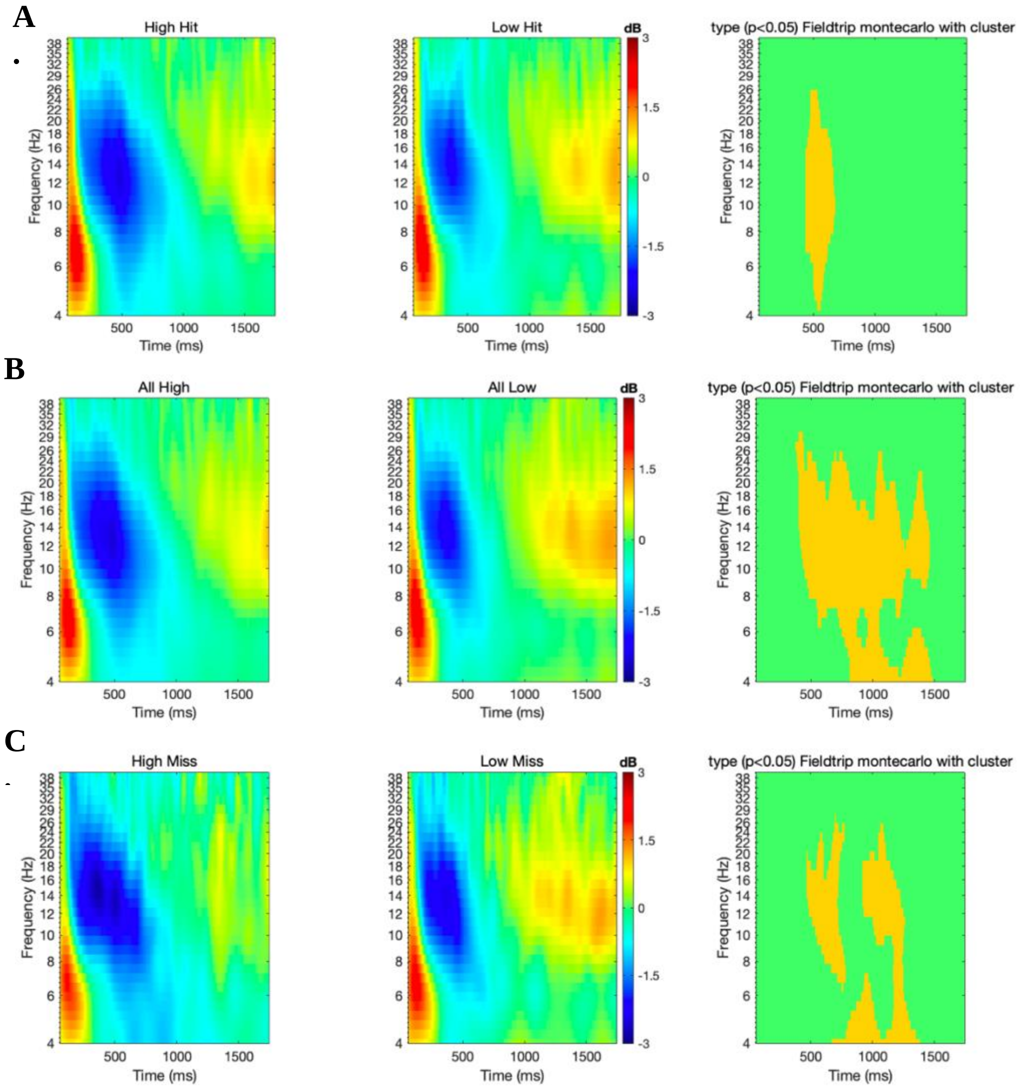


Figure 1. (**A**) Dipole locations for the clustered components contributing to the alpha desynchronization in the occipital/temporal cortex.
(**B**) Scalp maps for the clustered components contributing to the alpha desynchronization in the occipital/temporal cortex for hit vs miss and high versus low value conditions at encoding.

