Murdock free recall experiments explained with presentation rate dependent logarithmic decay in the Tagging/Retagging Model. Presentation rate dependence similar to intracellular Ca catalysis of endocytosis.

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Abstract:

I show that the free recall data of Murdock (1962) can be explained by the Tagging/Retagging model of short term memory in which a short term memory item is a tagged long term memory item. The tagging (linear in time) corresponds to the synaptic process of exocytosis and the loss of tagging (logarithmic in time) corresponds to synaptic endocytosis. The Murdock recent item recall probabilities follow a logarithmic decay with time of recall. The slope of the decay increases with increasing presentation rate. This is consistent with endocytosis since higher presentation rates lead to a higher frequency of exocytosis which increases the intracellular concentration of Ca ions which in turn increases the speed of the endocytosis process (Sankaranarayanan and Ryan, 2001). The initial Murdock items, with an effective low presentation rate, decay with the slowest logarithmic slope.

Since a slower presentation rate leads to a slower decaying short term memory presentation rate is presumably an important factor in determining the probability of items entering long term memory.

Introduction

In this contribution I show how my Tagging/Retagging model of short term memory (see below) in which short term memory arises from synaptic exocytosis/endocytosis, can explain Murdock's free recall data. Just like for cued recall and recognition data, the probability of free recall decays logarithmically with time, giving rise to the recency effect, but with the added twist of sufficient increases in presentation rates speed the logarithmic decay. The primacy effect comes about because early items have an effectively lower presentation rate and their logarithmic decay slope is closer to the low presentation rate decay found by Tarnow (2008) in the data of Rubin et al (1999).

The Tagging/Retagging model (Tarnow, 2008 and Tarnow, 2009) states that a short term memory is a tagged long term memory. When a word is read from a display the tagging level increases to 100% and after the word is no longer displayed the tagging level decreases logarithmically to 0%. The tagging level is the probability that a word will be recalled during cued recall and the deviation of the tagging level from 100% is proportional to the subjects' response time delay (explaining the term "retagging") because the word needs to be retagged. The proportionality constant is related to the meaningfulness of the word – the more meaningful, the longer it takes to retag the word. Meaningless words can take 0.3 seconds to tag and meaningful words can take 1.8 seconds to tag (Tarnow, 2008).

In Tarnow (2009) the Tagging/Retagging model was related to the underlying biochemistry. It was proposed that when a word is read by a subject it causes prolonged firing which depletes the Readily Releasable Pool (RRP) of neurotransmitter vesicles at presynaptic terminals (see Fig. 1). The pattern of depleted presynaptic terminals represents the long term memory trace of the word and the depletion itself (the tagging) of this trace is the short term memory. After the action potential firing has slowed down, endocytosis causes the word to decay from short term memory. If the endocytosis is allowed to finish (the word is not read again and is not being rehearsed), the pattern of exhausted postsynaptic terminals becomes invisible and, in our model, the short term memory of the word is gone. The long term memory remains as the metastable pattern of the neuronal excitations.

The Tagging/Retagging explains the linear relationship between response time and response probability for cued recall and recognition (Tarnow, 2008). The evidence for tagging increase/decrease being related to exocytosis/endocytosis includes the shape of the exocytosis and endocytosis curves (linear and logarithmic with time) and also the slopes. The logarithmic decay for cued recall and recognition of words in the high statistic experiment by Rubin, Hinton and Wenzel (1999) has an associated slope of -0.11/second and endocytosis of a variety of cells in mouse hippocampus varies between -0.11 and -0.14/second. Exocytosis takes place in a quasi linear increase with a time. In one example (Dobrunz, 2002) the associated time constant is about 1 second, similar to my finding of 0.3-1.8 seconds for words (going from nonsense to meaningful).

