

6-2-2016

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Kamp, Siri-Maria; Lehman, Melissa; Malmberg, Kenneth J.; and Donchin, Emanuel, "A Buffer Model Account of Behavioral and ERP Patterns in the Von Restorff Paradigm" (2016). *Psychology Faculty Publications*. 2390.
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Research article

A Buffer Model Account of Behavioral and ERP Patterns in the Von Restorff Paradigm

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Abstract: We combined a mechanistic model of episodic encoding with theories on the functional significance of two event-related potential (ERP) components to develop an integrated account for the Von Restorff effect, which refers to the enhanced recall probability for an item that deviates in some feature from other items in its study list. The buffer model of Lehman and Malmberg (2009, 2013) can account for this effect such that items encountered during encoding enter an episodic buffer where they are actively rehearsed. When a deviant item is encountered, in order to re-allocate encoding resources towards this item the buffer is emptied from its prior content, a process labeled “compartmentalization”. Based on theories on their functional significance, the P300 component of the ERP may co-occur with this hypothesized compartmentalization process, while the frontal slow wave may index rehearsal. We derived predictions from this integrated model for output patterns in free recall, systematic variance in ERP components, as well as associations between the two types of measures in a dataset of 45 participants who studied and freely recalled lists of the Von Restorff type. Our major predictions were confirmed and the behavioral and physiological results were consistent with the predictions derived from the model. These findings demonstrate that constraining mechanistic models of episodic memory with brain activity patterns and generating predictions for relationships between brain activity and behavior can lead to novel insights into the relationship between the brain, the mind, and behavior.

Keywords: Episodic memory; event-related potentials; Von Restorff effect; buffer model; free recall

1. Introduction

Lehman and Malmberg [1,2] recently proposed a mechanistic model of episodic memory, which posits that a multidimensional memory trace that consists of item, context, and associative features is episodically encoded when an item is studied. The contents and nature of the memory traces are influenced by two control processes that operate upon the information representing the items being studied: (1) *rehearsal* maintains item representations in an active state [3], and (2) *compartmentalization* removes an item from a state amenable to encoding [2]. As in the Atkinson and Shiffrin model [3], the goals and tasks demands of the subjects influence the number of items rehearsed, which items are compartmentalized and when, and the manner in which they encoded. In the present study we combined this model with theories on the functional significance of two event-related potential (ERP) components and tested an interpretation of the behavioral and ERP patterns in the “Von Restorff paradigm” [4] derived from the model.

According to the buffer model, the number of items that are co-rehearsed has important implications for how and to what extent new memories are formed. When items are co-rehearsed, memories representing their individual occurrence also represent their co-occurrence in the form item-to-item associations. If several items are rehearsed simultaneously, resources for encoding item and context features are divided among traces being formed, leading to weaker contextual representations than if only one item is in the buffer. The fewer items rehearsed, the stronger the inter-item associations will be. Rote rehearsal is a special case in which a single item is rehearsed, perhaps resulting in no item-to-item associations, and weak item-context associations. Elaborative rehearsal, in contrast, may involve encoding inter-item associations among list items, as well as extra-list items generated by access to general knowledge. Thus, the relative strengths with which item, context, and associative information are encoded depend on the nature of the encoding task, the goals of the subject and prior knowledge, among other factors.

Three characteristics of the model are worth emphasizing with respect to free recall, where the subject recalls items from a study list in any order they choose. First, it is assumed free recall is initiated with a retrieval cue consisting of a representation of the study list context only because no other cues are available to the subject. The greater the match between the retrieval cue and contents of a memory trace, the more likely the trace is to be retrieved (e.g., [5]). For delayed free recall, the context in the trace representing the first item on the study list tends to match the context in the retrieval cue better than context stored in any other trace, because the first item on the study list is rehearsed by itself initially and therefore is most strongly associated with study context. This mechanism accounts for the primacy effect in free recall [1].

Second, items in adjacent study positions tend to be rehearsed simultaneously unless there is reason for them to be processed as individual stimuli. Last, temporal context is assumed to change only slowly over time, and therefore traces of items encountered quickly one after another contain

features of the same, or a very similar, context. The result is that temporal contexts may associate relatively large numbers of traces stored in memory.

The buffer model of encoding was tested by Lehman and Malmberg [1], who observed that patterns of free recall are influenced dramatically by the temporal dynamics of the study list. For example, when subjects are presented with items one at a time, they tend to rehearse several items simultaneously, creating a series of traces related via their contextual and associative similarity. However, when subjects study pairs of items, subjects tend to rehearse the pair and compartmentalize that pair when the next pair is presented, creating memory traces in which only two items are associatively related.

1.1. Behavioral predictions for the Von Restorff paradigm

In the Von Restorff paradigm, a series of items are studied, but one item may be distinguished based on its physical or semantic characteristics. For instance, items from the category “fruit” may constitute all but one item of the study list, and the remaining item is a member of the category “animals”. Typically, subjects are more likely to freely recall this “isolate” compared to the other list members (“standards”), as well as compared to the same item placed within a list in which it is not deviant, for example the word “elephant” in a list of several animals.

The Von Restorff effect is interesting to consider within the framework of the buffer model: Is the isolate treated like the standards during encoding or does the isolate result in the compartmentalization of the prior study items? Prior results suggest that that subjects would tend to continually rehearse items creating associative relationships between a long series of memory traces prior to the isolate. If the isolate is treated just like the prior items then the associative chain would continue. If this is this case, it is unclear how the buffer model accounts for Von Restorff effect. On the other hand, if the isolate results in compartmentalization of the prior items then this associative chain would be disrupted, and it is possible that the trace representing the isolate would only be contextually, but not associatively, related to the traces representing the standards. If consistently so across trials and subjects, the isolate is in effect treated like the first item on the study list, and the Von Restorff effect is accounted for in a similar way as primacy via stronger item-to-context association for isolates than for standards. As a result, if prior items were being rehearsed, some or all of the resources devoted to encoding their occurrence should be allocated to the isolate. This is consistent with the notion that the presentation of the isolate, as a novel event, captures the attention of the subject, perhaps because there is an adaptive advantage to identifying unexpected stimuli (e.g., [6,7]). Hence, upon the encounter with the isolate, rehearsal of the prior items is halted (compartmentalization) in order to devote resources to encoding item and context features of the novel information. Together, these factors result in the enhanced probability to recall the isolate.