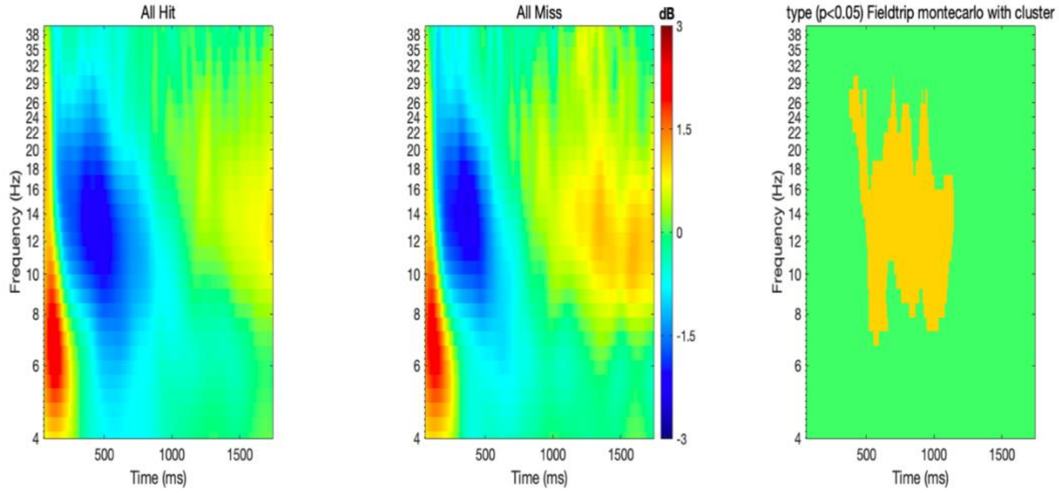
Event-Related spectral Perturbation (ERSP) map differences were found when encoding items assigned high or low point values in the bilateral occipital/temporal cortex cluster (**Figure 1**). High value conditions sorted for subsequent memory during retrieval exhibited greater alpha desynchronization in the bilateral occipital/temporal cortex from 400 to 600 ms post stimulus onset compared to the low value conditions **(Figure 2; A**). Outside of subsequent memory, conditions sorted for all high value items and all low value items during encoding exhibited significant differences in alpha desynchronization along with significant differences in beta (450- 1500 ms) and theta (600-1500 ms) for high value conditions (**Figure 2; B**). For conditions of subsequent misses for high and low value conditions during encoding, significant differences were



detected for alpha and beta frequencies form 450 – 700 ms. Differences in theta were observed from 650 -1400 ms post onset of stimulus with greater desynchronization for these frequency bands in high value conditions **(Figure 2; C**).

Figure 2. **(A)** Event Related Spectral Perturbation (ERSP) maps during the successful encoding of High value (High Value Hit) versus Low value (Low Value Hit) conditions in the occipital/temporal cortex. The color reflects changes in power values from pre-stimulus baseline with red indicative of increases and blue indicative of decreases in power(dB). The third map represents areas of significant difference (p-value <.05) between high and low value conditions. There is greater alpha desynchronization for high value hit conditions compared to low value hit conditions at 400 to 600 milliseconds (ms) post onset of stimulus. Additionally, this effect extends into the upper theta (3-8 Hz) and lower Beta (12.5-30 Hz) frequency ranges. **(B)** Event-related spectral perturbation maps during the encoding of high (All High Value) and low (All Low Value) value conditions irrespective of subsequent memory in the occipital/temporal cortex. The third map reflects the areas of significant difference (p-value .05) between the low value miss and high value miss conditions. Greater alpha- and beta-band desynchronization is seen for the high value vs low value condition from 450 – 1500 ms. As well, significant

In purely subsequent memory conditions during encoding sorted for later successful or unsuccessful retrieval, greater alpha desynchronization for hit conditions compared to miss conditions at 400 to 600 ms post onset of stimulus was detected. Additionally, beta (12.5-30 Hz) frequency range differences were observed with more desynchronization for subsequently remembered items during encoding.