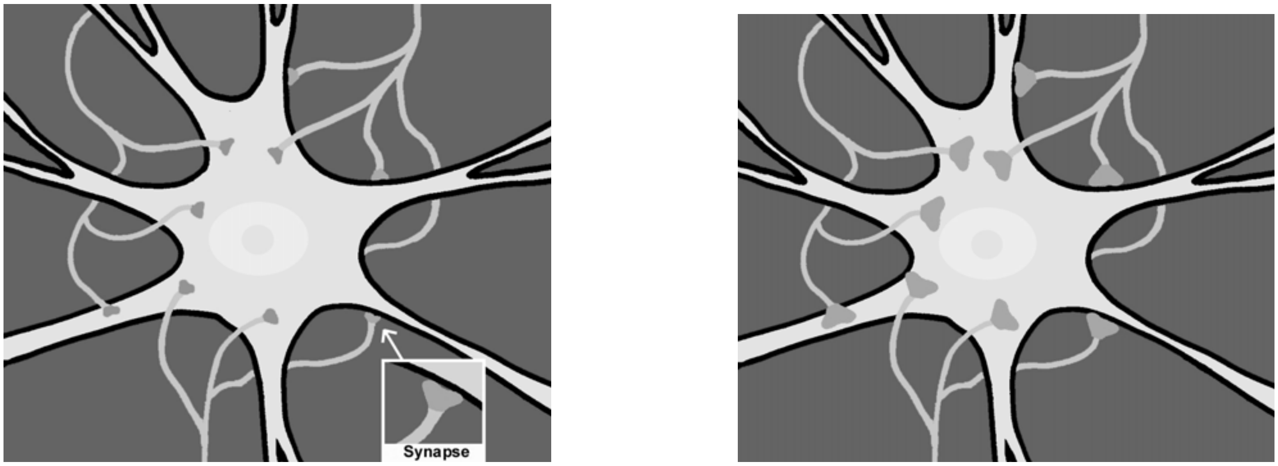

Fig. 1. Stylized drawings of proposed short term memory. In the left panel is shown a neuron with synapses before tagging/exocytosis. In the right panel is shown the same neuron with expanded synapses after tagging/exocytosis (The synapses are shown as expanded since the vesicles fuse with the presynaptic membrane increasing its surface area). In the right panel the neuron is part of a tagged long term memory trace.

A separate contribution will describe the difficulties of accounting for the Murdock free recall data using the standard model (Tarnow, in preparation).

The Murdock (1962) data reanalyzed

The Murdock (1962) data can be downloaded from the Computational Memory Lab at University of Pennsylvania (http://memory.psych.upenn.edu/DataArchive). I calculated the average recall positions for the various items to get as accurate an estimate possible of the exact time that an item was recalled (a one second average delay for each recall position was added). The results, in which the probabilities are displayed against recall time are shown in Figs. 2 (a) and (b). In Fig 2(a) we see the results from the three experiments with the 0.5 items/sec presentation rate. Without the initial three items (right panel) all the remaining items form a straight line, a logarithmic time dependence, just as is found for high statistic short term memory experimental data (see Tarnow, 2008 for a discussion of the Rubin et al, 1999 data). In Fig 2(b) we see the results from the three experiments with a 1 item/sec presentation time. The initial logarithmic time constant is the same for the three experiments with the 1 item/sec presentation rate and higher than for the 0.5 item/sec presentation rate. With the exceptions of the three initial items, items with the same presentation rate lie on the same curve. The curve for the higher presentation rate looks for low recall probabilities a little different, with more of a "hockey stick" shape. This latter shape may be due to the search time starting to add ??? for items that are almost forgotten.

We try a separate logarithmic time decay also for the initial three items, see Fig. 3. Here is shown the fitted decay of the first list items, second list items and third list items grouped together with the average of the most recent list item (which did not decay yet and is a good initial point). For the 0.5 items/second presentation rate the decay appears to be logarithmic across the three experiments; the fit is not as good for the 1 item/second presentation rate. It seems that for recall probabilities of 0.2 and lower the logarithmic fit may break down which suggests that another mechanism starts to dominate such as the search. If it does not break down, it gives us an upper limit in time for recall when the curve crosses the t axis. For the fit in Fig. 2 (a) it is 70 seconds and for the fit in Fig. 2 (b) it is 15 seconds. Beyond these times there are no more short term memory left.

