

AN ACTIVATION-BASED THEORY OF IMMEDIATE ITEM MEMORY

EDDY J. DAVELAAR & MARIUS USHER

School of Psychology, Birkbeck College, University of London

We present an activation-based computational model of immediate item memory, which is proposed to underlie activation based processes within the pre-frontal cortex (mediating primary memory) that trigger episodic learning processes in the medial temporal cortex (secondary memory). We show that the model is able to capture a range of basic phenomena such as Brown-Peterson forgetting functions and serial position functions in cued and free-recall. The model makes unique predictions for presentation rate and list length effects, which were tested (and supported) in subsequent experiments.

1 Introduction

The concept of neural activation is central in computational models of information processing. In this chapter, we present a neurocomputational model based on the maintenance of activated memory representations and apply this model to a range of basic memory phenomena. We report predictions made by the model, which have been tested and supported in subsequent experiments.

2 Model

In previous work, we presented a model that addresses the active maintenance of information in short-term memory (STM) [1,2]. According to this framework, a lexical-semantic component of STM corresponds to the activated part of (long-term memory) representations in prefrontal cortex [3]. The current model extends this work by introducing a system that forms episodic traces, assumed to be mediated by rapidly changing connection weights between frontal and medial temporal areas (see figure 1). The full model that includes both memory components, activation-based STM and weight-based episodic LTM is presented below.

Active memory (PFC). Neuroscientific investigations have revealed that frontal areas are activated in delayed-match-to-sample tasks [4] and in working memory tasks that involve manipulation of lexical-semantic information [5,6]. Neuropsychological studies have also found that frontal lobe damage may result in the inability to retain lexical-semantic information in immediate memory tasks [7].

Here, we build on these findings by representing the frontal system as a system with competing central (lexical-semantic) representations. Units are updated in parallel according to a standard equation where for every representation, i , (modelled here in a localist fashion), its neural current [8] or input activation, $x_i(t)$, (labelled as net_input in connectionist terminology) at time t , depends on the neural current in the previous time-step, $x_i(t-1)$ and the recurrent input (self-excitation and lateral inhibition).

$$x_i(t+1) = \lambda x_i(t) + (1 - \lambda)[\alpha F(x_i(t)) - \beta \sum F(x_j(t)) + I_i(t) + \text{noise}] \quad (1)$$

This set of equations corresponds to the numerical solution of differential equations [8] with an Euler integration step ($dt = 1 - \lambda$; the parameter λ which is smaller than unity, corresponds to neural leakage). The parameter for self-recurrent excitation, α , can be thought of as the intra-connectivity within the cell assembly. The parameter β represents the lateral inhibition, I_i is the sensory input to unit i (coming from the posterior system) and $F(x) = \frac{x}{1+x}$ (for $x > 0$) is the output activation function. As discussed in [8], threshold-linear response functions produce fits close to the neurophysiological recordings at low firing rate, while the nonlinearity $x/(1+x)$ is helpful to ensure firing rate saturation at high input. The activation of the unit is supplemented with zero-mean Gaussian noise of standard deviation σ .

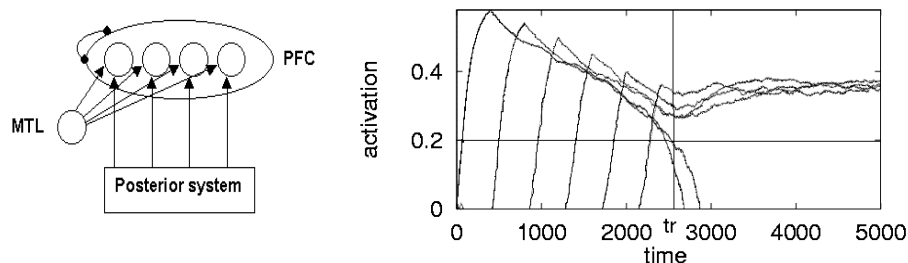


Figure 1: (A) Model description. Items in the capacity-limited short-term memory system, associated with the prefrontal cortex (PFC), are represented by cell assemblies, which receive sensory input from the posterior system and episodic reactivations from the medial temporal lobe (MTL). (B) Activation trajectories of PFC unit for a sequential presentation of six items; only the last four items are retained.

