

Running head: comparing mechanisms of sequential selection

Sequential Retrieval and Inhibition of Parallel (Re)Activated Representations:
A Neurocomputational Comparison of Competitive Queuing and Resampling Models

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Abstract

Sequential behavior is observed in various domains of cognitive psychology, including free recall paradigms. In this paper, within a neurocomputational framework resampling (RS) mechanisms are compared to competitive queuing (CQ) mechanisms. While both types of implementations select the most active representation, the subsequent inhibition is at the level of selection for RS-models and at the level of (re)activation for CQ-models. It is shown that despite the overwhelming success of CQ-models in serial recall (with regard to types of sequencing error), RS-models outperform CQ-models with regard to interresponse times (IRT) in a free recall task. Additional analyses show that decay of response suppression reduces the difference between the models. The RS-model is sensitive to the size of the search set and accounts for memory selection performance in patients with Alzheimer's dementia or Huntington's disease. Finally, a non-mnemonic clustering behavior is observed, which is related to the dynamical process of selection mechanism.

Keywords: Competitive queuing; memory retrieval; recall latencies; resampling; Alzheimer's dementia; Huntington's disease

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1 Introduction

In many complex systems that exhibit sequential ordering of actions, a selection mechanism converts simultaneously activated representations into a sequence of actions. The simplest form this selection mechanism can take is one by which one action is selected and then executed, after which another action is activated (from zero), selected and executed and so on. However, research within psychology has demonstrated that this type of selection mechanism is inconsistent with detailed error analyses in serial recall (Henson, et al, 1996) and typing (see Salthouse, 1986), as it would, for example, be unable to account for the smooth transitions between successive actions. Instead, evidence points towards a two-stage mechanism by which in the first stage, all task-appropriate representations are activated in parallel (instead of sequentially) and in the second stage representations are selected one at a time to produce its corresponding action. Although most of the initial knowledge was gathered from motor behavior, with typing as one familiar example (see the review by Salthouse, 1986 and its references), researchers have suggested that this two-stage mechanism may also be central to other forms of sequential behavior, from walking through a room or grasping a mug to producing speech, preparing coffee, or even memorizing words. Given this centrality of serial ordering in our daily lives, it may come as no surprise that computational modelers have developed models through which simultaneously activated representations produce serially ordered actions. Two of these models are highlighted in this paper and relate to sequential retrieval from memory.

The reason for focusing on memory retrieval is two-fold. First, a long tradition of mathematical sampling models has led to a wide range of memory models that are currently used to account for memory phenomena. During the 1990s, a new generation of models emerged that were embedded in a connectionist framework and used a particular mechanism called “competitive queuing” that is able to transform an activation gradient over to-be-reported memoranda into a sequential order of reports. As will

be argued in this paper, the two mechanisms make different predictions with regard to the timing of actions. This difference may be important beyond the memory literature in other areas in which sequential selection of parallel-activated actions is a common implementational choice. A modeler would need to know which mechanism to use to account for a particular type of data and empirical researchers (psychologists, biologists) would need to know what the behavioral signatures of these mechanisms are. For example, it is useful to know that if a certain mechanism underlies higher-order behavior (e.g., parallel activation and sequential selection), specific implementational details may lead to different behavior at a more finer-grained level (in this paper, the profile of the timing between successive actions). Second, in recent years evidence has been found that favors some components and disfavors other components of competitive queuing. Given the wide applicability of a two-stage activation-selection mechanism, it could be beneficial to reexamine the components with computational-analytic tools that are currently available. This paper aims at directly comparing two well-known mechanisms that were never before compared in this way. The memory literature contains much of the data needed for this comparison; this paper uses this data in an attempt to validate these models.

In this paper, the term “action selection” is used loosely and relates to the selection of representations that when executed has a behavioral consequence. Within this definition, retrieving a word from memory will eventually lead to the spoken or typed version of that word. Similarly, retrieving a plan of actions (e.g., making coffee) will eventually lead to the selection of a series of goal-directed movements. This paper therefore deals only with situations in which a higher-order action plan (retrieving memoranda) activates lower-order plans (produce a word) that eventually lead to a behavioral response that can be measured in real-time. The paper does not deal with situations that require unpacking of a motor sequence, such as walking or throwing a ball.

The next section outlines the competitive queuing and sampling-mechanisms, which is then followed by a brief introduction of the retrieval latencies that differentiates these mechanisms. A generic computational model is presented in which both mechanisms are implemented. This model is then used to

demonstrate the impact of the different mechanisms on retrieval latencies and is used to show its ability to qualitatively account for psychological data through a number of simulations. The paper closes with implications of the computational evaluation for models of memory, action selection, and other domains.