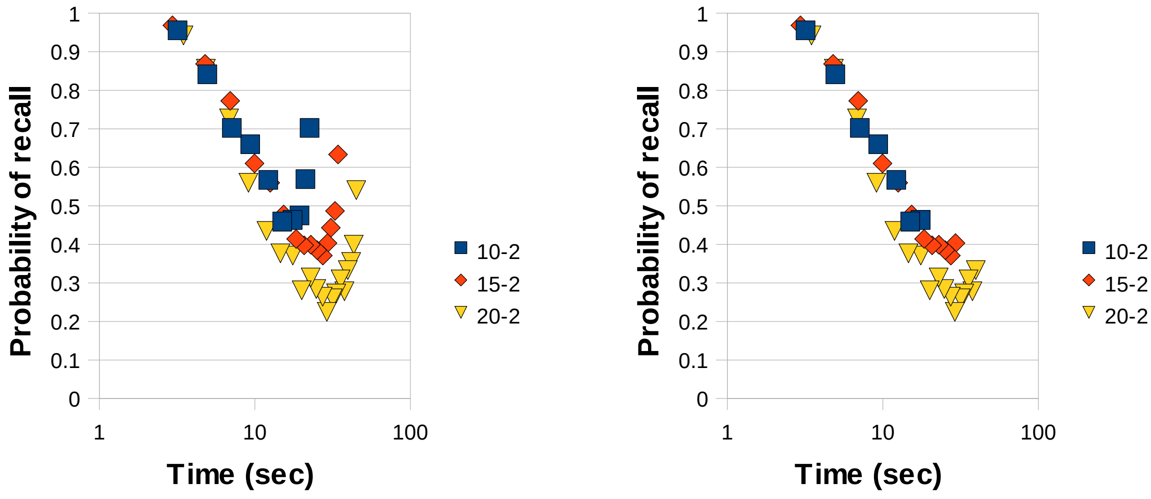

Fig. 2 (a). Probability of recall of an item as a function of the difference in time between study time and actual recall time for the three conditions with presentation rate of 0.5 items/second. The time axis is logarithmic. The interrecall time was estimated at 1 second. The left panel includes all data points, the right panel includes all but the initial three data points. Note the common logarithmic dependence (a straight line) that appears without the initial three data points. The labels 10-2, 15-2 and 20-2 stand for 10, 15 and 20 words at a presentation rate of one every two seconds.

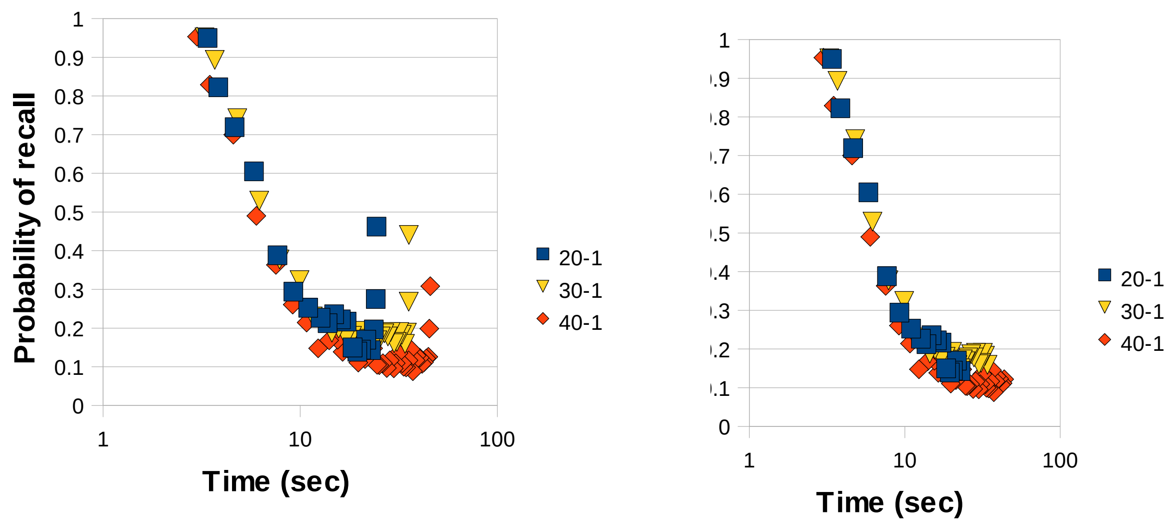

Fig. 2 (b). Probability of recall of an item as a function of the difference in time between study time and actual recall time for the three conditions with presentation rate of 1 item/second. The time axis is logarithmic. The interrecall time was guessed at 1 second. The left panel includes all data points, the right panel includes all but the initial three data points. Note the common logarithmic dependence (a straight line) that appears without the initial three data points. The labels 20-1, 30-1, 40-1 stand for 20, 30 and 40 words at a presentation rate of one every second.