The latter model therefore makes two predictions for free recall patterns in this paradigm. First, similarly to the first item [1], a stronger link to its encoding context may lead to an enhanced probability to recall the isolate first (if this context is used to cue recall). Notably, lists of the Von Restorff type have both an isolate and an item in the first position, so which item is recalled first

should depend on retrieval strategies: To cue recall, some subjects may reinstate the encoding context of the isolate, while others may use the context of the beginning of the list. In other words, individual differences in these output patterns are to be expected. Which strategy participants use to cue recall should also be associated with other behavioral outcomes, such as the total number of words recalled from a list (see also [1]). Secondly, if the buffer is emptied upon its encounter, the isolate should not be rehearsed simultaneously with the items that preceded it, resulting in a reduction in the item-to-item associations stored between the isolate and the preceding items. Therefore, the isolate should be less likely to be recalled immediately after the item that preceded it at encoding, compared to regular words in similar serial positions.

It is worth noting that these ideas do not directly conflict with existing theories on the Von Restorff effect, such as Hunt and Lamb's proposal [8] that differences between the isolate and other items as well as similarities among the remaining list items must be processed in order for a Von Restorff effect to occur. In fact, this idea is entirely consistent with the predictions from the model: On the one hand, if the isolate was not processed as different, subjects would not re-direct processing resources towards it. On the other hand, if the subject used a strategy that leads to rehearsal of single items rather than a (perhaps similarity-processing based) strategy of co-rehearsing multiple items, compartmentalization would be elicited after each individual item so the isolate would not be encoded differently from any other list item. The model is, however, distinguished from Hunt and Lamb's proposal by positing a specific mechanism invoked during the presentation of the list and upon encoding of the isolate, which may lead to the Von Restorff effect.

Taken together, the Von Restorff paradigm provides an excellent opportunity to test predictions from the model. A further advantage is that ERP patterns elicited in this paradigm have been well characterized in prior research and can therefore be integrated with the mechanisms of the model.

1.2. *ERPs as Indices of Rehearsal and Compartmentalization*

1.2.1. P300, Context Updating and Compartmentalization

Further insights can be gained by examining ERP components that, based on a wealth of prior research, are likely neural indices of the two control processes of the buffer model. Thus, the P300 [9] is a parietal positivity elicited by events that violate expectancies (for a review, see [10]). According to the "context updating hypothesis", the P300 occurs when incoming information is at odds with an internal schema of all currently relevant information, and consequently the schema is updated [10,11]. The overlapping terminology illustrates the conceptual parallel of P300 function to the encoding context in the buffer model. In the Von Restorff paradigm, encoding context may thus change, resulting in the need for updating, when a novel or unexpected event like the first list item or the isolate occurs. If so, both the first item and the isolate should elicit a P300, and there is indeed some evidence supporting this [12,13]. Taken together with the reasoning outlined in the previous section, context change should signal the subject to compartmentalize in order to devote resources to encoding the new information. As in the buffer model this leads to a strong item-to-context

association, if the respective context is used to probe recall, larger P300 amplitudes should be correlated with a higher probability to initiate recall with the isolate (or the first item in a list) that elicited the P300. On the other hand, P300 amplitude is inversely correlated with the subjective probability of the eliciting event [14], and varies with the allocated attentional resources [15]. Thus, if the buffer is emptied upon encounter with the isolate in order to allocate encoding resources to it, and if this is reflected by P300 amplitude, then larger P300 amplitudes should index reductions in inter-item associations between the isolate and the preceding list items. Therefore, larger P300 amplitudes should be associated with a lower probability of recalling the isolate immediately after the item that preceded it at encoding.

1.2.2. Slow Waves and Rehearsal

ERP slow waves are sensitive to the working memory load imposed by a task [16,17], and their scalp distribution depends on the type of information held active [18] (for a review, see [19]). Thus, when sequences of meaningful stimuli are to be held in an active state, for example when sentences are presented word by word [20], or sequences of object-location combinations are encoded into working memory [21], frontally distributed negative-going frontal slow waves increase in amplitude as the sequence progresses. In episodic encoding tasks, frontal slow waves may thus index maintenance- and control processes underlying the formation of associative links between items: More positive-going slow waves are typically elicited by subsequently episodically retrieved, versus not retrieved, item pairs [22–24]. Furthermore, in sequentially presented word lists, amplitudes of frontal slow waves are correlated with subsequent free recall [12,25,26], a test format that relies heavily on item-to-item associations [1,27,28]. Taking these patterns together, ERP slow waves developing over the course of the list as words enter the buffer are an obvious candidate to index the rehearsal process, which in the model is responsible for the encoding of item-to-item associations. It is important to note that it is not necessary to assume that the slow wave is directly indicative of the rehearsal process. It is also quite possible, and even likely, that its functional significance lies within some other cognitive process that, through its effect on the rehearsal mechanism, influences encoding of associations. Regardless, the slow wave should be more pronounced when associative encoding is active.

If the idea is correct that the slow wave co-varies with the encoding of associations through the rehearsal mechanism, then slow wave amplitudes should progressively increase over the course of the list until the capacity of the buffer is reached (which for visual information may be after 4–6 items [29]). Furthermore, its amplitude should differ between lists in which subjects subsequently recall many words, compared to only a few. Finally, slow wave amplitudes should correlate with the extent to which associations are formed between items rehearsed simultaneously, and should therefore predict the sequential retrieval of items that were studied in adjacent serial positions.

1.3. *The Present Study*

We tested these behavioral and ERP predictions by re-analyzing data we collected in two prior experiments [30,31], in which subjects encountered sequentially presented word lists of the “Von Restorff” type while their EEG was recorded. Immediately after each list, subjects freely recalled all words they remembered.

2. Materials and Methods

All procedures were in line with the Declaration of Helsinki. The USF Institutional Review Board approved all procedures and all subjects provided informed consent.

2.1. Subjects

A combination of data from two prior studies resulted in sufficient artifact-free ERP data from 45 native English speakers. Their age ranged between 18 and 45 years ($M = 22.2$), 15 were male and 4 were left-handed.

2.2. Study Lists

In addition to the word lists of the “Von Restorff” type that are of interest for the present study, the experiments contained lists of varying word frequencies ($n = 24$, [30]) or emotional content ($n = 21$, [31]), which are not reported here. The “Von Restorff lists” contained 15 words that were between 3 and 8 letters long and of medium frequency (10–50 lemma occurrences per million; [32]). One word in each list, placed randomly between serial positions 6–10 in order to avoid interactions with primacy and recency effects and for the purpose of consistency with prior studies [12,25,26], was displayed in a larger font than the other words (the “isolate”). The other words from the Von Restorff lists are here referred to as “standards”. In prior ERP studies using the Von Restorff paradigm, isolates were compared to standards as well as to control words that came from lists in which no isolates were included [12]. Since the results for the standards were comparable to the control words, in the present report we compare isolates only to standards from the Von Restorff lists.