2 Competitive queuing versus resampling

This section presents the two mechanisms that will be compared in a generic model. Before describing these mechanisms, it should be noted that models of recall memory fall into either one of two almost separate literatures. On the one hand are the models that deal with serial recall, while on the other hand are models that deal with free recall. Each literature has its own debates, model implementations, empirical methods and focus on what is relevant in the data. This paper focuses on free recall or sequential selection in any order for three reasons. First, neurocomputational models of free recall are being developed (Davelaar, et al, 2005, 2006), but still rely on the non-dynamic retrieval process, as used in current mathematical models. The question is how to extend this new neurocomputational work by borrowing dynamical mechanisms of sequential selection from the literature on serial recall. Second, detailed analyses of retrieval latencies exist for free recall (see section 3) that form a benchmark against which to evaluate the model. Although data for serial recall exists (Farrell & Lewandowsky, 2004; Kahana & Jacobs, 2000), similar rigorous analyses have not yet been conducted. Third, as free recall is per definition free from any constraints on output order, the task is highly suitable to investigate mechanisms of sequential selection. Like the properties of inherent circadian rhythm in agents (man, animal, plants) can be investigated by taking away external cues of time, so can the sequential selection mechanism of agents be investigated by taking away external constraints of sequencing (i.e., the requirement to produce actions or report words in a pre-specified order). Given that sequential selection is central to behavior in general, the analyses in the following support the view that measuring latencies between successive behaviors can provide insight into the type of the underlying selection mechanism that led to the sequence of behaviors.

2.1 Competitive queuing

Grossberg (1978a,b) developed a model in which sequential output can be obtained from parallel activation in a dynamical model with feedforward excitatory and feedback inhibitory connections. The basic architecture is shown in Figure 1. The profile of activations in the activation layer is fed into the selection layer. This profile may originate from an activation-based short-term buffer, or from long-term memory with or without a static signal. There are three critical components. First, the activation profile shows the degree of activations for all yet-to-be executed plans, with the desired sequential order being from most active to least active. Second, the activations compete, i.e., the representations in the activation layer all inhibit each other. A nonspecific arousal signal arrives at the selection layer which brings the activations above a response threshold. Third, as soon as a plan is selected (e.g., for moving the fingers to the desired key for typing, or flexing the muscles for articulation of a word), the representation in the selection layer inhibits the representation it received input from. This prevents perseverative behavior and allows the next-strongest representation to become selected for output.

This two-layer output module produces all actions corresponding to the activated representations in the correct serial order with smooth transitions from one selected action to the next. In addition, by adding noise to any of the three critical components, it can account for errors in sequencing seen in human behavior, such as seen in typing (e.g., Salthouse, 1986) and memory for serial order.

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In the 1990s, starting with Houghton (1990), this architecture received much attention in the memory literature (Brown, Preece & Hulme, 2000; Burgess & Hitch, 1999; Henson, 1998; Page & Norris, 1998; see for a review, Page & Henson, 2001) and related areas (planning: Cooper & Shallice, 2000;

spelling: Glasspool & Houghton, 2005; speech production: Hartley & Houghton, 1996) leading to a range of models employing the select-then-inhibit dynamics (see for review, Glasspool, 2005). The models are collectively referred to as competitive-queuing (CQ) models, as the activations are placed in a competitive queue before being selected.¹

It should be noted, however, that these models of serial ordered recall are different than the original Grossberg's model (1978) in at least two critical aspects. First, in Grossberg's model, the inhibition of the representation in the activation layer is complete (i.e., total response suppression), whereas the CQ-models were aimed at capturing errors such as repetitions and thus assumed a need for a gradually decaying inhibition (for a non-decaying inhibition account, see Farrell & Lewandowsky, 2002). If the set of activated representations in the activation layer is called the search set, then Grossberg's model could be referred to as a sampling-without-replacement model and the CQ-models could be referred to as sampling-with-delayed-replacement models. Second, whereas Grossberg's model focuses on producing sequential behavior given a single activation gradient, the aforementioned CQ-models (except the primacy model by Page & Norris, 1998 which follows Grossberg in this regard) have addressed various forms of changing the source of activation during the course of retrieval. A contextual representation is incorporated in those models that changes along a certain dimension (e.g., temporal, absolute, or relative position in the list) and gets linked with the representations of the to-be-remembered items. During retrieval this context signal is replayed leading to serial recall. Not surprising, this context signal may contribute greatly to variations in the timing of actions. However, these models have yet to be extended to account for retrieval latencies.²

