A Neural Index Reflecting the Amount of Cognitive Resources Available during Memory Encoding: A Model-based Approach

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Abstract

Humans have a limited amount of cognitive resources to process various cognitive operations at a given moment. The Source of Activation Confusion (SAC) model of episodic memory proposes that resources are consumed during each processing and once depleted they need time to recover gradually. This has been supported by a series of behavioral findings in the past. However, the neural substrate of the resources is not known. In the present study, over an existing EEG dataset of a free recall task (Kahana et al., 2022), we provided a neural index reflecting the amount of cognitive resources available for forming new memory traces. Unique to our approach, we obtained the neural index not through correlating neural patterns with behavior outcomes or experimental conditions, but by demonstrating its alignment with a latent quantity of cognitive resources inferred from the SAC model. In addition, we showed that the identified neural index can be used to propose novel hypothesis regarding other long-term memory phenomena. Specifically, we found that according to the neural index, neural encoding patterns for subsequently recalled items correspond to greater available cognitive resources compared with that for subsequently unrecalled items. This provides a mechanistic account for the long-established subsequent memory effects (SMEs, i.e. differential neural encoding patterns between subsequently recalled versus subsequently unrecalled items), which has been previously associated with attention, fatigue and properties of the stimuli.

A Neural Index Reflecting the Amount of Cognitive Resources Available during Memory Encoding: A Model-based Approach

Humans are only able to process and maintain a relatively small amount of information at any given moment and one explanation, common to many models of working memory, is that processing depends on a limited amount of cognitive resources (Anderson et al., 1996; Ma et al., 2014; Oberauer et al., 2016). Even though, in contrast, long-term memory is often considered to have unlimited capacity, at least some theories assume that the rate of encoding in long-term memory depends on the amount of working memory resources available at the time of encoding (Atkinson & Shiffrin, 1968; Popov & Reder, 2020; Reder et al., 2007). For example, the Source of Activation Confusion (SAC) model of episodic memory (Popov & Reder, 2020; Reder et al., 2000; Reder et al., 2007) assumes that each time an item is stored in long-term memory (LTM), its encoding depletes a fixed proportion of the currently available resources and that the strength of the resulting memory trace is proportional to the amount of resources assigned to it. The amount of resources is not infinite, and once depleted it needs time to recover gradually (i.e. resource-depletion-and-recovery assumption). This resource assumption has been supported recently by numerous behavioral findings (Kowialiewski et al., 2021; Mizrak & Oberauer, 2021; Popov et al., 2019; Popov & Reder, 2020; Popov et al., 2021). Despite the behavioral evidence, this resource-depletion-and-recovery assumption has never been tested on neural data and we currently do not know what the biological or neural substrate is of the proposed limited resources.

In this paper, we establish a neural signature of resource availability, providing further support for the proposed limited resources. Additionally, this index can serve as a tool for directly measuring the amount of available resources during encoding and an example of its application is demonstrated at the end. To **determine such a neural index of resource availability**, we used a free recall paradigm where participants were asked to remember a list of consecutive presented words and later to recall all the words

from the list in any order. We used the power spectrum pattern of the EEG signal during the encoding of a word as the key neural signature to derive the amount of available cognitive resources. According to the SAC's resource-depletion-and-recovery assumption, the available cognitive resources are at their fullest at the beginning of each list. We therefore defined the power spectrum pattern of encoding the first word in the list as a template pattern for maximum resources. We then measured how much the encoding patterns of other words are similar to this template pattern. We used the *pattern similarity* as an index of resource availability - we reasoned that the more a pattern is similar to the maximum possible resources, i.e. first serial position template pattern, the more resources are available and the higher the resource availability index value will be.

To **validate the neural index of resource availability**, we used a model-based approach. We fit the SAC model to two recall behavioral findings that according to the model can be explained by differential resource consumption during encoding - the primacy serial position effect (Murdock, 1962) and the sequential effect of word frequency (Popov & Reder, 2020). Based on the fit to the recall data, the model infers the amount of resources are available during the encoding of each word on the list. If the identified neural signature represents resource availability, it should index an amount of available cognitive resources consistent with that inferred from the recall performance using the SAC model. This will both validate the neural index of resource availability and provide a strong test of the SAC's resource-depletion-and-recovery assumption as a different portion of the data is used (i.e. neural data during the encoding phase) compared with the behavioral studies (i.e. behavioral data during recall phase). The two relevant behavioral effects are:

1. *Primacy serial position effect* - a key aspect of delayed free recall is the primacy effect - recall probability is often highest for the first presented item and it decreases gradually with the serial position until it asymptotes in the middle of the list (Murdock, 1962). According to the SAC model, the primacy effect occurs because the amount of available resources decreases as cognitive operations move forward. For

example, when asked to remember a list of words shown on screen one after another, participants have their full pool of cognitive resources at the beginning. Encoding the first word depletes a portion of the resource pool. Since resources recover only gradually over time, participants will have a partially depleted resource pool when they start to encode the second word and such depletion accumulates as the list moves forward. Eventually, the proportion of resources depleted by each word and the amount recovered between words balance each other, leading to an asymptote of available resources, mirroring the behavioral asymptote. We anticipate such accumulation of depletion will be reflected by the changes in the neural index of resource availability, i.e. the neural index decreases as the list continuously moves forward until it reaches the asymptote.