Words were presented one at a time in white Arial font on a black background for 250 ms and a fixation cross was displayed for 2000 ms between two words.

2.3. Procedure

Subjects were asked to memorize each list by silently rehearsing the words, and immediately after the end of each list subjects were signaled by the onset of a grey triangle to write down all words they could remember in any order. There was no distractor task in between encoding and recall. The recall phase lasted at least 45 seconds, but there was no upper time limit for recall. A total of 40 word lists in the first session, and either 30 (experiment 1) or 40 (experiment 2) lists in the second session, were studied. Of these, a total of 20 were “Von Restorff lists”, which were randomly

interspersed among the other list types. At the beginning of the first session subjects completed two practice lists. Self-paced breaks were allowed after each set of 5 lists.

2.4. *Analysis of Behavioral Data*

Behavioral measures were calculated for all serial positions and analyzed separately for the primacy (1–5), plateau (6–10) and recency (11–15) positions, as well as for isolates.

2.4.1. Recall rates

Recall rates represent the proportion of words that were successfully retrieved in the test phase.

2.4.2. Conditional recall probabilities (CRPs)

CRPs are an index of the contribution of item-to-item associations to recall: They represent the probability with which items that are recalled at adjacent output positions were also studied in adjacent serial (input) positions. For example, the CRP at lag 1 represents the probability that, given that an item is successfully recalled, it is output immediately after the item that occupied its preceding serial position at study (for more detail, see [1,28]).

2.4.3. First recall probabilities (FRPs)

FRPs represent the conditional probability that, given that an item was successfully recalled, it was recalled in the first output position.

We further explored individual differences in FRPs. As outlined in the introduction, Von Restorff lists have both a first word and an isolate and subjects may differ in the extent to which they use the two contexts to cue recall. Therefore, we created two groups of subjects that were either more likely to begin recall with the first word ($n = 21$), or to begin with the isolate ($n = 17$; the division was done by determining whether FRPs were higher for isolates or words in position 1 while disregarding all other serial positions). Seven subjects who exhibited FRPs of zero for both isolates and the first word, were disregarded in this analysis.

2.5. *EEG Recording and ERP Analysis*

The EEG was recorded with a 128-channel hydrocel EGI system (Eugene, OR), amplified at 0.01 to 100 Hz, digitized at 250 Hz, and referenced to electrode Cz. Off-line, bad channels were replaced by mathematical interpolation. Using self-written Matlab code, we conducted two ERPs analyses, the first one to analyze the P300, and the second one to quantify frontal slow waves. To insure comparability to prior results in paradigms with similar logic, the P300 analysis used principal component analysis (PCA; [30,31]), while in the slow wave analysis we calculated mean amplitudes [20,21].

2.5.1. P300

The EEG was band-pass filtered at 0.3–20 Hz and cut into segments of 300 ms before to 1200 ms after the onset of words in serial positions 1–10. Eye blinks were removed by independent component analysis implemented in J. Dien’s toolbox [33]. Then, subject ERP averages were calculated for isolates (collapsed over serial positions) and standards (separately for serial positions 1–10) based on only artifact-free trials, re-referenced to linked mastoids and baseline corrected. Then, we submitted to a spatio-temporal PCA [34] all subject ERPs of the 11 word types. Twenty spatial factors with six temporal factors each were extracted, accounting for a total of 88% of the variance in the data. For the spatial PCA step, we calculated “virtual ERPs”, the temporal progression of factor scores over time for each trial type of interest [34]. Virtual ERPs can be conceptualized as ERP activity that is associated with a specific spatial PCA factor. In both PCA steps we used Promax rotations without Kaiser normalization. In the present manuscript we only report the spatial factor (SF) whose spatio-temporal characteristics correspond to the P300.

2.5.2. Frontal Slow Wave

The EEG was low-pass filtered at 10 Hz and cut into segments of 1000 ms before the onset of the first word to 2250 ms after the onset of the last word of each list. The segments were re-referenced to linked mastoids and baseline corrected, and artifactual segments were excluded (artifact detection and rejection was done separately for the P300 and the slow wave analysis). For each participant, the lists were divided into “high recall” and “low recall” lists by performing a median split on the number of words recalled per list, and ERP averages were calculated for a frontal electrode cluster centered around Fz (EGI hydrocel electrodes 4, 5, 10, 11, 12, 16, 18, 19). For statistical analysis we averaged the amplitudes separately for three time windows, spanning the presentation of the first five words (primacy positions; 0–11.25 s), words 6–10 (plateau), and words 11–15 (recency).

In an additional analysis, the slow wave in each of the three time windows was baseline corrected using the 1000 ms preceding the onset of the respective time window. The goal of this analysis was to examine the increase of the slow wave within the primacy, plateau, and recency positions separately.

2.6. *Statistical Analysis*

To analyze these dependent measures, we conducted paired samples t-tests and ANOVAs. A Greenhouse-Geisser correction was applied when the assumption of sphericity was violated.

3. **Results**

3.1. *Behavioral data*

3.1.1. Recall Rates

There was a recall advantage for standards in the primacy, $t(44) = 6.87, p < 0.01, d = 1.02$, and the recency, $t(44) = 10.67, p < 0.01, d = 1.59$, compared to the plateau positions of the list (Figure 1A, left panel). Isolates were recalled at a higher probability than standards in the plateau positions, $t(44) = 7.33, p < 0.01, d = 1.09$: The Von Restorff effect.