Neurophysiological studies support the dynamics assumed in these types of models. For example, Averbeck and colleagues (2002) trained macaque monkeys to draw geometric figures (triangle, square, trapezoid, inverted triangle). After training, the recorded neural firing patterns of neurons in the prefrontal cortex during drawing suggested that representations of all segments of a figure were coactivated before the initiation of the first action. During drawing, the neurons corresponding to the upcoming action

increased and then decreased in firing rate before and after the action, respectively, in the same manner as predicted by Grossberg's model and CQ-models that use a single context representation. However, the results did not show that the activation of the selected-and-then-inhibited representations gradually increased, as is critical in CQ-models to account for repetition errors. Although it is certainly possible that the motor task of drawing figures by monkeys is not comparable to human memory performance, recent research on human memory has questioned the existence of a gradual decaying inhibition and employed other forms of response suppression (Duncan & Lewandowsky, 2005; Farrell & Lewandowsky, 2002, 2004). Nevertheless, the simulation study in this paper (specifically in the Appendix) will consider both the sampling-without-replacement (CQ^0) and the sampling-with-gradual-replacement (CQ^Δ) versions.

2.2 Resampling models

Although the CQ-models gained much success, a different approach to producing sequential retrieval has been employed in global memory models, such as Search of Associative Memory (SAM; Raaijmakers & Shiffrin, 1980, 1981), MINERVA 2 (Hintzman, 1984), and Theory Of Distributed Memory (TODAM; Murdock, 1982). Here, SAM is used to exemplify the retrieval process, which is broken down into three critical components. First, a search set is defined based on available retrieval cues, which in most models is the list context, but could also be categories (e.g., Gronlund & Shiffrin, 1986) or chunks (e.g., Anderson, et al., 1998; Anderson & Matessa, 1997). Second, a single trace is selected (sampled) from the search set and used to recover the full memory representation. This could correspond with recovering the phonemic representation in order to utter the word or the execution of the motor plan for typing the word. Third, after successful recovery, the trace is allowed to compete for resampling if the same cue is used to probe the memory system, but will not produce an output. Due to the possibility of resampling (but not re-recovery) of an item, SAM could be seen as a resampling (RS) or selection-with-replacement model. In order to compare the CQ-model with the RS-model, it is assumed that the first two components of both models are equivalent, and that the critical difference lies in the post-response suppression mechanism.

The assumption in SAM that a resampled representation never leads to an output can be relaxed and the assumption of gradual decay of inhibition could be used instead. Such a model has never been used in the SAM framework, but will be used in the simulation study for completeness.

Functional imaging data supports the view that the brain has separate components for activation and selection (Badre, et al., 2005). For example, in a study by Badre and colleagues, participants performed a number of tasks that have previously been used in investigations on memory retrieval and have been argued to rely to different degrees on the ability to select the correct response among distractors. The authors were interested in whether selection and activation mechanisms are subserved by the same or by different neural substrates. Factor analysis on the behavioral results produced two factors that were labeled as a selection and a non-selection component. These behaviorally-defined factors were associated with variance in different brain regions, with the anterior ventrolateral prefrontal cortex (aVLPFC) and the inferior-temporal cortex (IT) related to activation of information and the mid-ventrolateral prefrontal cortex (mVLPFC) related to selection of task-appropriate representations. This two-stage model of retrieval supports the global memory models, but does not necessarily falsify the CQ-mechanism. Nevertheless, the retrieval dynamics are different for the two mechanisms, as will be discussed in the next section.

3 Retrieval dynamics

This section summarizes the data patterns that will be used to compare and validate the above two models. Recall latencies provide information on the underlying memory processes and distinguish different patient populations.

3.1 Recall latencies

In a series of analytical studies, Rohrer and Wixted (Rohrer, 1996, 2002; Rohrer & Wixted, 1994; Wixted & Rohrer, 1993) investigated the temporal dynamics in free recall of words. This work, which extends the limited number of previous empirical investigations (e.g., Murdock & Okada, 1970; Patterson, Meltzer &

Mandler, 1971; for a review see, Wixted & Rohrer, 1994), provided critical insight regarding the sampling and recovery of items. In a typical experiment, a participant memorizes a number of words and after a distractor task reports as many words as possible in any order. During the retrieval phase, the time taken to retrieve an item is measured as the main dependent variable. The basic findings are as follows. The time needed to retrieve an item increases with the number of items that were memorized (set size effect). The inter-response time (IRT), the elapsed time between two consecutive responses, increases during the retrieval phase and is a function of the number of words yet to be recalled (see Figure 2). These findings have been interpreted to support the RS-mechanism of selection, where the recall latency reflects the size of the search set. The larger the search set, the longer it takes to select an item from the set.