2. *Sequential effect of word frequency* - the sequential effect of word frequency in episodic memory is another important behavioral evidence for the SAC's resource-depletion-and-recovery assumption. Popov and Reder (2020) discovered that the word frequency of a specific word, X_k, where k represents the word's position on a study list, affected memory for the items that followed it on the study list, i.e. items X_{k+1}, X_{k+2}, etc. Specifically, memory performance was better across a variety of test types (item and associative recognition, cued and free recall) for item X_{k+1} when the preceding X_k item was a high-frequency word rather than a low-frequency word. Based on prior work (Diana & Reder, 2005; Reder et al., 2007) (for a review, see Popov and Reder (In press)), the SAC model assumes that encoding low-frequency words requires more resources than high-frequency words, leaving fewer resources to process subsequent information and therefore impairing memory performance. If the identified neural index in fact represents resource availability, it should index a lower amount of cognitive resources during encoding X_{k+1} after encoding a low-frequency word X_k compared to a high-frequency word X_k. Moreover, the SAC model can also capture a stronger effect of word frequency on the memory of

the immediate subsequent item X_{k+1} compared with the next subsequent item X_{k+2} since the resources have less time to recover by the time an item is presented for X_{k+1} than X_{k+2} (Popov & Reder, 2020). Therefore, a valid neural index of resource availability should index a larger difference at X_{k+1} compared with X_{k+2} between the resource availability following the encoding of a low-frequency word and a high-frequency word at position k.

Once we have a validated neural index of resource availability, we can **use it to propose novel hypotheses regarding other long-term memory phenomena** that might be influenced by available cognitive resources during encoding. For example, successfully recalled items are associated with different neural patterns during encoding compared with those of unrecalled items. These differences are known as subsequent memory effects (SMEs) and they consistently appear across various brain regions, memory tasks, and imaging technologies (Kim, 2011; Paller et al., 1988; Paller & Wagner, 2002). Though SMEs has been long established and robust, the interpretation of SMEs remains unclear (Halpern et al., 2021; Long et al., 2014; Paller & Wagner, 2002). What are the underlying neural mechanisms during encoding that contribute to better recall performance? Multiple accounts have been provided in the past, linking SMEs to either endogenous factors such as attention and fatigue (Aly & Turk-Browne, 2016; Lohnas et al., 2020; Uncapher & Rugg, 2009) or external factors reflecting stimulus and task-related variables (Bainbridge et al., 2017; Craik & Lockhart, 1972; Fellner et al., 2013; Hanslmayr et al., 2009; Hanslmayr & Staudigl, 2014; Otten & Rugg, 2001a, 2001b; Sanquist et al., 1980). More recent efforts aim to further disentangle endogenous factors with external factors (Halpern et al., 2021; Kahana et al., 2018; Weidemann & Kahana, 2021).

In the current work, we show that the amount of available resources during encoding provides an alternative account for subsequent memory effects. Consistent with the SAC's resource-depletion-and-recovery assumption, more available resources should relate to a more efficient encoding process and thus a better memory for an item. If the

amount of available resources during encoding contributes to the observation of subsequent memory effects, we should observe a higher resource availability index for subsequently recalled items compared with subsequently unrecalled items. Moreover, according to the SAC's resource-depletion-and-discovery assumption, as the resources recover gradually, the amount of resources available on one trial is correlated with the amount of resources at the preceding trial. Thus, we make a novel prediction about a potential sequential effect associated with the subsequent memory effect, which we termed as the "sequential subsequent memory effect": if we split the subsequently recalled and subsequently unrecalled words and examine the neural activity when encoding the preceding item (in contrast to neural activity when encoding the given word as analyzed in standard "subsequent memory effect"), the resource availability index should be higher at encoding the preceding word among words that are subsequently recalled than words that are subsequently unrecalled.

In the remaining paper, we provide the background of the SAC model from which we infer the amount of available resources during encoding and describe the procedure to obtain the neural index of resource availability from the EEG data. Then we validate the neural index of resource availability by comparing it against the inferred resources from the SAC model. Finally, we use the validated neural index as a tool to test a novel hypothesis that the subsequent memory effect is associated with the amount of available resources during encoding. Overall, these results provide converging support for the SAC's resource assumption and a future tool for directly monitoring the amount of available resources from neural data.

Method

Participants

We analyzed the data from Experiment 4 of the Penn Electrophysiology of Encoding and Retrieval Study (PEERS) (Kahana et al., 2022). The PEERS comprises 4

experiments and the datasets have been used in many other previous studies (Healey & Kahana, 2016; Healey et al., 2019; Lohnas et al., 2015). We excluded the participants for whom we could not find corresponding behavioral data and the final sample included 88 participants (age between 18-35) each with at least 20 completed sessions. This study was not preregistered. We obtained pre-processed EEG data from Weidemann and Kahana (2021) and behavioral data from the lab that conducted the PEERS (http://memory.psych.upenn.edu). The analysis code can be found at: https://rutgers.box.com/s/jkk490sabd43meg7hff62cq47aax4gzu.

Delayed free recall experiment

Participants performed a delayed free recall experiment with several experimental sessions consisting of 24 lists of 24 words. For each list, participants were asked to consecutively remember the word presented on the screen after which they performed a distractor task followed by a free recall task where they had 75 seconds to recall just-presented items in any order after 1200 - 1400 ms. At the beginning of each list, there was a 1500 ms delay before showing the first word. The presentation time for each word was 1600 ms, and the inter-stimulus interval between words randomly jittered between 800 - 1200 ms (uniform distribution). The distractor task lasted 24 seconds during which participants solved math problems in the form of A+B+C=? where A, B, and C are integers ranging from 1 to 9, and participants were given bonuses based on their speed and accuracy. Half of the lists were randomly chosen in each session (excluding the first list) and a pre-list distractor task was added where participants performed the same math problem described above for 24 seconds before the presentation of the first word with an interval jittered between 800 - 1200 ms.

The experiment used a subset of 576 words drawn from an original word pool used in other PEERS experiments. For every participant, each session used these same 576 words but randomly assigned them to 24 lists. We obtained the word frequency of each

word from the pre-generated word frequency data set from Semenov et al. (2015).