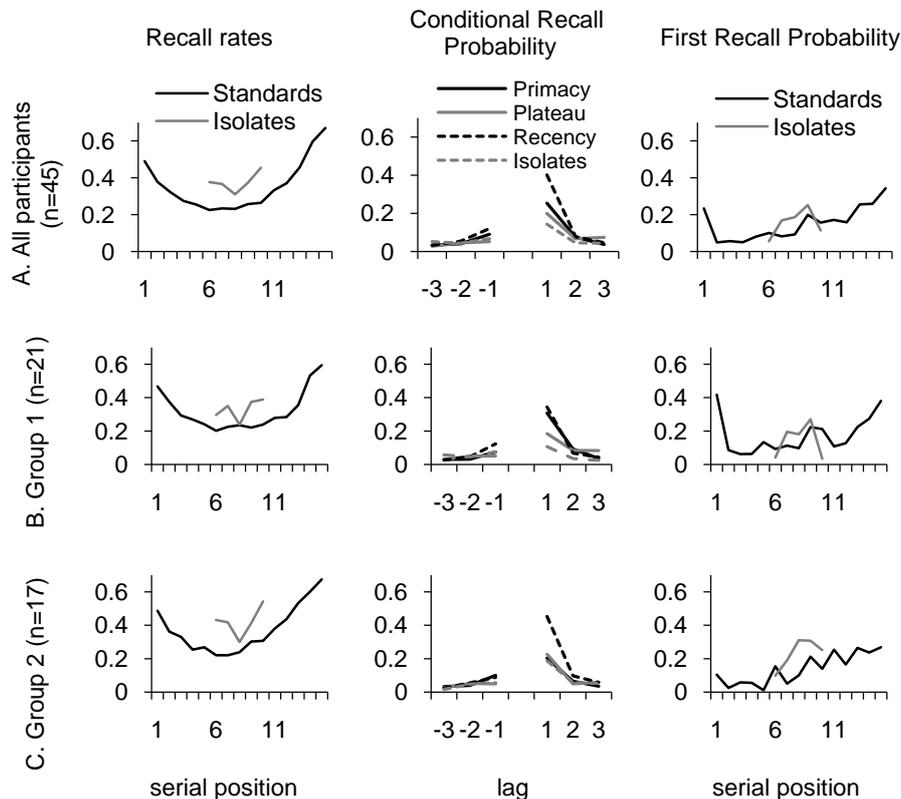


Figure 1. Behavioral data. Left panels: serial position curves of recall probabilities. The horizontal axis shows the input position within the list, the vertical axis the proportion of words recalled. Middle panels: conditional recall probabilities depending on study list position and word type. The horizontal axis indicates a given lag. For example, lag 1 means that a word was recalled immediately after the word that preceded it at encoding, while lag -1 means that a word was recalled after the word that followed it at encoding. The vertical axis displays the probability of recall at a given lag. Right panels: first recall probabilities. The horizontal axis shows the input position within the list, the vertical axis the proportion of words recalled from this serial position in the first output position. (A) Data for the entire sample. (B) Data for the group of participants that tended to begin recall with the first study word. (C) Data for the group of participants that tended to begin recall with the isolate.

3.1.2. CRPs

Subjects were more likely to recall words at adjacent output positions when they were encoded at adjacent input positions, with a tendency toward forward (lag 1) over backward (lag-1) transitions

(Figure 1A, middle panel). This pattern was evident in all analyses, but the CRP at lag 1 was higher for words studied in the recency- than the primacy and plateau positions. In support of this, an ANOVA with the factors study position (primacy vs. middle vs. recency) and lag (6 levels: -3 to 3) revealed two main effects [study position: $F(1.67,73.66) = 37.06, p < 0.01, \eta^2 = 0.46$; lag: $F(1.89,81.73) = 127.16, p < 0.01, d = 0.74$] and an interaction, $F(3.98,175.05) = 14.54, p < 0.01, d = 0.25$.

Importantly, the CRP at lag 1 (but not at lag -1) was reduced for isolates compared to standards in the plateau positions, that is, standards in comparable serial positions as the isolates (Figure 1A, middle panel; Figure 2): A 2 (isolate vs. standard) by 6 (lag) ANOVA supported this by two main effects [word type: $F(1,44) = 12.61, p < 0.01, \eta^2 = 0.22$; lag: $F(3.76,165.49) = 3.14, p = 0.02, \eta^2 = 0.07$] and an interaction, $F(5,220) = 10.8, p < 0.01, \eta^2 = 0.2$. This indicates that, whereas standards were likely to be recalled following recall of standards studied in close temporal proximity, isolates were far less likely to be retrieved after the standards that preceded them in the study list.

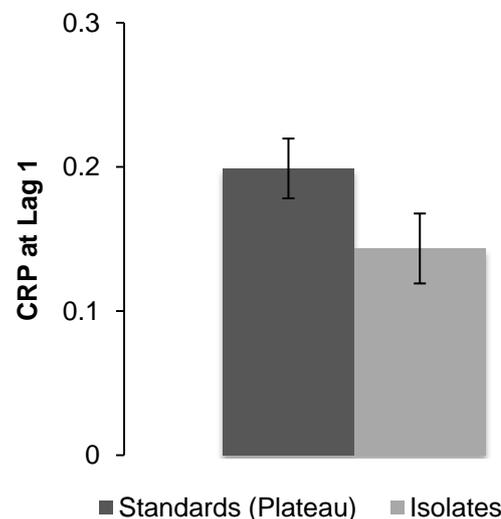


Figure 2. Conditional recall probabilities at lag 1 for isolates and standards in the plateau positions. An isolate is less likely to be recalled after the word that preceded it at encoding than a standard in a similar serial position. Error bars represent the standard error of the mean.

3.1.3. FRPs

Words were more likely to be recalled first when they were studied in the recency, compared to the plateau, positions, $t(44) = 5.72, p < 0.01, d = 0.85$ (Figure 1A, right panel). Furthermore, there was an increased probability to begin recall with the first, compared to second word, $t(44) = 5.48, p < 0.01, d = 0.82$. For the whole sample, the FRP for isolates did not differ from the standards in the plateau positions ($t < 1.35$). This suggests that in the whole group, context cues used to initially probe memory tended to consist of context features that were present when recall was initiated or

reinstated context features associated with the conditions present during the early portion of the study list.

3.1.4. Individual Differences

The group of subjects that tended to begin recall with the first word (group 1; Figure 1 B, right panel) exhibited a larger FRP for serial position 1 than 2, $t(20) = 6.22$, $p < 0.001$, $d = 1.36$, but FRPs did not differ between isolates and standards in the plateau positions ($p = 0.29$). The group that tended to begin recall with the isolate (group 2; Figure 1 C, right panel) exhibited significantly larger FRPs for isolates than standards in comparable serial positions, $t(16) = 4.07$, $p < 0.001$, $d = 0.99$, as well as for position 1 compared to position 2, $t(16) = 3.07$, $p < 0.01$, $d = 0.74$. Notably, both groups exhibited larger FRPs for the recency- than the plateau positions (both $p < 0.01$).