All Hit

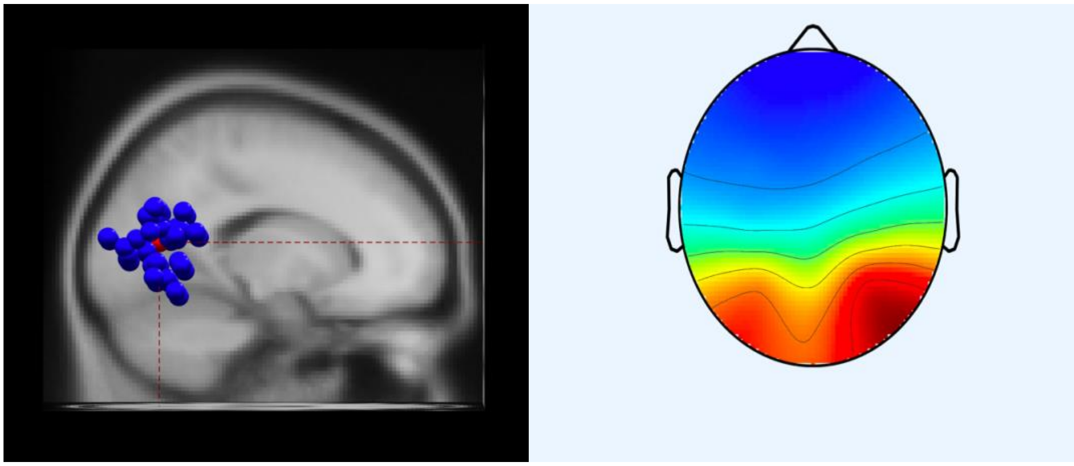
All Miss

type (p<0.05) Fieldtrip montecarlo with cluster

Figure 3. Event Related Spectral Perturbation (ERSP) maps during the successful encoding (“hit”) compared to unsuccessful encoding (“miss”) conditions in the occipital/temporal cortex. The color reflects changes in power values from pre-stimulus baseline with red indicative of increases and blue indicative of decreases in power(dB).

The third map represents areas of significant difference (p-value <.05) between hit and miss conditions. There is greater alpha desynchronization for high value hit conditions compared to low value hit conditions at 450 to 1100 milliseconds (ms) post onset of stimulus. Additionally, this effect extends into the lower Beta (12.5-30 Hz) frequency ranges.

Lastly, the contrasts of subsequent “remember” and “know” conditions during encoding revealed minimal alpha-desynchronization in the upper frequencies of the alpha band from 600-700 ms and 1100-1200 ms post stimulus onset for “remember” conditions. Additionally, greater beta-desynchronizations occurred from 500- 1200 ms post onset. For high value remember/know conditions, no significant differences were observed. For low value remember/know conditions during encoding, similar dynamics were observed. Limitations of this are discussed.



A. **B.**

Figure 4. (**A**)Dipole locations for occipital/temporal cortex component clusters in the recognition and familiarity design during encoding. **(B**) Average scalp maps for all conditions in the recognition and familiarity design for the respective dipole locations in the occipital/temporal cortex cluster.