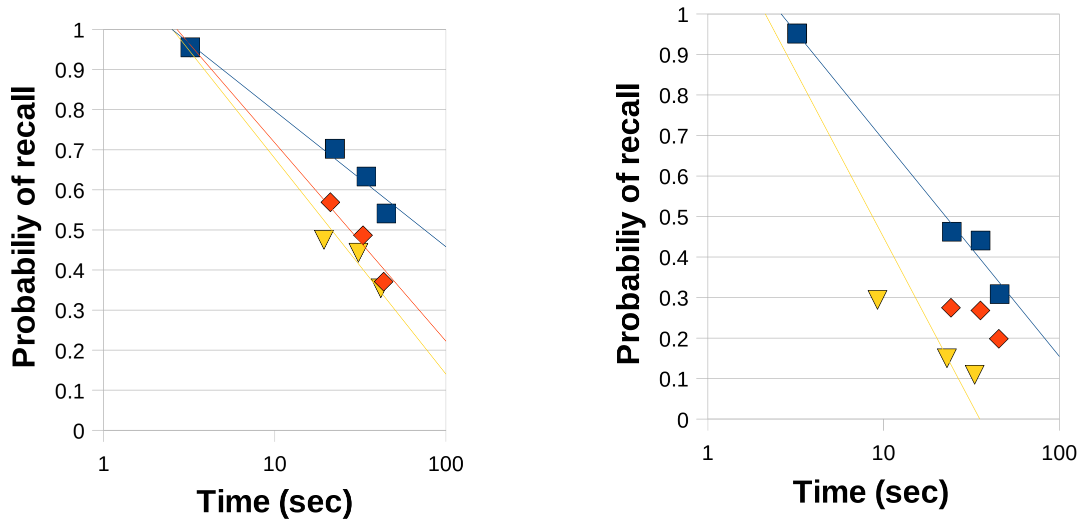

Fig. 3. Probability of recall for the initial three items (first items in squares, second items in diamonds, third items in triangles) in the three conditions with presentation rate of 0.5 items/second (left panel) and 1 item/second (right panel). Note the slower decay associated with the 0.5 item/second presentation rate and also associated with the item order (lowest for the first item).

The slope of the logarithmic curve for a high statistic measurement by Rubin, Hinton and Wenzel (1999) calculated in Tarnow (2009) was -0.11/second (see Fig. 4). The presentation rate was 0.17 items/sec (5 second word display and 1 second null display). The slopes resulting from the Murdock (1962) data show well defined trends, see Table 1. The slopes vary from small to large presentation rates. It also vary from the first item (least steep) to recent items (steeper). Since the first item did not have an item preceding it, it effectively has a lower presentation rate explaining the shallower slope.