EEG data collection and processing

Two systems, a 128 channel Biosemi Active and a 129 channel Geodesic Sensor (Electrical Geodesics, Inc.; EGI), were used in the experiment to record EEG data. Each participant used the same system for all their experimental sessions. The MNE package (Gramfort et al., 2013) and custom python codes were used to execute the raw EEG data. A 0.1 Hz high-pass filter was applied to both systems and the EEG data were then re-referenced based on average. The epoch of interest started from 800 ms before each word shown on the screen to the end of its presence. A 1200 ms buffer zone was applied to both sides of the epoch during wavelet transform after which a power spectrum analysis was conducted based on the logarithmically spaced 15 frequencies ranging from 2 to 200 Hz. A log-transform was applied to the power, the time was down-sampled to 50 Hz. and z-transformed powers were calculated across all trials within each session for each participant. For EGI system, the power at electrodes 4, 5, 12, 13, 19, 20, 24, 28, 29, 37, 42, 52, 53, 54, 60, 61, 78, 79, 85, 86, 87, 92, 93, 111, 112, 117, 118, and 124 were aggregated together, and for Biosemi system, electrodes A5, A6, A7, A18, A31, A32, B2, B3, B4, B18, B19, B31, B32, C2, C3, C4, C11, C12, C24, C25, D2, D3, D4, D12, D13, D16, D17, and D28 were aggregated together for subsequent analysis. These electrodes that located in superior regions were selected because they were used before and were shown to be relevant to SMEs (Paller et al., 1988; Weidemann & Kahana, 2021).

Neural index of resource availability

The SAC model assumes that participants have their largest amount of available cognitive resources at the beginning of each list. Therefore, we used the power spectrum pattern (i.e. neural signature) at encoding the first word in lists as a template and benchmark patterns under other conditions against it by calculating Pearson correlations on their corresponding power in log frequency space. The Pearson correlation coefficient

was then used as the resource availability index indicating how much cognitive resources are available. A larger divergence of a neural signature from the template corresponds to a lower index, indicating fewer cognitive resources available at that moment. The neural index varies between -1 and 1 with -1 indicating least resources and 1 indicating max resources. We compared the index in phenomena of interest across participants using paired t-test. Note that, in every session, half of the lists had a pre-list distractor task, which might cause additional depletion of cognitive resources at the beginning, making the amount of resources at encoding the first word no longer the largest. To eliminate this influence, we calculated the template and the neural signature at different serial positions only across lists without a pre-list distractor task. For other conditions, neural signatures were calculated across all lists since possible resource depletion would offset each other during comparison.

SAC model of resource availability

In the current work, we apply the SAC model of episodic memory to infer the amount of available resources during encoding, based on behavioral data during recall. The resource assumption in the SAC model has been supported by numerous behavioral findings (Kowialiewski et al., 2021; Mizrak & Oberauer, 2021; Popov et al., 2019; Popov & Reder, 2020; Popov et al., 2021). The inferred resource availability will then be used to validate the neural index of resource availability, obtained from the neural signal during encoding. The current work does not represent novel model development - instead, it uses an existing model and validates one of its assumptions (resource-depletion-and-recovery) with neural data.

We employed a simplified version of the SAC model (Popov & Reder, 2020) described below, that keeps the major assumptions about how the resources deplete and recover. The actual SAC model is more complicated than this and involves assumptions about memory decay, contextual fan, and others; however, these assumptions are not

relevant for the current project. Thus we decided to simplify the model in order to clearly demonstrate the resource-depletion-and-recovery assumption. This should allow for other computational models of memory to capture the same set of behavioral findings as long as the below assumptions of resources are incorporated into their models.

The model assumes that encoding information in LTM depletes a limited resource pool ($W_{max} = 1$) and that the strength of the LTM trace is proportional to the amount of resources dedicated to it. In the model information is represented as a network of nodes that vary in strength between 0 and 1. Words have pre-existing semantic nodes whose strength is a continuous function of word frequency:

$$B_{sem} = 0.4 - 0.2e^{-0.1WFpermillionwords} \tag{1}$$

Based on this equation, we estimated that in the current experiment the strength of LF words was 0.22, and the strength of HF words was 0.40. When encoding a word in a studied list, two processes occur. First, the activation of the semantic node is raised to 1, which depletes the following amount of resources:

$$W_{sem} = \tau(1 - B_{sem})^2 W \tag{2}$$

where τ is a scaling parameter and W is the amount of currently available resources. Thus, HF words having higher base-level strength require less of the resource to be activated ($(1 - 0.40)^2\tau = 0.360\tau$) relative to LF words ($(1 - 0.22)^2 = 0.608\tau$). After the word is encoded, an episodic node is created which represents the binding between the word and the list context. The creation of the episode node depletes a proportion *delta* of the available resources, and its strength, B_{epi}, is proportional to the amount of resources it consumed:

$$W_{epi} = \delta W \tag{3}$$

$$B_{epi} = \sqrt{W_{epi}} \tag{4}$$

The resource pool recovers linearly over time t_i between item presentations at a rate of r per second until it reaches W_{max}:

$$W_{i+1} = \min(W_{max}, W_i - W_{sem} - W_{epi} + rt_i) \tag{5}$$

Finally, the model posits that successful recall of item i occurs probabilistically if the episode node's strength is above the retrieval threshold:

$$P(recall)_i = P(B_{epi} \geq \theta_{epi} | \sigma_{epi}) \tag{6}$$

where θ_{epi} is the retrieval threshold and σ_{epi} is the standard deviation of normally distributed noise added to the episodic node's strength.