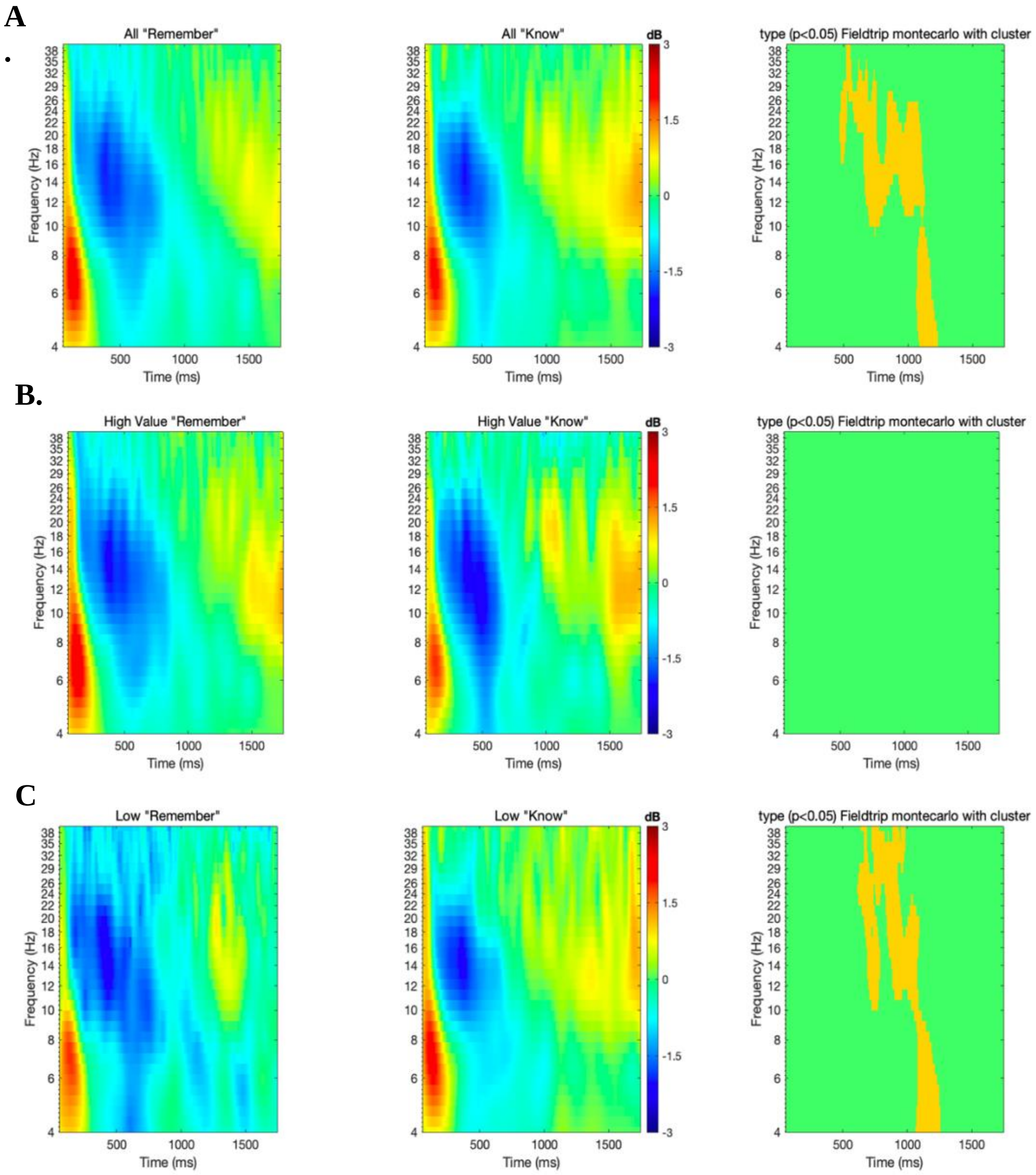


Figure 5. Event Related Spectral Perturbation (ERSP) maps during the successful recognition versus subsequent familiarity during retrieval in all value conditions for occipital/temporal cortex. The color reflects changes in power values from pre-stimulus baseline with red indicative of increases and blue indicative of decreases in power(dB). The third map represents areas of significant difference (p-value <.05) between hit and miss conditions. (**A**)There is greater upper alpha desynchronization for high value hit conditions compared to low value hit conditions from 600 to 700 ms and post onset of stimulus. Additionally, this effect extends into the Beta (12.5-30 Hz) and upper theta (3-8 Hz; 1100-1200 ms) frequency ranges. (**B**) No significant differences for high remember or know conditions during encoding. (**C**) Similar differences for low value remember/know conditions seen in pooled all values.

CHAPTER 5

DISCUSSION

The first main finding from this study is that participants were observed to have a significant decrease in alpha desynchronization during encoding of subsequently remembered high value items compared to low value items from 450 to 650 ms post onset of stimulus. As well, significant desynchronization in upper theta and beta activity was displayed during this period. Second, during encoding of subsequently remembered or missed trials, participants displayed a sustained alpha desynchronization from 450 - 1100 ms post onset of stimulus. Significant differences in beta (12.5 - 30 Hz) were detected within this same time window. Lastly, the subsequent "remember" versus "know" conditions across all values displayed upper alpha desynchronization from 600-700 ms and theta effects at 1100-1200 ms post onset of stimulus. Subsequent "remember" and "know" under high value conditions revealed no difference while low value conditions paralleled pooled value conditions; however. limitations for interpreting this are discussed.