An illustration of the active maintenance in this system is shown in figure 1b, where the inputs to the model are activated sequentially (for 450 iterations) corresponding to the presentation of a sequence of words in a STM experiment. Notice that at each iteration, all units are updated and not only the one which receives input. When $F(x)$ is above a certain threshold, φ ($\varphi = 0.20$ for all simulations), the item is said to be in active memory.

As can be seen in figure 1b, after stimulus offset, the representations are still active in the absence of further input. This is consistent with neurophysiological data showing sustained neural activity during the delay interval between presentation of items and recall probe [4,9].

Episodic memory. We assume that when an item is in active memory it is encoded in episodic memory [10,11]. In our model, the episodic trace strength S is a function of the time that the item was in active memory and its activation level during that time as computed by

$$S_i = \int_0^t \theta[F(x_i) - \phi] dt \quad (2)$$

$$\theta(x) = x, \text{ for } x > 0 \text{ and } \theta(x) = 0, \text{ otherwise}$$

When an item is retrieved from active memory, its episodic strength is increased from its original value to a higher value S^r . This is a simple way of implementing the episodic learning during retrieval and a mechanism of output interference.

Retrieval. At retrieval, an item can be reported when i) it is in active memory (AM) with probability $P(AM)$ or ii) it is not active, but retrieved from episodic memory (EM) with probability $P(EM)$. Within a specific trial, we assume that when an item is in AM there is a probability of 1 that the item will be reported (collapsed across trials, however, this will average to a continuous probability), whereas recalling from EM is probabilistic (even within a trial). The probability, $P(\text{recall})$ of correctly recalling item i at time of retrieval, t_r , is thus computed as:

$$P_i(\text{recall}) = P_i(AM) + [1 - P_i(AM)]P_i(EM) \quad (3)$$

where

$$P_i(AM) = 1 \text{ for } F[x_i(t_r)] > \phi, 0 \text{ otherwise}$$

$P(EM)$ is determined by assuming that all episodic traces are reactivated with a parameter c , which can be seen as the cumulative output of the medial temporal context system. We also assume that retrieval from episodic memory is a competitive process between all traces of retrieved (rS^r , where r is the number of retrieved items) and non-retrieved items of the current trial, n , and between the traces of items from previous trials, m .

$$P_i(EM) = cS_i \frac{S_i}{\sum(S_j) + rS^r + Z^n}, \text{ for } P_i(EM) < 1 \quad (4)$$

$$P_i(EM) = 1, \text{ otherwise}$$

Where the term Z^n is defined by $Z^n = \sum[\delta^{n-m} \sum (S_{j,m})]$. According to equation 4, the retrieval probability $P(EM)$ is a function of the relative and the absolute strength [11]. The term Z^n in the denominator, which changes from trial to trial, n , refers to the absolute strength of episodic traces of previous trials, consisting of an exponentially decreasing weighted summation from previous trials, m , with δ ($\delta < 1$) as the parameter governing the extent with which traces from previous trials interfere with the retrieval of items from the current trial. This term becomes relevant when we discuss proactive interference.

The parameter values used in the simulations in this chapter were kept as similar as possible to those used in previous work [2] with $\lambda = 0.99$, $\alpha = 2.0$, $\beta = 0.15$, $I = 0.33$, $\sigma = 0.8$, $c = 0.02$, $\delta = 0.4$, $S^r = 350$, and presentation duration for each item is 500 iterations¹. In all simulations reported below, the number of competing units in the system exceeds the number of list items.

3 Brown-Peterson Forgetting Functions

The activation-based system described has a limited capacity [1, 2]. When this capacity is exceeded, either by incoming new information related to the task, or by material related to another (distractor) task, forgetting occurs. This is consistent with the memory literature that suggests that forgetting is due to displacement of items from active memory and to increase in competition at retrieval from episodic memory. Here we focus on a forgetting paradigm that attracted a lot of attention and provided important insight in the nature of forgetting.

3.1 Displacement

In the paradigm known as the Brown-Peterson task, participants are presented with a short (subspan) list of items, which they have to report after a filled distractor interval of varying duration. The typical finding (averaged over repeated trials) is a decrease in recall performance with increasing distractor duration. Brown [12] and Peterson and Peterson [13] explained this pattern of results in terms of decay-based forgetting of information over time. However, later work has shown that this view can not account for several effects in the forgetting paradigm, which can readily be accounted for by a displacement type of forgetting [10,14].