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3.2 Utility of retrieval latencies

The analysis of recall latencies has provided an empirical tool for measuring the size of the memory search set, dissociating the effect of episodic and semantic cues (Rohrer, 2002), and measuring the loss of semantic memory in patients with Alzheimer’s dementia (AD). Rohrer and colleagues (1995), after analyzing the recall latencies (minus the first recall latency), argued that AD-patients have a structural memory deficit. The loss of neural tissue in AD leads to a smaller size of the memory set, which in turn is observed as shorter recall latencies for AD-patients compared to controls. This is in contrast with the longer recall latencies observed in patients with Huntington’s disease (HD) (Rohrer, et al., 1999).

Whereas both AD- and HD-patients have lower total recall compared to controls, the retrieval latencies revealed marked differences.

3.3 Model predictions

As mentioned above, CQ- and RS-models have a stage in which all target representations are activated by a cue. It takes time for the first item to be selected and produce an output. Given that no differences exist

between these two models at this initial stage, both models will produce the same first retrieval latency. However, after the first item is retrieved, in CQ-models the representation of this item is inhibited (is deleted from the queue). As every output is followed by inhibition of the retrieved item representation, there is an ever-decreasing competition during the retrieval phase. This model therefore predicts that the time needed for selecting a new item decreases: IRTs become shorter. In RS-models, the item representation is still activated by the cue and can therefore be sampled, even though it will not be output. The more items have been output the lower the probability (and therefore the longer it will take) that a new not-yet retrieved item will be sampled. This model predicts that the time needed to report the next item depends on the activation gradient and therefore reflects the size of the memory set. This model therefore predicts that the time needed for selecting a new item increases: IRTs become longer.

4 Generic model

In order to evaluate the mechanisms, a generic model is presented in which RS- and CQ- mechanisms can be explored. The main dependent measures are the IRTs and the distributions of recall latencies. As Simulation 1 makes clear that the CQ-mechanism does not capture the IRTs, simulations 2, 3, and 4 only address the RS-model to illustrate its applicability.

4.1 Model architecture

The model consists of 4 layers (see Figure 3). Each layer contains 20 localistic representations that are connected to corresponding representations in other layers. Each unit corresponds to a large number of neurons that together participate in the neural code for that particular representation. For every unit in each layer, its current activation depends on the activation value on the previous time-step, the self-recurrent excitation, the inhibition felt from every other unit in the same layer, the external input and some random noise. The activations of all units in the model are updated at each time-step according to the following differential equation (see also Davelaar, et al., 2005, 2006; Usher & McClelland, 2001):

$$x_i(t+1) = \lambda x_i(t) + (1-\lambda)(\alpha F(x_i(t)) + I_i(t) - \beta \sum_j F(x_j(t)) + \xi) \tag{1}$$

Here, x represents the internal activation, $\lambda=0.98$, α is the self-recurrent excitatory connection, $F(x) = x/(1+x)$, for $x>0$ represents the output activation function. $I_i(t)$ represents the external input at time-step t to unit i . Units in each layer compete for activation, which is governed by the within-layer inhibition parameter β . Each unit receives inhibition from every other unit in the same layer. The activation of each unit (only in the memory layer) is supplemented with zero-mean Gaussian noise ξ , with standard deviation σ . The parameter values vary between layers, but are chosen to minimize epiphenomenological dynamics that may obscure the comparison between the CQ- and RS-mechanisms. For example, in order to compare the models, each model should be able to produce an output. If the connection between the activation and selection layer is too weak, the CQ-model, but not the RS-model, produces an output, and if the response suppression is too weak, the RS-model, but not the CQ-model, produces an output. Each layer can be interpreted as representing a set of brain areas that have been implicated in memory activation, memory selection, and action selection.

Figure 4 shows the influence of the parameters α and β on the activation of the representations, which eventually govern the overall system behavior. Figure 4A shows for a variety of values for α and β , the average number of representations (out of 10, $I_i=0.33$ for all) that are still activated above a fixed threshold (0.2, as used in previous work) after 2000 iterations over 100 simulation runs ($\sigma = 0.1$). Figures 4B-D show for three points from the Figure 4A, the corresponding activation trajectories. As can be seen, increasing the self-recurrent excitation will increase the number of representations that are still active above threshold at the end of the simulation. However, this is only true for low levels of inhibition, as an intermediate level of inhibition dampens the overall activation, putting an upper bound to the total number of activated representations. With high inhibition, the system goes into a winner-take-all selection mode.