The central finding of this study is greater alpha-desynchronization in association with high value word pairs in the occipital/temporal cortex (**Figure 2**, **A**). This finding directly replicates previous findings for oscillatory activity and value-driven effects during encoding (Forner- Phillips, 2021; Nguyen, 2019). In this work increased occipital/temporal cortex alpha desynchronizations were associated with high value over low value items, and previous research has provided evidence for alpha-oscillatory desynchronizations in association with allocation of attentional resources to a stimulus (Bonnefond et al., 2017; Fries, 2005; Hanslmayr et al., 2016, 2012; Jensen & Mazaheri, 2010; Klimesch et al., 2012; 1996). Considering this and the replication of alpha oscillatory activity in VDR paradigms, it could be a reward driven allocation of greater attentional resources toward high value items is a driver of these dynamics. Of interest, the temporal dynamics of this oscillatory activity correspond to the latency observed in the previous ERP study which found the P3 component to be observed from 450 to 650 ms post stimulus onset (Elliott, 2020).

It is therefore warranted to further explore the previous ERP findings and how the data fits with the present time-frequency findings. Encoding results indicated that the ERP P3 component was correlated and scaled linearly with participants' sensitivity to value when subsequently tested in the recognition test or their "Selectivity Index" at the PZ electrode sight (Elliott, 2020). It is important to consider that the P3 component is thought to represent reward driven dopaminergic processes or the allocation of attentional resources (Walshet al., 2012; Gruber, 2017). As previously discussed, alpha band desynchronizations have been also thought to underlie the process of allocating attentional resources (Bonnefond et al., 2017; Fries, 2005; Hanslmayr et al., 2016, 2012; Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 1996). Together, these ERP and ERSP findings display similar temporal dynamics and are measured from similar locations on scalp, potentially in support of the reward driven attention resource allocation hypothesis; however, future experiments with similar design and utilization of methods with greater spatial resolution, such as event related fMRI, may help to confirm whether the P3 component and alpha-oscillatory activity observed have similar neural generators.

With respect to the encoding of subsequent hit versus miss trials, subsequent hits were observed to produce a sustained decrease in alpha band activity compared with misses. This is concurrent with other research, which reports widespread alpha desynchronization in task relevant areas associated with enhanced performance on memory tasks (Hanslmayr et al. 2009, 2016, 2012; Klimesch et al., 1996; Minarik et al., 2018). The more exclusive desynchronization at 450-650 ms differences for high and low value hit conditions points to a more specific allocation of resources for higher value items over low value items. As well, unanticipated significant differences in beta and theta band desynchronization activity for hit trials were observed. While much of the previous research has focused on synchronization of beta-band oscillations for episodic memory, previous research in studies investigating subsequent memory with EEG have noted desynchronization findings.

Beta oscillation (13 -30 Hz) have been observed in subsequent memory designs (Hansylmar et al., 2016, 2012; Greenberg et al, 2015). These beta desynchronizations have been positively related to enhancing the richness of information represented in the brain, which encourages the encoding into long term memory. Increases in complexity for firing patterns in underlying neuron populations are seen as beta power decreases and with this may lead to more detailed information being encoded. (Hansylmar, 2012; 2014; 2016). In the context of value directed remembering, greater beta-desynchronization for high value items may lead to increased complexity of the information stored. This could help to explain previous observed effects such as recalling values paired with memory and other contextual elements in greater detail (Knowlton et al., 2022). Future studies examining beta activity during encoding of value-based stimulus could help to elucidate if the effects seen underlie an element of this process. Theta frequency band differences were also seen with respect to memory and value conditions.