Recall rates (Figures 1B and C) in the primacy- and plateau positions did not differ between the groups (both $t < 1.36$). However, compared to group 1, group 2 exhibited a recall advantage for the isolates, $t(16) = 2.53$, $p < 0.01$, $d = 2.53$, and words in the recency positions, $t(16) = 2.88$, $p < 0.01$, $d = 2.88$ (Figures 1B and C, left panels). Finally, group 1 exhibited higher CRPs in the primacy, while group 2 exhibited higher CRPs in the recency, positions (Figures 1B and C, middle panels). Accordingly, a mixed ANOVA with the factors list portion (primacy vs. recency) and group revealed an interaction, $F(1,36) = 10.84$, $p < 0.01$, $\eta^2 = 2.3$. CRPs at lag 1 for isolates or standards in the plateau positions did not differ between groups ($t < 1.5$).

3.1.5. Summary and Discussion: Behavior

Isolates showed a recall advantage over the standards, but an isolate was less likely than a standard to be recalled immediately after the item that preceded it at encoding. The model can therefore explain the Von Restorff effect in free recall such that upon encounter with the isolate the buffer is emptied of its prior content. Our prediction that due to a strong item-to-context association, subjects tend to use the context of the isolate as a retrieval cue and therefore FRPs will be enhanced for the isolate, was not supported in the whole group. However, there were individual differences in retrieval patterns, revealing that subjects differed in the extent to which they used the beginning-of-the-list context (group 1) vs. the context of the isolate (group 2) to probe recall. A strengthened item-to-context association may therefore indeed be encoded for the isolates, but it only leads to enhanced FRPs if concordant retrieval strategies are used.

Importantly, the two strategy groups differed on other recall patterns as well. The relative enhancement of CRPs for the primacy- and recency positions in groups 1 and 2, respectively, suggests that the word that is recalled first serves as an “anchor” to probe recall of the words that followed it: Recalling the first word first leads to “chained” recall in the primacy positions, while recalling the isolate first leads to a “chain” of recall that extends into the recency positions. Furthermore, group 2 demonstrated higher recall rates for isolates and words in the recency positions. This is in line with prior reports that initiating immediate free recall with the first word of the list is

not the most successful recall strategy [1]. The performance advantage for isolates of those subjects who began recall with the isolate further supports the idea that compartmentalization occurred with the presentation of the isolate and contributed to the improved recall of the isolate. The enhanced FRPs for both isolates and words in position 1 point to a reason for group 2's superior recall: In addition to the end-of-the-list context and beginning-of-list contexts (which both groups used), only group 2 had the context of the isolate available to flexibly cue recall.

We next investigated the P300 and frontal slow wave as potential physiological indices of the context updating/compartmentalization and the rehearsal mechanisms. To reiterate the hypotheses, as a correlate of context updating and therefore of compartmentalization, the P300 should be elicited by words in position 1 and by isolates. As a consequence of this process, associations to the item preceding the isolate should be reduced and P300 amplitude elicited by the isolate should be negatively correlated with the CRP at lag 1. On the other hand, the frontal slow wave should differ between lists in which subjects recall many words as opposed to few. Furthermore, as an index of simultaneous rehearsal of multiple items, its amplitude should be correlated with CRPs in the corresponding serial positions. With regard to the two strategy groups, if ERP amplitudes differ between the groups, this would indicate that different encoding mechanisms are engaged. However, if there is no evidence for ERP differences, the behavioral differences are likely due to differences in retrieval strategies rather than encoding mechanisms.

3.2. *Event-related potentials*

3.2.1. P300

Spatial factor 4 exhibited the parietal scalp distribution of the P300 (Figure 3). Its virtual ERPs [34] exhibited a positive peak 600 ms after word onset, captured by temporal factor 2. Both isolates, $t(44) = 3.98$, $p < 0.01$, $d = 0.59$, and words in serial (input) position 1, $t(44) = 3.35$, $p < 0.01$, $d = 0.5$, but not words in serial (input) position 2 ($t < 0.81$) elicited larger P300 amplitudes than standards in the middle serial positions. P300 amplitude did not differ between isolates and words in position 1 ($t < 0.42$), and there were no differences between the strategy groups in P300 amplitude for either word type (both $t < 0.57$).

Importantly, the P300 elicited by the isolates¹ negatively correlated with the CRP for isolates at lag 1, $r(43) = -0.29$, $p < 0.05$, but not at lag -1 ($|r| < 0.1$). This indicates that subjects with larger P300 amplitudes were less likely to produce the isolate immediately after the standard that preceded it at encoding than subjects with smaller P300 amplitudes (Figure 5A). Although there was a tendency for the negative correlation to be especially strong for group 2 (which also tended to initiate recall with the isolate; $r(15) = -0.52$), the correlation coefficient did not significantly differ between the strategy groups.

¹ Each participant's P300 was calculated by subtracting the amplitude for standards in the middle serial positions from the amplitude elicited by the isolates.