We fitted the model to the averaged behavioral recall data over serial position and word frequency of the preceding word (5 model parameters and 28 data points; limited to serial positions 2-15, because serial position 1 was not preceded by another word and because a recency effect was observed in the last serial positions and the simplified model does not include a recency mechanism). Five parameters were estimated via a grid search ($\tau = 0.2$, $\delta = 0.26$, $r = 0.08$, $\theta_{epi} = 0.367$, $\sigma_{epi} = 0.256$) minimizing the root-mean-square error (RMSE) of the observed and predicted free recall probability. We then used this model with the same set of parameters to infer the availability of cognitive resource at encoding the words with increasing serial position and at those preceded by words with different word frequency.

Finally, we introduced normally distributed noise in the *delta* parameter on each trial i:

$$\delta_i \sim \mathcal{N}(\delta, 0.1) \tag{7}$$

This variability represents variation in how well the resource is used on each trial and is a new addition to the model. This addition is useful because available cognitive resources can be affected by both experimental factors such as serial position and word

frequency which we have explicitly accounted for, but also idiosyncratic variation from time to time.

Results

Although the resource-depletion-and-recovery assumption of the SAC model has been supported by a series of behavioral findings (Kowialiewski et al., 2021; Mizrak & Oberauer, 2021; Popov et al., 2019; Popov & Reder, 2020; Popov et al., 2021), its neural underpinnings are yet to be found. We extracted a neural signature from EEG data and defined a corresponding neural index indicating the resource availability. To validate this resource availability index, we compared it with the resource availability inferred from the SAC model that captured the primacy serial position effect and the sequential effect of word frequency.

Validation of resource availability index

First, we fitted the SAC model with the recall data so as to see whether this simplified version based solely on the resource-depletion-and-recovery assumption could capture the behavioral pattern during recall. The model provided good fits to the free recall data (Fig. 1; RMSE = 0.006, $R^2 = 0.989$), with its estimated parameters consistent with previous SAC models (Popov & Reder, 2020). Specifically, as shown in the Fig. 1, the model, presented in the dash line, successfully captures the primacy serial position effect where the recall probability is the highest for the first presented word and decreases gradually with the serial position regardless of the word frequency of the preceding words. Meanwhile, at each serial position, the model captures the sequential effect of word frequency where the recall probability is higher when the word was preceded by a high-frequency word rather than a low-frequency word.

With the SAC model fitted to the recall period of the behavioral data, we can infer the amount of available resources during encoding according to the SAC model and compared it with the neural index of resource availability (calculated separately from the

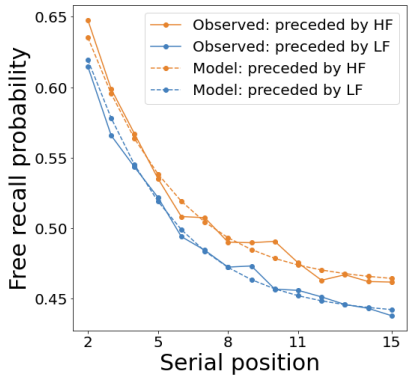

Fig. 1. Primacy serial position effect (recall probability is at its highest at the beginning of the list) and sequential effect of word frequency (recall probability is higher when preceded by high-frequency words than low-frequency words), as captured by the SAC model. $\tau = 0.2$, $\delta = 0.26$, $r = 0.08$, $\theta_{epi} = 0.367$, $\sigma_{epi} = 0.256$.

encoding period of the neural data). Fig. 2a shows the amount of available resources at the beginning of encoding each serial position in SAC. At the beginning of the list resources are at their maximum, and they decrease gradually with each serial position, until they asymptote approximately after item 15. If the neural index indeed reflects the amount of available resources, it should follow the same pattern.

Fig. 2b shows the power spectrum pattern of neural patterns when encoding words at different serial positions (among lists without a pre-list distractor task). We assumed that the available cognitive resources are at their fullest at the beginning of each list and proposed that the power spectrum pattern of encoding the first word in the list as a template pattern for maximum resources (Fig. 2b). We then measured the neural index of resource availability as how much the encoding patterns of other words are similar to this template pattern (Fig. 2c).

The template, i.e. serial position 1, has the lowest power value at the middle-frequency band and the highest value at the low- and high-frequency bands. As the serial position increases, the value at the middle frequency band becomes larger and the value at the low- and high-frequency bands become lower (Fig. 2b). In other words, the

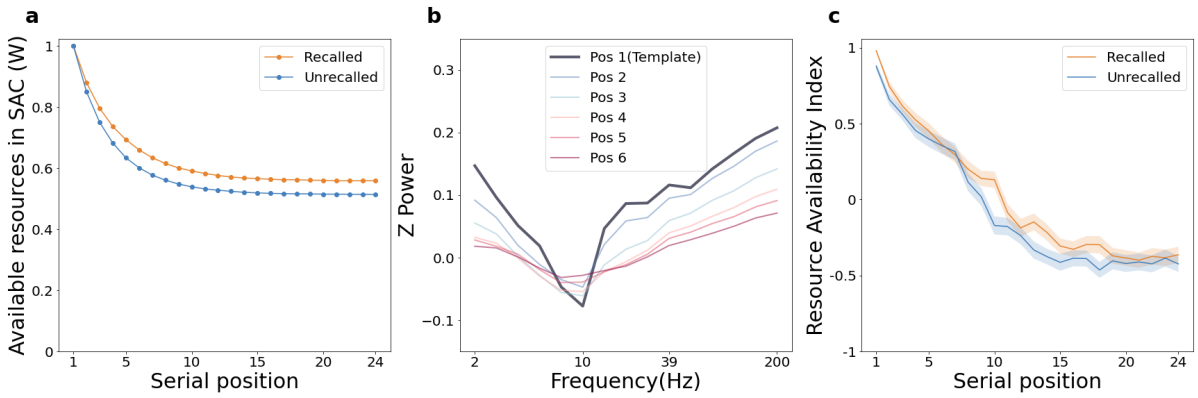

Fig. 2. The effect of serial position on available cognitive resources during encoding. a. Available resources in the SAC model for different serial positions partitioned by whether words were subsequently recalled. b. The power spectrum pattern when encoding words from serial position 1 to 6 (in lists without a pre-list distractor task). c. Neural index of resource availability for different serial positions (in lists without a pre-list distractor task), partitioned by whether words were subsequently recalled. Note that: (1) figure a represents resources inferred from the model fitted to the recall data while figures b and c were measured from EEG data during the encoding period in the free recall task; (2) resources in the SAC model vary between 0 and 1, while the neural resource availability index varies between -1 and 1. These two notes also apply to corresponding sub-figures in Fig. 3, 4, and 5.