Displacement refers to the process whereby items are removed from active memory whenever new items enter the system, exceeding its limited capacity (illustrated in Fig 1b). The forgetting functions (recall as a function of the number of intervening distractor items processed) predicted by the model are shown in

¹ The actual values of the parameters do not change the qualitative pattern of simulations, although different paradigms require some deviations from these values reflecting task procedural differences. Wherever parameter values deviate from the ones listed here, it is mentioned in the caption of the corresponding figure and briefly discussed in the text.

Figure 2a,b. The asymptote defines performance when the items are retrieved from episodic memory only, while the forgetting rate is a function of displacement from active memory². A number of effects in the Brown-Peterson forgetting paradigm found in the literature are simulated below.

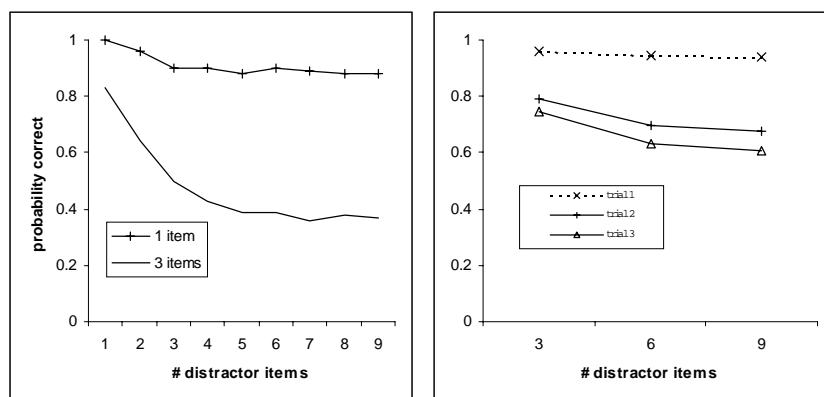


Figure 2: The effects of (A) listlength (1 items vs 3 items; $t = 400$, $c = 0.003$) and (B) proactive interference in the Brown-Peterson paradigm.

3.2 Listlength and Proactive Interference

The probability of items being displaced increases with listlength. Figure 2a shows results of a simulation of the listlength effect obtained in a Brown-Peterson task³. As found in experiments, longer lists reach a lower asymptote than shorter lists [16]. In the model, items in long lists not only compete with distractor items but also with each other. When all items are displaced from active memory, only the episodic memory trace contributes to performance. The lower asymptote for longer lists is due to more competition at retrieval from episodic memory.

Investigators [16,17] have pointed out that performance decreases with increasing number of previous trials. This proactive interference (PI) is strongest at long retention intervals (figure 2b). Research focusing on response times distributions suggest that PI is due to a memory search through a larger set than the set of list items [18]. Episodic traces of previous trials exert competitive influence during retrieval of current list items. In the model, PI is incorporated by allowing

² Displacement is different from retroactive interference, being insensitive to the similarity between list items and distractor material [15].

³ The smaller number of iterations (compared to the default value) reflects the presentation modality of the words, where auditory presentation is relatively fast compared to typical presentation duration in the visual modality. The small value for the contextual output reflects the short time participants received for giving their response.

episodic traces from previous trials to compete with the traces from the current trial, n , with a factor δ^{n-m} , where $\delta < 1$ and m is the trial number of the competing trial (see equations 4 and 5). As the effect of PI is only present for trials 2 and onwards, the first trial shows a strongly attenuated forgetting function. However, with increasing trial number, the competition increases, but has its effect only at long retention intervals as only then all items are displaced from active memory and performance relies exclusively on retrieval from episodic memory. These two processes, displacement from active memory and competition in episodic memory underlie the model's ability to produce the interaction between trial number and retention interval.

4 Modelling Free Recall

Free recall is one of the most studied forms of recall from immediate memory and it is beyond the scope of the present chapter to review all of the results reported in the literature. We focus here on how the activation-based model accounts for primacy and recency effects in immediate, delayed and final free recall and effects of variables that influence retrieval from episodic memory (listlength and proactive interference)⁴.