Theta frequency activity (4-8 Hz) has long been implicated in learning and memory; however, the full picture of its role has been more complicated. With some studies observing increases and other studies observing decreases in power related to successful memory encoding (Herweg et al., 2020). VDR paradigms have observed increases in frontal theta in association with low value items compared to high value items (Nguyen, 2019). Post-hoc exploration of frontal theta in the present study found no evidence for frontal theta differences in value conditions; however, the paradigm used in this task varied in that they were free recall. It is possible that different aspects of strategic encoding are employed depending on the task explaining this inconsistency (Knowlton et al, 2022). Rather than frontal theta differences, observed theta desynchronizations were found in the bilateral/occipital cortex.

While many studies have noted theta power increases are predictive of episodic memory, many others have reported theta desynchronizations in association with successful memory. In a review of theta oscillations in memory by Herweg et al. (2020), dozens of studies showing apparent opposite effects for theta in memory were analyzed. To explain this, theta effects and successful memory were divided in two cognitive processes. One of these processes was the deployment of attentional resources leading to general decreases in low frequency power. In a study examining primacy effects in electrocorticographic recordings from neurosurgical patients, widespread brain regions exhibited lower theta frequency in the beginning of lists that gradually increased. This was explained to be the possible result of primacy effects where attention is higher for items presented in the beginning of a sequential study list (Serruya, 2012). EEG research examining oscillatory encoding dynamics of the primacy effect displayed similar results of a lowered theta power gradually increasing over the serial task as well as alpha band power (Sederberg, 2006). Further, wide-spread cortical theta power decreases predicted successful memory for items occurring in later serial positions (Herweg, 2020). These results suggest that as resources are divided among numerous list items, focus is turned to divided item processing and attention is strained. A certain inhibition of rehearsal of previous items and allocation of attention is then required for successful encoding of middle position items (Sederberg, 2006). Considering this research, observed theta effects in the present task could potentially be indicative of the greater allocation of attention driven effects observed in high value compared with low value conditions in the value and memory-based conditions. Further analysis of spectral dynamics during encoding of value in serial positions task could help to further understand the specific process of value-driven theta-desynchronization and alpha-desynchronization through examination of spectral differences of subsequent value effects interacting with known primacy and serial load effects.

ERSP maps were also examined for high value, low value, and combined high and low value for a conditional breakdown of subsequent remember/know during encoding. A direct limitation to these comparisons is the disproportionate responses for high values compared with low values for recollection and familiarity responses. The behavioral data indicated the effect of value was on recollection alone with no effect on familiarity seen in other VDR studies (Adcock et al., 2006; Elliott et al., 2020). Participants exhibited value-driven gain in “remember” responses with no influence on “know” responses. Linear trend analysis showed a significant interaction of response type with value, revealing accuracy of remember responses alone increased as a function of value (Elliott et al., 2020). While the disproportionate results limit inferences, a possible future route of exploration could be to decouple value-based effects from memory-based effects utilizing a VDR subsequent recognition memory paradigm and neuroimaging.

In decoupling the effects of value and memory, the distinction of the alpha-band desynchronizations for value-based trials to a more restricted latency compared to the more sustained alpha desynchronization accompanied by beta and theta differences are considered. While numerous strategies are known to contribute toward successful memory such as rote rehearsal (repetition), elaborate rehearsal, and others, it is of interest which specific processes lead to value-driven effects. While models of elaborate rehearsal have been proposed to explain the observed value-driven effects, the current results do not seem to provide evidence in support of this view; however, the full picture of value-driven gain is yet to conclude. It could be that different contexts of value elicit differential encoding strategies (Knowlton et al., 2022). It is certain however, that mental processes have limited capacity which forces memory to be selective in how information is prioritized in a specific way. Consistent with the behavioral results, participants exhibited greater alpha-desynchronization for high value items, sharing similar temporal dynamics to the P3 component. These results overall support the preferential allocation of attentional resources via reward-driven dopaminergic-mid brain hypothesis. Value can certainly influence memory gains; however, there is a specific way in which it can augment cognitive processes leading to enhanced encoding of information.

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