neural signature diverges more from the template as the serial position increases, giving rise to decreased amount of resource availability as measured by our proposed neural index in Fig. 2c. This pattern holds for both recalled and unrecalled words, demonstrating that the trend is not a trivial consequence of having higher accuracy at earlier serial positions. We fitted a linear mixed model to test the relationship of indexes with serial positions. The effect of serial position is significant and negative in both recalled (beta = -0.056, 95% CI [-0.063, -0.048], $t(2111)$ = -14.611, $p < 0.001$; Std. beta = 0.004) and unrecalled condition (beta = -0.054, 95% CI [-0.062, -0.046], $t(2111)$ = -13.341, $p < 0.001$; Std. beta = 0.004). As the serial position number increases, the continuously decreasing index indicates fewer

and fewer available cognitive resources during encoding, which matches the pattern of resource availability inferred from the SAC model in Fig. 2a.

Next, we plotted how the available resources inferred by SAC change based on the frequency of the preceding word. Fig. 3a shows the effect of word frequency at position k on the resource availability while encoding the immediately subsequent item (position k+1) or the item after that (position k+2). Specifically, studying low-frequency words at position k leaves fewer resources available when the next words are presented, and this effect is more pronounced during the encoding of words at position k+1 ($W_{high-frequency} = 0.60$, $W_{low-frequency} = 0.57$) than during the encoding of words at position k+2 ($W_{high-frequency} = 0.58$, $W_{low-frequency} = 0.56$), as the latter has more time to recover the pool of cognitive resources. If the neural index we identified represents resource availability as we hypothesized, then it should show similar patterns as a function of word frequency as the SAC model's inferred resources based on recall performance.

Fig. 3b and c show the power spectrum patterns when encoding words at position k+1 and k+2. While the previous analyses of neural data were only across lists without a pre-list distractor task, in order to maximize statistical power the following results were across all lists, except the calculation of the template that was still calculated across lists without a pre-distractor task. We split trials into 5 bins based on their word frequency at serial position k (k range from 1 to 22) and compared the corresponding neural signatures in bins of the highest and lowest word frequency. In both Fig. 3b and Fig. 3c, high-frequency words at serial position k are associated with a more template-like neural signature of the sequential words (i.e. a lower value at the middle-frequency band; the template that represents maximum resources can be found in Fig. 2b). Because the neural index of resource availability is defined as the similarity to the template, this means that there are more resources available when word encoding is preceded by a high-frequency word (Fig. 3d). To formally test this, in comparison to encoding low-frequency words (M=-0.601, SE=0.040), encoding high-frequency words (M=-0.416, SE=0.048) at serial

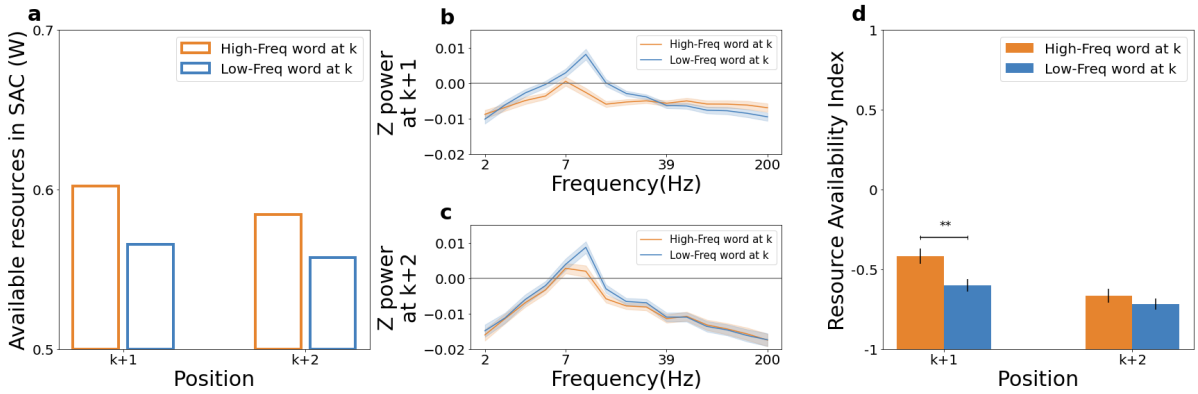

*Fig. 3. The effect of word frequency of the preceding word on available cognitive resources during encoding. a. Available resources in the SAC model during encoding at positions k+1 and k+2 depending on the frequency of the word at position k. b. The power spectrum pattern when encoding words at position k+1 depending on the frequency of the word at position k. c. The power spectrum pattern when encoding words at position k+2 depending on the frequency of the word at position k. d. Neural index of resource availability during encoding at positions k+1 and k+2 depending on the frequency of the word at position k. Asterisks indicate a significant difference between groups (**p < .01).*

position k is associated with a significant higher resource index value (t(87)=-3.081, p=0.003, d=0.328) at serial position k+1. Encoding words of different word frequencies does not have a significant effect on the neural index at the k+2 position. Altogether, high-frequency words at serial position k are related to more available cognitive resources at serial position k+1 and a smaller, even though non-significant, facilitation at serial position k+2, which matches the pattern of resource availability inferred from the SAC model in Fig. 3a.