4.1 Serial Position Functions

When participants are presented with a sequence of items and are requested to recall those items (in any order), a typical pattern emerges. This pattern shows better recall for items at the beginning (primacy) and end (recency) of the list (figure 3b, solid line). Many investigators have put forward different accounts for the shape of the serial position function obtained in free recall. The activation-based model explains this shape in similar terms as dual-store models [10,19,20].

The model accounts for *primacy* effects because when items are activated, episodic traces are formed until the items are deactivated below the threshold ϕ through displacement. The very first item will reach a higher level of activation than the second, since it does not need to compete with already active representations (see figure 1b); the second item receives inhibitory influence from the first one when it is activated and every subsequent representation has to counteract the inhibitory influence of the already active ones. This results in decrease in level of activation and thus of the episodic strengths (see equation 2) over the first serial positions and thereby of the recall probability of these items generating primacy.

The *recency* effect is due to the fact that the final items of the list are in active memory at the time of retrieval and have a high probability of being output, resulting in the (S-shaped; [21,22]) end peak of the serial position function. As the

⁴ The noise parameter in the simulations of free recall was increased to 1.0 to reflect the increased task complexity (i.e strategies) that are likely to amplify fluctuations in activation levels.

middle-list items have been displaced from active memory, they do not benefit from primacy nor from recency, resulting in the flat middle portion.

When recall is prompted immediately, the episodic strengths of the recency items are lower than those of the pre-recency items. This is due to the shorter duration that the recency items were in active memory when retrieval started (t_r) and therefore the less time was available for episodic encoding (see equation 2 and figure 1b). Figure 3a shows the contributions from active and episodic memory. In figure 3b (solid line) these contributions are put together (using equation 3) to create the total serial position function. Although the final items have lower episodic strengths than pre-recency items their presence in active memory ensures higher probabilities of recall accounting for an overall recency effect (Fig 3b, solid line).

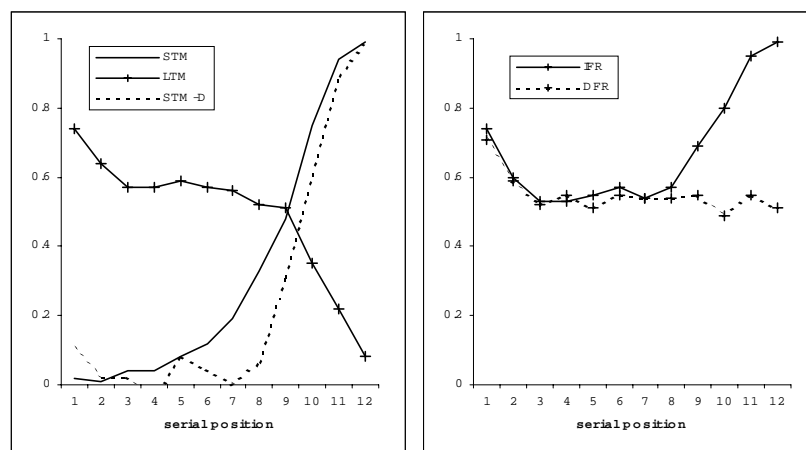


Figure 3: (A) The contributions of LTM (solid line with crosses) and the actual and estimated (from delayed recall) contribution of STM (solid and dotted line respectively). (B) Serial position functions of immediate (IFR) and delayed free recall (DFR).

4.2 Delayed and Final Free Recall: flat versus negative recency.

When a distractor task is interpolated between list presentation and recall, a flat serial position function, at the recency positions is found [23; figure 3b dotted line]. The model explains performance in a delayed recall task similarly to the way it explained forgetting in the BP task. When distractor items are presented, the final list items are displaced from active memory by new items of information related to the distractor task. We assume that during this displacement, episodic traces are still formed (according to equation 2), resulting in similar episodic strengths for recency as for pre-recency items (figure 3b). As performance in this task is mediated primarily by retrieval from episodic memory, a flat 'recency' portion is obtained.

In some experiments, participants are required at the end of the experiment (after performing a series of trials of immediate free recall) to report all items seen during the experiment. The typical result is a *negative recency* on the *final recall* test for items that were not reported during the immediate free recall trials [24]. This effect can be naturally explained in the model, as a result of the negative recency of the pure episodic traces (Fig. 3a; solid line with +s). To do this we only have to assume that unlike in the typical distractor tasks, memory retrieval interferes with episodic encoding. It is possible that typical distractor tasks interfere less with memory encoding than retrieval operations, because participants do not immediately start with the distractor task (switching time), whereas at retrieval the start of the process is much faster, causing the episodic traces to be ‘frozen’. Consistent with this, when distractor tasks are presented at a fast rate, negative recency can be obtained in delayed free recall [25].