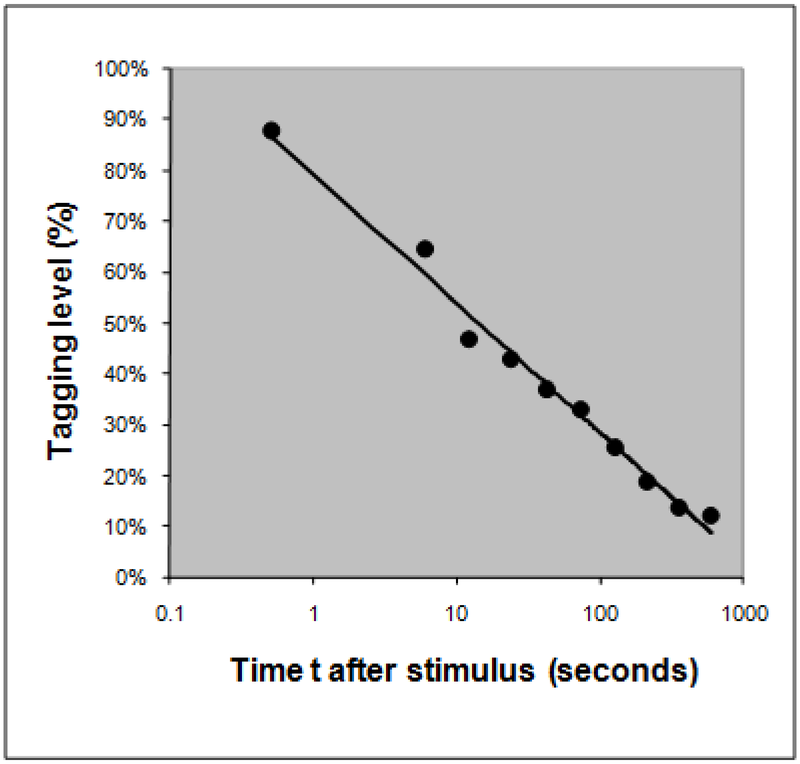

Figure 4. Tagging remaining averaged over recall and recognition memory items from Tarnow (2008). The curve represents a two parameter logarithmic fit, moving t=0 seconds to t=0.5 seconds to avoid a divergence.

That short term memory decay of a particular item is strongly related to the presentation rate makes intuitive sense. If we increase the presentation rate more items are injected into short term memory but they decay faster. Thus when reading a paragraph of text, a presentation rate of several words per second, most of us probably do not remember the individual words.

Presentation rate (items/second)	First item decay rate (items/second)	Second item decay rate (items/second)	Third item decay rate (items/second)	Recent items decay rate (items/second)
0.17*				-0.11*
0.5	-0.15	-0.21	-0.23	-0.29
1	-0.23	-0.29	-0.36	-0.69

Table 1. Slopes of logarithmic fits to data from Murdock (1962) and Rubin, Hinton and Wenzel (1999). The * denotes a recognition and cued recall experiment.

Presentation rate and Ca catalyzed endocytosis

Sankaranarayanan and Ryan (2001) showed how intracellular calcium ions regulate the speed of endocytosis. They found that the higher the calcium concentration the faster the endocytosis proceeded. In Fig. 5 we see that the decay rates almost double as the intracellular calcium concentration is doubled (see also Table 2). Exocytosis is triggered by the influx of calcium ions and repeated exocytosis increases the intracellular calcium concentration. High presentation rates would increase the amount of exocytosis per unit time with the associated increase in intracellular calcium ions speeding up the endocytosis.

The effect of the presentation rate is related to the finding that increases in exocytosis lead to increases in intracellular calcium which leads to increases in the rate of endocytosis. Sankaranarayanan and Ryan (2001) found that intracellular levels of calcium tightly regulates the speed of endocytosis.

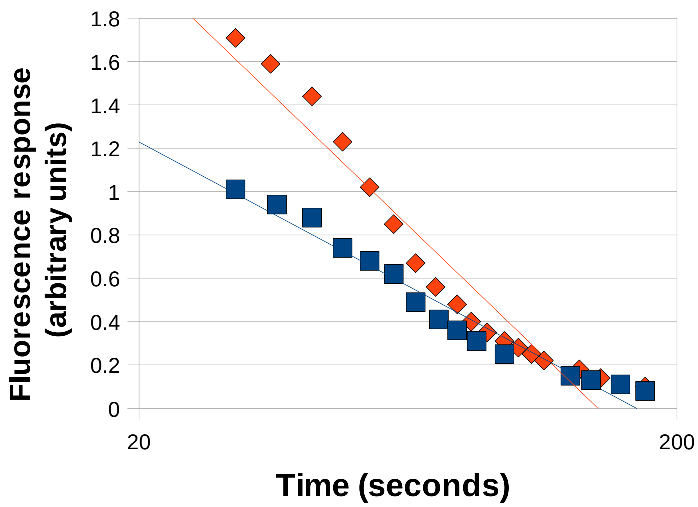

Fig. 5. Data from Fig. 4C in Sankaranarayanan and Ryan (2001) of flourescence (arbitrary units) and time (seconds). For a 1 mM concentration of Ca (squares) the logarithmic fit decays with a -0.6 items/second slope, for a 2 mM concentration of Ca (diamonds) the slope is -1.0 items/second.