Both the evidence from the primacy serial position effect and the sequential effect of word frequency validated that our proposed neural index of resource availability reflects cognitive resource availability. After the validation, we then were interested in whether the neural index can serve as a tool to examine long-term memory phenomena that might be influenced by available cognitive resources during encoding.

An alternative account for subsequent memory effects

Subsequent memory effects (SMEs) refer to the observation that neural patterns of encoding subsequently recalled items are different with that of encoding subsequently unrecalled items. Multiple accounts have been proposed in the literature, associating SMEs with attention, fatigue and properties of stimuli. In our analysis, we would like to consider the hypothesis that observed SMEs are associated with different amount of available cognitive resources during encoding.

We first produced in Fig. 4a the subsequent memory effects commonly observed in the literature, where the neural patterns for subsequently recalled words are different than those for subsequently unrecalled words. Consistent with prior studies (Gruber et al., 2004; Hanslmayr et al., 2012; Sederberg et al., 2006; Sederberg et al., 2003; Summerfield & Mangels, 2006), Fig. 4a demonstrates that the power spectrum pattern associated with subsequently recalled words has a lower value at the middle-frequency band and higher values at the low-frequency and high-frequency bands. Unique to our current analysis, however, is our ability to interpret these patterns as how similar they are to the template that represents maximum resources, i.e. there is a smaller divergence from the first encoded word template among the recalled words compared to unrecalled words, indicating that there are more resources available when encoding words that are subsequently recalled. This is more clearly seen in Fig. 4b, where there is a significant higher neural index of resource availability ($t(87)=10.125$, $p<0.001$, $d=1.079$) at encoding subsequently recalled words ($M=0.459$, $SE=0.051$) than subsequently unrecalled words ($M=-0.517$, $SE=0.048$). These neural results support our hypothesis that the differential neural patterns at encoding for subsequently recalled versus unrecalled words could be a result of participants having different cognitive resources available during encoding. We also simulated available resources during encoding of subsequently recalled or subsequently unrecalled words according to the same SAC model we fitted before (Fig. 4c). Fig. 4c shows that the available resources in SAC are higher during encoding subsequently recalled

words compared to subsequently unrecalled words ($W_{recalled} = 0.67$, $W_{unrecalled} = 0.55$), consistent with the neural index pattern.

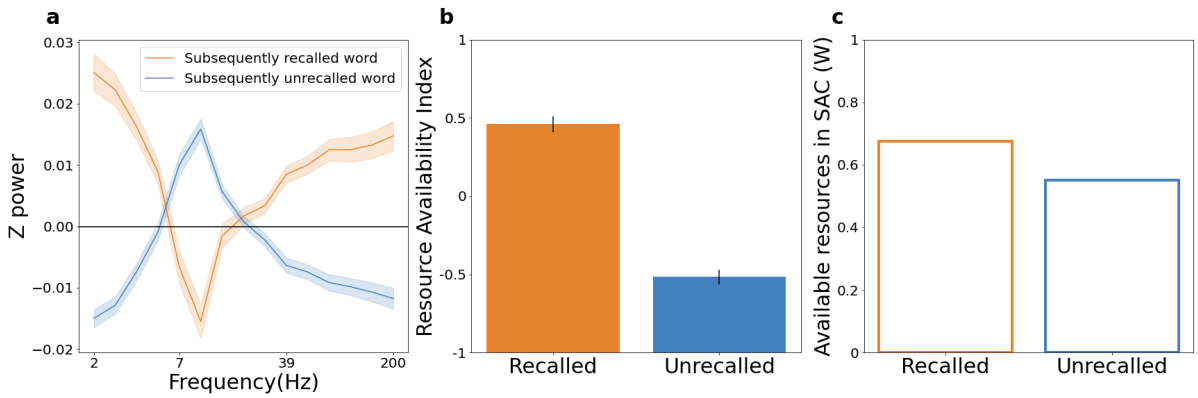

Fig. 4. Explaining subsequent memory effects by cognitive resources available during encoding. a. Different power spectrum patterns for encoding subsequently recalled versus unrecalled items (i.e. subsequent memory effects). b. The neural index of resource availability of subsequently recalled versus unrecalled words. c. Available resources in the SAC model during the encoding of subsequently recalled versus unrecalled words.

To further support our hypothesis that the subsequent memory effects could be a result of participants having different cognitive resources available during encoding, we made a novel prediction of a phenomenon that is closely related to the subsequent memory effects, which we call the "sequential subsequent memory effects" - subsequent better memory for item X_{k+1} is associated with different neural patterns when encoding X_k (instead of X_{k+1} as in standard subsequent memory effects). This is shown in Fig. 5a where the power spectrum pattern for encoding words at position k is different for subsequent recalled versus unrecalled items encoded at position k+1; this holds either when items encoded at position k were subsequently recalled (Fig. 5a) or unrecalled (Fig. 5b). Thus, the sequential subsequent memory effect is not simply due to auto-correlation in recall probability between items in nearby serial positions. Importantly, we also predict that better memory for item X_{k+1} is associated with more resources during the encoding of the preceding item X_k, as the available resources during encoding at position k only change

gradually and could carry over to position k+1.

We tested this prediction by plotting the neural index of resource availability during encoding of X_k given whether X_{k+1} were subsequently recalled or not (Fig. 5c). When the word X_k was recalled, more resources are related to successful recall of the word X_{k+1} (M=0.548, SE=0.050), with a significantly higher index value (t(87)=6.49, p<0.001, d=0.692) in comparison to where the word X_{k+1} was not recalled (M=0.171, SE=0.054). When the word X_k was unrecalled, the resource availability indexes are not significantly different from each other (Fig. 5c) - possibly due to an already nearly fully depleted resources indicated by the preceding state where participants had already failed to recall. Altogether, these neural results show that more cognitive resources available at encoding preceding words relate to better memory of current words, indicating that the amount of resources available at any point is associated with not only the memory of the item encoded at that point, but also the memory of items encoded in the near future. Even when there are enough resources at time k to encode item X_k successfully, having even more available resources would leave enough for encoding the subsequent item X_{k+1}.