4.3 Estimating STM Capacity

Investigators have used various methods to estimate the contribution of short-term memory in immediate free recall. When the long-term memory contribution is known, the short-term memory contribution can be estimated by using equation (3). However, because of negative recency in episodic trace strengths immediately after the list, the actual contribution of short-term memory will be underestimated (see [26] for discussion) when the performance for middle-list items [20] or performance in delayed free recall [27] is used as an estimate of the long-term memory contribution. To illustrate this, we plot the STM contribution estimated by using the performance in the delayed free recall as an estimate of the LTM contribution (dotted line in figure 3a). The actual contribution of STM (solid line) is 3.99 while the estimated contribution is 3.08, an underestimation of 0.91 items. This explains the lower estimate of STM capacity using these methods (in the range of 2-3 [14]) than those using a diversity of other converging methods (in the range of 4 ± 1 [28], see [26] for other methods).

4.4 Listlength and Proactive Interference

One of the robust findings in memory literature is the listlength effect [21,22]. With increase in the number of items to be retained, performance for pre-recency items decreases, while no effect is found at recency. The model explains this effect (figure 4a) through the increase in competition at retrieval from episodic memory (see equation 4). As the recency items are reported from active memory, listlength does not affect the recency portion of the serial position function.

As discussed in the previous section, proactive interference also affects retrieval from episodic memory. Therefore it will only affect the pre-recency portion of the serial position function (figure 4b [29]). In the simulations, the contribution from episodic memory decreases from 5.92 to 4.39 (normalised to 12

items) with increase in listlength and from 5.92 to 4.23 due to proactive interference. The contribution from active memory is constant (3.99) for all conditions.

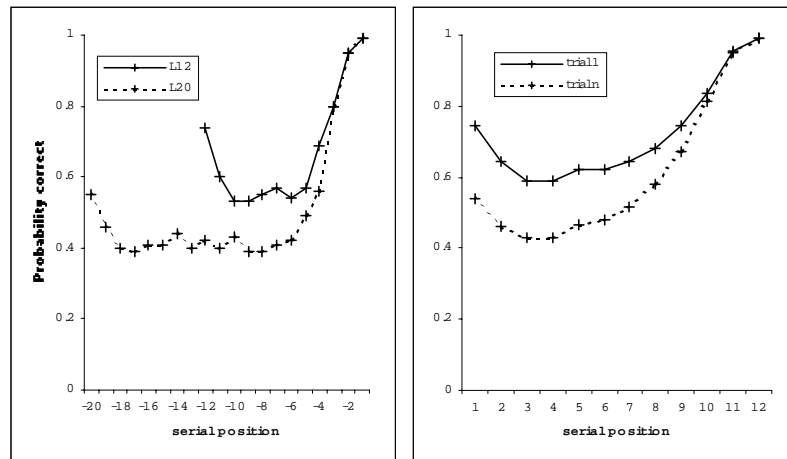


Figure 4: Simulations of the effect of (A) listlength and (B) proactive interference in immediate free recall.

5 Modelling Cued Recall

In the model, forgetting within a single trial is due to the dynamics of self-excitation and lateral inhibition. In this section, we concentrate on two predictions made by the model, which were tested in experiments and can be understood through the complementary dynamics within the system. Category cued recall was used in order to avoid the complexities related to strategy selection and competition between items at retrieval. Therefore the probability of retrieving item i from episodic memory equals cS_i (eliminating the competitive factor in equation 4)⁵.

5.1 Listlength Effects

The lateral inhibitory mechanism in the model can be seen as two different types of inhibition; forward and backward. Backward inhibition can be considered the force behind the displacement process such that previous activated items will be deactivated by the backward inhibitory influence from newly activated

⁵ As only one speeded response is needed in cued recall, the contextual output contributes less to the overall performance, as would have been when more time for retrieval is available (as in free recall). Therefore the parameter reflecting contextual output is substantially smaller than in the previous section.

representations. However, the forward inhibition causes newly activated representations to reach a lower level of activation than if that representation was activated in the absence of already active representations. The model predicts, in contrast to decay-based theories and theories based on retroactive interference only, that the probability of correct recall is lower with increasing number of previous items. Figure 5a shows a simulation of data obtained by Haarmann and Usher [1]. As in the data, when the two listlengths are equated for the time to and the number of items between presentation and recall, it can be seen that listlength interacts with serial position. This pattern is due to the forward inhibition of items already in active state.