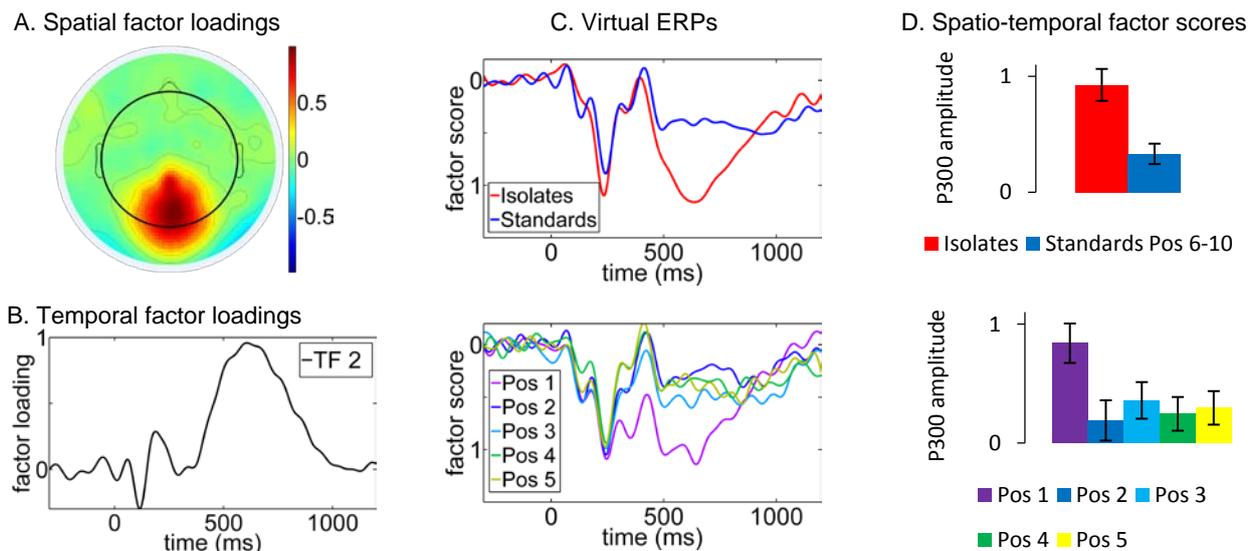


Figure 3. PCA factor representing the P300. (A) Spatial factor loadings, indicating the spatial distribution of the factor that captures the P300. (B) Temporal factor loadings, indicating the time course of the temporal factor that represents the P300. (C) Virtual ERPs (ERP activity corresponding to the spatial factor capturing the P300) for the word types of interest. (D) spatio-temporal factor scores, as a measure of P300 amplitude, for the word types of interest. Error bars represent the standard error of the mean. Note. Pos = serial (input) position.

3.2.2. Frontal Slow Wave

The ERPs at the frontal electrode cluster were characterized by a negative-going slow wave that increased over the course of the list (Figure 4A): In support of this, a 3 (time window) by 2 (low-vs. high recall list) ANOVA on the mean amplitudes revealed an effect for time window, $F(1.21, 53.06) = 11.98$, $p < 0.01$, $\eta^2 = 0.21$. The slow wave appeared to differ between lists from which subjects recalled many (“high recall”), compared to few (“low recall”) words (Figure 4), but the main effect for recall level was not significant, $F(1, 44) = 3.68$, $p = 0.068$, $\eta^2 = 0.08$. Figure 3A suggests that only in the first time window (covering serial positions 1–5) the slow wave for low recall lists increased more steeply than for the high recall lists, while subsequently the slow waves converged and then evolved in parallel. To test this, we re-calculated the ANOVA after baseline correcting the amplitudes for the middle- and the late time windows, using as baselines for each window the preceding 1000 ms (Figure 4B). Indeed, the ANOVA revealed an interaction, $F(1.72, 75.52) = 4.9$, $p < 0.05$, $\eta^2 = 0.1$: The slow wave was larger for low- than for high recall lists in the first time window, with the reverse pattern in the second, but no difference in the third time window (Figure 4B). The magnitude of the difference did not differ between the two sub-groups in any time window ($p > 0.19$).

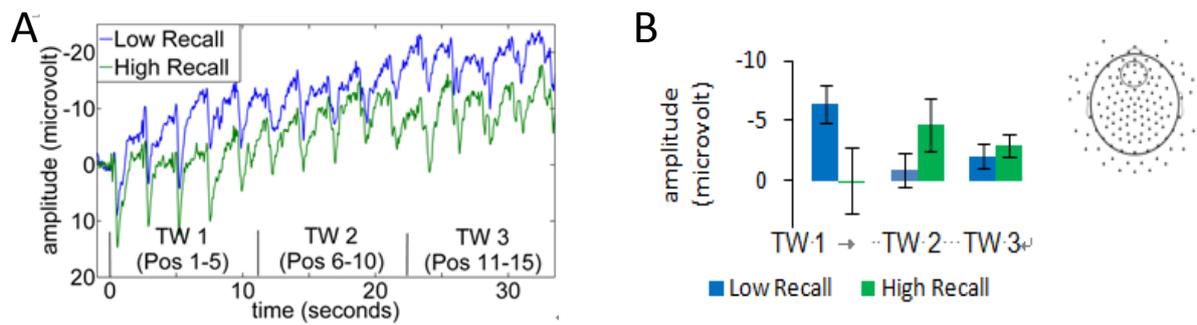


Figure 4. Frontal slow wave. (A) Grand average ERPs across the study list for high- and low recall lists at the frontal electrode cluster. Words were presented every 2.25s; the positive peaks therefore represent stimulus-locked activity. (B) Baseline-corrected mean amplitudes in the three time windows. Error bars represent the standard error of the mean.

Furthermore, the overall amplitude of the frontal slow wave in the late time window (relative to the baseline of 1000 ms before the onset of the first word of the list) negatively correlated with the CRP at lag 1 for words in the recency positions, $r(43) = -0.39$, $p < 0.01$ (Figure 5B). This indicates that larger slow wave amplitudes were associated with a higher probability of recalling items in a similar sequence to the order in which they were presented at encoding, at least for words in the recency positions.

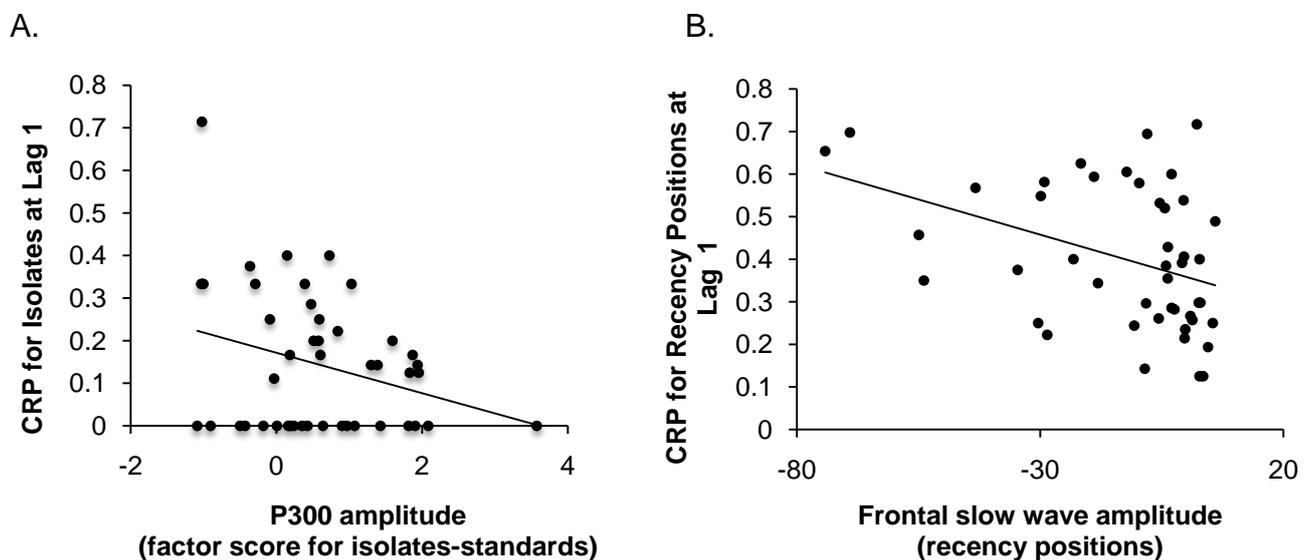


Figure 5. Scatter plots of (A) P300 amplitude elicited by isolates and the CRP at lag 1 for isolates and (B) frontal slow wave amplitude in the recency time window and CRPs at lag 1 for standards in the recency positions.