Intracellular calcium concentration (mM)	Decay rate (items/second)
In vivo	-0.11 to -0.14
1*constant	-0.58
2*constant	-1.04

Table 2. Slopes of logarithmic fits to data from Sankaranarayanan and Ryan (2001). The intracellular calcium concentration was manipulated via the extracellular calcium concentration. The actual intracellular calcium concentration is not known except that it was shown to be proportional to the extracellular calcium concentration.

Summary

Previously (Tarnow, 2008) I showed that the Tagging/Retagging model explains the slow presentation rate in the cued recall and recognition experiments by Rubin et al (1999). The free recall experiments of Murdock (1962) adds another level of complexity in the bowing of the curve of recall probability versus item number. In this paper I showed that the bowing is a result of presentation rate dependence of short term memory. The faster the presentation rate the steeper is the logarithmic decay curves. When the presentation rate is not well defined, for the initial three items, the probabilities fall on separate logarithmic curves consistent with an effectively lower presentation rate.

I related the presentation rate dependence to a known intracellular calcium dependency of the endocytosis rate (Sankaranarayanan and Ryan, 2001): a higher presentation rate leads to more exocytosis which leads to a higher intracellular calcium rate which leads to a steeper logarithmic decay of short term memory.

The question arises when is the presentation rate optimal in the sense of the subject remembering the maximum number of items per unit study time? A high presentation rate with high information input leads to quick decay while a low presentation rate limits the information input but keeps information in memory longer. In the word memory experiments used for this paper the number of words in the initial logarithmic part of the curve remembered increases as the presentation rate is lowered from 1 item/second (3 words) to 0.5 items/second (8 words) to 0.17 items per second (more than 100 words).

Optimizing short term memory is presumably crucial for long term memory retention: There must be a relationship between how long an item stays in short term memory and the probability of the appropriate association making it into long term memory with the associated protein synthesis (Kandel 2001). A memory item that lasts 2 minutes in short term memory should be much more probable to have an association added to it in long term memory than an item that lasts 20 seconds. In other words, if we want to increase long term retention the data suggests that decreasing the presentation rate is crucial.

The importance of a decreased presentation rate on long term cannot be emphasized enough. It suggests a basis for memory loss in adults with a lot of things going on, a basis for the importance of slow music practice, a basis for long term memory deficiencies for people with attention deficits who may be artificially increasing the presentation rates of their surroundings.

References

LE, Dobrunz. (2002) Release probability is regulated by the size of the readily releasable vesicle pool at excitatory synapses in hippocampus. : Int. J. Devl Neuroscience Vols. 20: 225-236.

Kandel, E.R. (2001). The Molecular Biology of Memory Storage: A Dialogue Between Genes and Synapses. Science, pp. 1030-1038.

Murdock Jr., Bennet B. The serial position effect of free recall. Journal of Experimental Psychology. Vol 64(5), Nov 1962, 482-488.

Rubin DC, Hinton S, Wenzel A.(1999). The Precise Time Course of Retention. Journal of Experimental Psychology: Learning, Memory and Cognition, Vols. 25:1161-1176.

Sankaranarayanan S, Ryan TA (2001). Calcium accelerates endocytosis of vSNAREs at hippocampal synapses. Nature Neuroscience 4, number 2, 129-136.

Tarnow. (2008). Response probability and response time: a straight line, the Tagging/Retagging interpretation of short term memory, an operational definition of meaningfulness and short term memory time decay and search time. Cognitive Neurodynamics, 2 (4) p. 347-353.

Tarnow. (2009) Short term memory may be the depletion of the readily releasable pool of presynaptic neurotransmitter vesicles of a metastable long term memory trace pattern. Cognitive Neurodynamics.