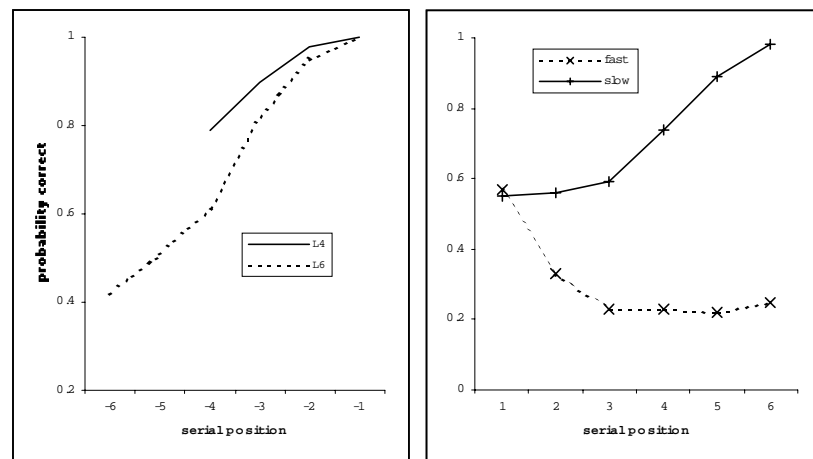


Figure 5: (A) Simulation of the listlength effect in category cued recall, $c = 0.001$. (B) Presentation rate effects in category cued recall. All parameters were equal as in (A) except for stimulus duration (150 vs 400 iterations per item).

5.2 Presentation Rate Effects

Another prediction that the model makes is that at very fast presentation rates, early list items may generate forward inhibition that may prevent the activation of later items. With slow presentation rate, items can reach an activation level where it can overcome the forward inhibition of previous items (see figure 1b). In contrast, with very fast presentation rate, items will not have enough time to reach that level. In behavioural terms, the model predicts a shift from recency to primacy with increasing presentation rate. This prediction was tested and supported in an experiment by Davelaar and Usher [30] in a category cued recall test, where lists of six words were presented at 'slow' (800 ms) and fast (100 ms) presentation rates. Figure 5b shows simulation of the behavioural data in the experiment. This result challenges decay-based theories and theories based on temporal distinctiveness [31]

as these theories would predict that the serial position curve in the fast condition will still show a recency effect. It should be noted that this effect only occurs at very fast presentation rates. However, the model has also been used to model presentation rate effects in the normal domain [2].

6 Discussion

In this chapter, we have presented an activation-based theory based on neurocomputational work and applied it to a large body of memory data. We have shown that the model displays a displacement type of forgetting. The model's behaviour, driven by its lateral inhibition, was tested and supported in experiments and challenges models explaining forgetting as due to retroactive interference or decay only. The presented model is able to account for findings that are problematic for theories based on retrieval through temporal distinctiveness, such as presentation rate effects and negative recency.

The model inherits properties present in the theory of Search of Associative Memory (SAM; [11]), where an item-limited short-term buffer displays a displacement type of forgetting. In SAM, retrieval is i) from STM or ii) from episodic memory. However, the current model is based on activation levels of LTM representations. This feature makes the system sensitive to incoming items and flexible. In a model for selection from memory [32], this flexibility was used to transform the system from one where several representations are active to one where only one representation is active (through neuromodulation) according to the task requirement (active maintenance or response selection). More importantly, the system is not committed to a recency based displacement mechanism where old items are displaced first [21] or all items have equal probability to be displaced [11]. The model, as presented here, shows a more dynamic type of displacement, which depends on external variables like the presentation rate.

We have shown that the activation-based theory is capable of accounting for basic memory phenomena and can be used to make novel predictions. Future work taking into account the contextual [33] and temporal [34] retrieval dynamics and habituation mechanisms at encoding [35], should help to further the understanding of the activation dynamics of memory.

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