3.2.3. Summary and Discussion: ERPs

Isolates and words in position 1 elicited a P300, which according to the context updating hypothesis suggests that context change was elicited upon their encounter. Subjects with larger P300 amplitudes for the isolates were less likely to produce the isolate after the standard preceding it during encoding, providing some physiological evidence for the elicitation of the compartmentalization process purposed at directing attentional resources away from encoding the preceding items and toward encoding the isolate, while at the same time validating the assumption that this process is indexed by the P300.

Negative-going frontal slow waves developed over the course of the list and differed between lists in which subjects recalled many items compared to only a few. Their amplitudes increased faster for low- than high recall lists in the primacy positions, but in the middle positions, slow waves elicited in high recall lists converged with those of the low recall lists. Finally, participants with larger overall slow wave amplitudes exhibited higher CRPs, that is, they were more likely to show “chained” recall of words in the recency positions. This correlation further suggests that this ERP component is, as hypothesized, an index of the rehearsal process of the model.

There were no significant differences between groups 1 and 2 in ERP amplitudes, so there is no evidence that during encoding the isolate or other words were processed differently by the two groups. Therefore, the behavioral group differences may reflect differences in retrieval strategies rather than encoding processes.

4. Discussion

Combining the buffer model [1] with theories on the functional significance of the P300 and frontal slow wave components of the ERP, we developed an integrated model of the Von Restorff effect resulting in specific predictions for behavioral and ERP patterns in the paradigm. Behavioral and psychophysiological indices of episodic encoding generally supported these predictions. The buffer model thus accounts for the enhanced recall of the isolate by assuming that compartmentalization occurs upon the encounter of unexpected events. Our results support this, on the one hand, by demonstrating a reduced probability of recalling the isolate immediately after the item preceding it at encoding. On the other hand, a subset of the subjects exhibited a tendency to initiate recall by producing the isolate, and these subjects also exhibited better recall for the isolate than the other strategy group. Taken together, item-to-context associations appear to be strengthened for the isolate, and this mechanism may account for the Von Restorff effect in recall rates.

The P300 and the frontal slow wave patterns are consistent with their use as an index of the operations of the episodic buffer and therefore provide a means to “observe” its operations more directly than merely inferring them from output patterns. Next, we will discuss the ERP results in the light of the behavioral results and prior theory on their functional significance, and most importantly, the implications for the buffer model.

4.1. P300

The elicitation of a P300 suggests that the first word and the isolate elicited a context change. All but 7 subjects exhibited enhanced FRPs for one of these word types, indicating that they, at least in some lists, reinstated the respective context to initiate recall. There was no correlation between P300 amplitude and FRPs, so the magnitude of the context change (although it should according to the theory be correlated with compartmentalization and thus the strength of the item-to-context association) did not impact which context was reinstated during recall. Rather, this may be a strategic choice.

CRPs at lag 1 were reduced for the isolate and were negatively correlated with P300 amplitude. In other words, participants were less likely to produce the isolate immediately after the item that preceded it at encoding, compared to standards in similar input positions, and this tendency was even stronger for participants with larger P300 amplitudes. This is consistent with the idea that the P300 co-occurred with the compartmentalization mechanism posited by the model. However, isolates still exhibited enhanced CRPs at lag 1 compared to other lags, suggesting that to some extent associations with the preceding items had still been formed. With regard to the model this implies that compartmentalization is not always, or not completely, initiated when an isolate occurs, or that factors other than compartmentalization also contribute to the Von Restorff effect.

Many prior studies have shown that P300 amplitude elicited by isolates in the Von Restorff paradigm is correlated with subsequent recall success [12,25,26,30,35,36]. Our results strengthen the idea that P300 indexes a cognitive process that is in certain circumstances relevant for episodic encoding [10,11]. More precisely, the present study links the P300 to the roles of encoding context and compartmentalization in the buffer model. Our results therefore open a path for further empirical exploration of the precise circumstances under which the process indexed by the P300 is relevant for episodic encoding.

Notably, although isolates and words in serial position 1 elicited a P300, the ERPs also exhibited differences (Figure 2): For example, words in serial position 1, but not isolates, elicited an attenuated N400 [37]. Therefore, the conclusion to be drawn from these data is not that the first word and isolates elicit the same set of cognitive processes, but rather that context updating and compartmentalization are common to both.

4.2. Frontal Slow Wave

Most prior studies that have reported frontal slow waves in episodic encoding tasks cut the continuous EEG into segments around the presentation of one or two individual stimuli, resulting in the analysis of relatively small ERP time windows. By contrast, studies that have analyzed working memory processes in object-location encoding [21] or sentence comprehension [20] tasks have reported slow waves developing over longer sequences of stimuli. The present study demonstrates that such slow waves are also evident in episodic encoding tasks over the course of entire lists. This may reflect the increasing effort of rehearsal as items enter the buffer until its capacity is reached.

In the initial serial positions, less negative-going slow waves were observed for lists from which subjects recalled more words than their median recall level. It appears that lists of which subjects can recall many items are characterized by a more efficient use of the buffer, resulting in a slower rise of the negativity. Differences in rehearsal effort disappear when the capacity of the buffer is reached, resulting in convergence of the slow waves between high and low recall lists after the primacy positions. However, according to this logic, high and low recall lists should begin to diverge again as items are added to the buffer after compartmentalization due to the occurrence of the isolate. There was, however, no evidence for such a pattern (Figure 4), which may in part be due to the temporal variance of the onset of compartmentalization, induced by the random placement of the isolate between positions 6–10. This idea should be examined in future studies.

Overall frontal slow wave amplitude was correlated with CRPs in the recency positions, confirming that slow waves can serve as a window into “observing” the rehearsal process. Notably, subjects with more negative-going slow waves also exhibited a stronger tendency to produce items at adjacent output positions that had been encoded at adjacent input positions. At first glance, this may be at odds with the finding that less negative-going amplitudes were elicited for lists from which subjects recalled more items. This may be explained such that subjects that engage strongly in rehearsal and therefore show a strongly negative-going slow wave may indeed generate stronger item-to-item associations. However, for each subject it may be those lists that place a lower strain on the buffer that lead to higher levels of recall.