We also simulated how the resources change in such condition according to the already fitted SAC model (Fig. 5d). The simulation result has a close correspondence with the neural index (Fig. 5a). Specifically, more resources are available during encoding X_k when X_{k+1} was recalled rather than unrecalled and such effect is larger when X_k is recalled ($W_{recalled} = 0.76$, $W_{unrecalled} = 0.62$) compared to when X_k is unrecalled ($W_{recalled} = 0.60$, $W_{unrecalled} = 0.52$). The resource availability inferred from the SAC model (Fig. 5d) corresponds to that measured by our neural index during encoding (Fig. 5c), although the model does predict a small difference even when item X_k is unrecalled. Overall, the novel "sequential subsequent memory effects" that we observed and their corresponding neural index of resource availability served as further evidence that the amount of available cognitive resources provides an alternative account for the subsequent memory effects.

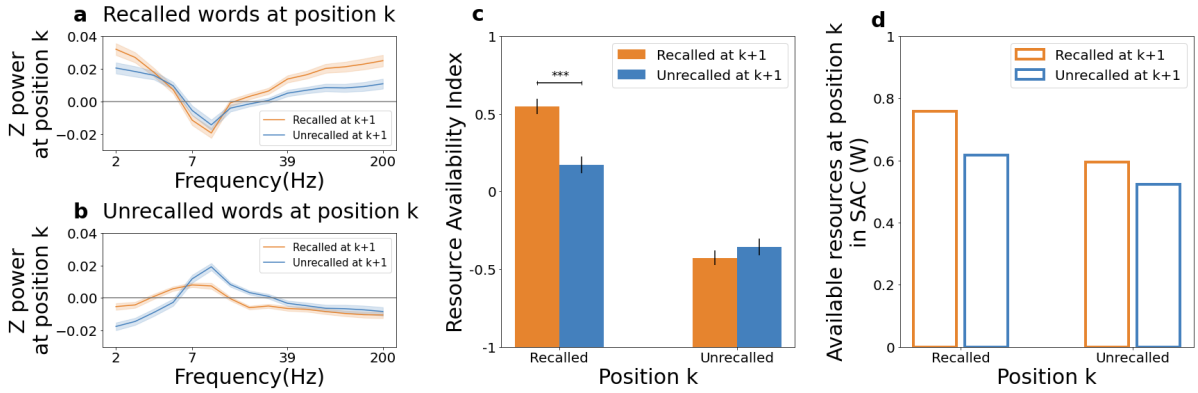

*Fig. 5 Explaining sequential subsequent memory effect by cognitive resources available during encoding. a. Different power spectrum patterns when encoding recalled words at position k for subsequently recalled versus unrecalled items encoded at position k+1, i.e. sequential subsequent memory effects, conditioned on when items at position k were subsequently recalled. b. Different power spectrum patterns when encoding unrecalled words at position k for subsequently recalled versus unrecalled items encoded at position k+1, i.e. sequential subsequent memory effects, conditioned on when items at position k were subsequently unrecalled. c. The neural index of resource availability when encoding items at position k, conditioned on whether items at position k and k+1 were subsequently recalled or unrecalled. Asterisks indicate a significant difference between groups (***p < .001). d. Available resources in the SAC model when encoding items at position k, conditioned on whether items at position k and k+1 were subsequently recalled or unrecalled.*

General Discussion

We proposed a neural index during word encoding in a free recall paradigm which can be interpreted as reflecting the amount of cognitive resources available for forming new memory traces. Based on the SAC model of episodic memory, which has been successful in modeling many benchmark behavioral findings in the past (Cary & Reder, 2003; Diana & Reder, 2005; Popov & Reder, 2020; Reder et al., 2000; Reder et al., 2007), we assumed that each memory encoding operation depletes a limited amount of cognitive resources, which in

turn recovers gradually over time. Based on this model, we proposed that the power spectrum pattern during the encoding of the first word on each list can be used as a template that reflects the maximum amount of available resources. Furthermore, we proposed that how much the encoding patterns of other words are similar to this template pattern could be interpreted as reflecting the amount of resources available during that time, termed as the "resource availability index". The obtained neural index is able to capture the primacy serial position effect and the sequential word frequency effect consistent with the SAC model. Moreover, we proposed a novel mechanistic account of the long-established subsequent memory effects, by showing that neural encoding patterns for subsequently recalled items correspond to greater available cognitive resources compared with that for subsequently unrecalled items. We now turn to the broader implications of these results.

A model-based approach to identify neural substrates

Typical cognitive neuroscience approaches focus on applying statistical models to determine which aspect of the neural data are associated with certain behavioral outcomes or experimental manipulations (Turner et al., 2017). For example, by contrasting neural patterns during a "2-back" working memory task and a control task that requires only perceptual and response processes, one can identify a set of brain regions responsible for working memory maintenance (see a review at Smith and Jonides, 1998). Such analysis can uncover useful information about the brain regions involved, however, it is challenging to interpret why these regions are involved and the exact mechanism of that involvement (Palmeri et al., 2017; Turner et al., 2017). What is more, sometimes it is unclear what behavior outcomes or experimental manipulations one should contrast the brain activity with. For example, to apply a similar approach, our current study could design an experiment with two conditions - corresponding to "high" and "low" demand of cognitive resources - and compare neural patterns between the conditions. However, cognitive

resource is a latent cognitive construct that we cannot easily postulate its connection with behavioral outcomes or experimental conditions. What could be designated as "high cognitive resources" and "low cognitive resources" conditions could involve other cognitive processes that result in complex relationship between the factors we are interested in the behavioral outcomes to predict (see an analysis that demonstrated such complication; Zhang et al., 2018).

To tackle this problem, we adopt a model-based approach by comparing our proposed neural index of cognitive resources with a latent quantity of cognitive resources in a computational model of memory, i.e. SAC. In contrast to cognitive neuroscience approaches, models of cognition have the advantage to characterize latent cognitive processes in precise mathematical terms. The amount of available cognitive resources in SAC during encoding were decided so that the model captures behavioral findings in free recall that are associated with the recovery and depletion of cognitive resources. Additionally, while models of cognition typically rely on comparing their fit to behavioral findings to test alternative theories (Roberts & Pashler, 2000), being able to identify the neural substrate of a cognitive process in the model can provide further support for the theory that specifies the cognitive process (Anderson et al., 2016; Nunez et al., 2019; Nunez et al., 2017; Padoa-Schioppa, 2011; Zhang et al., 2017). Since two different sources of data are used to identify the neural resource availability index (encoding) and the model's latent resource availability quantity (recall), this approach provides strong convergent evidence for the model's resource assumptions.

Reconcile accounts for subsequent memory effect: endogenous or exogenous factors

To better understand the neural mechanisms during encoding that contribute to SMEs, it is helpful to distinguish endogenous factors that reflect endogenously varying brain states with external factors reflecting stimulus and task-related variables

(Weidemann & Kahana, 2021). Weidemann and Kahana (2021) identified the effect of serial position on neural activity, i.e.neural activity at early serial positions is similar to those of subsequently recalled items and that at later serial positions resembles that of subsequently unrecalled items. These were taken as evidence that the standard subsequent memory analysis may be misleading (differences in neural activity between subsequently recalled and subsequently unrecalled items might reflect processes controlled by exogenous factors such as serial positions) and that one needs to analyze SMEs in a way that isolates exogenous factors from endogenous factors (Weidemann & Kahana, 2021). In a novel analysis approach of SMEs, Halpern et al. (2021) also emphasized the importance of adjusting for exogenous factors such as serial positions and item effects. However, our current work demonstrates that endogenous and exogenous factors may not be easily separable. This is because exogenous factors such as serial positions can directly covary with an endogenous factor such as fluctuations in the amount of cognitive resources available: according to the SAC's resource-depletion-and-recovery assumption, when resource depletion is faster than resource recovery, as the list moves forward, there are gradually less and less cognitive resources available. This also simultaneously explains why neural activity at early serial positions is more similar to those of subsequently recalled items than unrecalled items, since both the early serial position items and the subsequently recalled items are associated with more resources.

It is important to note that SMEs might represent a family of effects, rather than a single unified signal, and that multiple processes might be contributing to observed ERP patterns during the encoding of recalled vs unrecalled items (Van Petten & Senkfor, 1996). Our findings suggest that at least part of SMEs signal can be attributed not to encoding processes per se, but to the "readiness to encode", consistent with prior findings that EEG activity before an item is presented can predict subsequent memory of that item (Noh et al., 2014). The novel sequential SME effect we uncovered based on the SAC's predictions is particularly interesting in this regard. We showed that even when item X_k is successfully

recalled, the neural patterns during its encoding differ depending on whether the subsequent item, X_{k+1}, was recalled. If SMEs represented processes entirely related to the encoding of the current item, such as the attention devoted to it, or the strength of the resulting memory trace, then there is no reason to expect a difference based on the recall probability of the subsequent item.

A methodological tool to measure resource availability

In addition to providing the first neural support of the SAC's resource-depletion-and-recovery assumption, the current results also provide a methodological tool with which to study resource availability in the future. One drawback of behavioral studies is that differences in resource availability during encoding can only be inferred based on differences in subsequent recall performance. In the past this has significantly limited the questions we can ask about resource depletion. For example, for modeling simplicity, Popov and Reder (2020) assumed that resource depletion during encoding occurs instantaneously with the word presentation and that afterwards the resources recover linearly over time. As they noted in the conclusion section, these choices allowed the model to fit the data, but were otherwise arbitrary. With the currently proposed resource availability index, we could in the future potentially directly measure the time dynamics of resource depletion and recovery during encoding.

Limitations and future work

The SAC's resource-depletion-and-recovery assumption is agnostic about the nature of the cognitive resources - in it, resources are a latent quantity that gets assigned as "fuel" to each memory operation. In our current work, we demonstrated that this is more than just an abstract mathematical quantity but that it corresponds to concrete neural substrates. While the current results take us one step closer to understanding the neural underpinnings of cognitive resources, it is important to note that as of yet they do not unambiguously tell us what the nature of these resources is. Are these cognitive resources

the same resources that underlie one's limited capacity during working memory tasks (Anderson et al., 1996; Ma et al., 2014; Oberauer et al., 2016)? Are these cognitive resources related to the inner resources drawn during self-regulation in the influential "ego-depletion" account (Bratslavsky et al., 1998) (though recently called into question through multiple meta-analyses from Carter et al. (2015), Hagger et al. (2016), and Randles et al. (2017))? Both are excellent venues for future research.

Conclusion

While there have been numerous behavioral findings that support an account of limited resources during memory encoding, neural underpinnings of the resources are unknown. Our work fills this gap by identifying a neural index of resource availability extracted from EEG data. We validated this neural index by showing its consistency with inferred resource availability from the SAC model that was able to capture the primacy serial position effect and the sequential effect of word frequency. Further, we used this neural index as a tool for monitoring resource availability and showed it was able to provide an alternative account for the long-established subsequent memory effects. Together, these results provided converging support for the proposed limited resources in the SAC model and a future tool for directly monitoring the resource availability from neural data.

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