The correlation of frontal slow wave amplitudes with CRPs in the recency list position is thus in line with prior proposals (for a review, see [19]), that frontal slow waves reflect information being kept active in a temporary store which, in turn, leads to the formation of durable inter-item associative traces. This general pattern should not be specific to Von Restorff lists, but further research is necessary to substantiate this conjecture.

4.3. *Individual Differences in Retrieval Strategies*

Two groups of subjects differed in the extent to which different list contexts were flexibly used to cue retrieval. In immediate free recall tasks, the end-of-the-list context is highly similar to the context in which the last few list members were encountered, so recall is typically initiated by retrieving those items first [1]. In line with this, both groups exhibited enhanced FRPs for the last list items. In addition, in terms of reinstating the previous list context, group 1 used only the context of the beginning of the list, while group 2 evidently used both the context of the beginning of the list and the isolate in different trials to cue retrieval. Depending on the particular list and the success of the first retrieval attempt, this flexibility may be the reason for the better recall performance for group 2. There was no evidence that ERPs elicited at encoding differed between the two groups. The individual differences therefore appear to originate in retrieval, rather than encoding, mechanisms.

Our results thus strongly suggest that in free recall tasks episodic encoding and retrieval processes are not unitary, so for behavioral and electrophysiological analyses alike it is important to consider individual differences in strategic- and other aspects.

4.4. *Other Models of Episodic Encoding*

The goal of the present report was to integrate a mechanistic model of episodic encoding with theoretical models of ERP function, resulting in specific predictions that could be tested in the Von Restorff paradigm. The results were consistent with the predictions derived from the integrated model, demonstrating that combining mechanistic models with neuronal activity patterns is a fruitful approach to further our understanding of episodic encoding. It is however important to emphasize that our goal was not to examine whether other mechanistic models may also be able to explain the results we obtained, and whether specific ERP components could also in theory be used as indices for specific processes posited by other models. While this issue is far beyond the scope of the present article, it should be addressed in future work.

4.5. *Conclusions, Limitations and Future Directions*

A critic of the present study may speculate that the lists of words with positive, negative or neutral emotional content, or of low or high word frequency, which were presented in the two experiments, respectively, but which were not analyzed in the present report may have influenced the result patterns. While we cannot entirely rule out this conjecture, we consider it unlikely. First, the data came from two different studies in which the additional list types varied in quite different features (either emotional content or word frequency). Second, presentation order of the lists was randomized and different for each participant, so the Von Restorff lists analyzed in the present report were not consistently preceded by the same list type. Taken together, the nature of the preceding list types might have introduced noise that may have worked against the detection of statistically significant of result patterns, but a confounding or biasing effect is unlikely. Nevertheless, follow-up studies should employ only the Von Restorff lists of interest to test the hypotheses presented here to examine whether the same result patterns are obtained.

Another interesting question for further research is whether different FRP, CRP and ERP result patterns would be obtained if the isolate was presented in serial position 2 of the list, at which point the isolated nature of the stimulus cannot yet be noticed. Previous studies have reported enhanced recall rates for isolates in this position, suggesting that salience at the time of stimulus encounter is not necessary in order for a recall-enhancing effect to occur (e.g., [38]). This has been taken as evidence that processes located at retrieval, rather than encoding, are responsible for the Von Restorff effect (e.g., [39]). Indeed, if the participant only notices later on that the item in serial position 2 was in fact an isolate, the compartmentalization process can obviously not be elicited any more during its presentation at encoding. Therefore, the output patterns reported in the present study should be different for such isolates: CRPs at lag 1 should not be reduced, and the probability of recalling such isolates first should also not be different from a non-isolated control item in a similar serial position. Furthermore, if the deviant nature of the stimulus cannot yet be noticed, a P300 should also not be elicited. Resolving whether partially different mechanisms account for Von

Restorff effects at different parts of the serial position curve thus remains to be tested in future research.

The idea that the P300 is a physiological correlate of the compartmentalization process posited by the model leads to several other hypotheses that can be tested by employing other paradigms. For example, context updating may be induced in the middle of a study list by a feature that is independent of the study items themselves, such as by a suddenly onsetting noise. According to the model, this should lead to a more unique item-to-context association for the item following the context change. Therefore, large P300 amplitude, as an index of context change and consequently compartmentalization, should similarly to the present results be associated with a reduced probability of this item to be recalled immediately after the items that preceded it at encoding. Along the same line, in the list-based directed forgetting paradigm, reduced memory performance for the first of two lists when in between a “forget” instruction is given (as compared to no instruction), can also be explained by the model through a mental context change in between the first and the second list [1]. If P300 amplitude indexes this context change, then its amplitude should be correlated with stronger “forgetting” of the first list after the “forget” instructions.

Another important extension of the present results would be to employ different manners of isolation in Von Restorff-type lists. For example, isolates that are semantically deviant from an otherwise semantically related list should elicit the same effects as presented here. Perhaps the output order effects will be even more pronounced, because in semantically related lists associative strategies should be more likely to be used, and a semantically deviant item may therefore be even more likely to trigger the compartmentalization process. These and other studies should thus further explore whether P300 can serve as a physiological index of context change within the model, leading to the elicitation of the compartmentalization mechanism.

The idea that the frontal slow wave co-varies with and thus reflects the rehearsal process of the buffer model also needs to be further explored in paradigms other than the Von Restorff paradigm. An obvious next question is whether similar patterns to the ones observed here, especially the correlation of slow wave amplitudes with conditional recall probabilities, would also be observed when study lists do not contain an isolate. Furthermore, and more importantly, any experimental manipulation that affects how many items are co-rehearsed in the buffer, should also affect the magnitude of the slow wave. In one potential experimental design to test this, participants may, for example, encode information in chunks of different sizes. Based on the results of such studies, the model may also be modified to incorporate and account for the actually observed ERP patterns.

These and other studies in the same line of research may combine with the present study into a fruitful approach to gain a comprehensive understanding of the cognitive and psychophysiological characteristics of human episodic memory: Brain activity is utilized to constrain mechanistic models of episodic encoding and retrieval, which in turn can be used to generate predictions for the eliciting conditions and behavioral correlates of brain activity.

Acknowledgements

We thank the Cognitive Psychophysiology Laboratory of the University of South Florida, in particular Glen R. Forester and Ty Brumback, for their assistance.

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