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4.1.1 Activation layer

The activation layer contains representations of the words that are to be recalled. The memory representations may already be in an active state (they are in the short-term buffer; Davelaar, et al., 2005) or are (re)activated by a cue, which could be a category name (semantic cue, as in a verbal fluency task) or a contextual reference (episodic cue, as in a list memory task). In this paper, only cued activations are considered. The cue activates the first 10 items in the memory layer range from 0.28 to 0.37 (0.01 difference between units). The activated representations compete weakly with each other. In the simulations, zero-mean Gaussian noise is added to the activations of the memory units ($\alpha = 0$, $\beta = 0.1$, $\sigma = 0.1$).

4.1.2 Selection layer

The selection layer (modeled after Usher & McClelland, 2001) contains representations that receive weighted input, $W_{ms}F(x)$, from those in the activation layer, where W_{ms} represents the connection weight between the activation and the selection layer. The activated representations compete strongly, $\beta=1.0$, with each other, and have moderate, $\alpha = 1.0$, self-connections. Both the activation and selection layer could be implemented in prefrontal areas, such as the ventrolateral prefrontal cortex (Badre, et al, 2005; see for a recent discussion on prefrontal cortex and memory, Ranganath & Blumenfeld, in prep).

4.1.3 Output layer

The output layer contains representations that receive weighted input, $W_{so}H[F(x),0.4]$, from those in the selection layer, with $W_{so}=2.0$ and $H[F(x),0.4]=1$, when $F(x)>0.4$, 0 otherwise. The units are inert with no dynamics other than activation decay after a unit in the selection layer has provided a pulse to the output

layer. This allows for obtaining an exact point in time in which a response is initiated. The connection between the selection and the output layer represents the “direct pathway” or the “selection pathway” (Gurney, Prescott & Redgrave, 2001) in the basal ganglia.

4.1.4 Inhibition layer

The inhibition layer contains representations that receive input, $H[F(x), 0.4]$, from those in the selection layer. To maximize the influence of the inhibition layer on the retrieval dynamics and thereby make the whole system sensitive to differences related to the RS- and CQ-mechanisms only, units in the inhibition layer have strong self-excitation and do not inhibit each other ($\alpha = 2.0$, $\beta = 0$). This implements a form of output buffer in which all selected items are maintained throughout the retrieval phase and prevents perseverations and repetitions. The neural substrate of the inhibition layer is assumed to include subcortical areas of the basal ganglia that are in the “indirect” or “control” pathway. In addition, the self-recurrent connection may be interpreted as including cortical projections to the subthalamic nucleus. Recent work by Frank (in press; Frank, Sherman & Scheres, in press) suggests that a critical function of the subthalamic nucleus is to prevent (too early) responding.

4.2 Simulation 1: RS- versus CQ-mechanism

In the first simulation, the weighted output of the inhibition layer, $W_{inh}F(x)$, is sent to the selection layer or the memory layer to implement the RS- and CQ-model, respectively. Figure 5 shows a noise-less simulation of both implementations. As can be seen, of the 10 activated representations in the memory layer, only 8 produce a response in the RS-model, whereas all produce a response in the CQ-model. Figure 6A presents a comparison of the first recall latency and the subsequent IRTs for both noise-less simulations. The results are striking. The RS-model shows increasing IRTs throughout the retrieval phase, whereas the CQ-model shows a gradual decrease in IRTs. The RS-model produces increased IRTs because with each response the responsible unit in the activation layer keeps sending activation to the corresponding unit in the selection layer. As this unit is inhibited, the next-highest unit will win the competition, but as it receives less activation, it takes longer to reach the response threshold. This

continues throughout the recall phase, leading to ever-increasing IRTs. The CQ-model on the other hand reduces the number of activated units in the activation layer, thereby reduces the competition in the selection layer. With less competition, the units in the selection layer can more readily reach the response threshold, resulting in ever-decreasing IRTs.

The models were run with noise ($\sigma = 0.1$) in the activation layer. To obtain a wide range of total recall, 1000 simulations were run with $W_{ms} = [1.4 : 2.0, \text{step } 0.1]$, which is justified under the assumption that the activations of the memory representations are modulated by attentional (Usher & Davelaar, 2002) or motivational factors. Despite this range, the CQ-model produced all 10 responses in 99.2% of the simulations. Figures 6B and 6C show the IRTs as a function of the total recall and the recall interval for the RS- and CQ-model respectively. These figures mimic the noise-less results in Figure 6A. Human behavioral data are in accordance with the results of the RS-model (e.g., Murdock & Okada, 1970; shown in Figure 2).

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The results of Simulation 1 are expanded with additional analyses in the Appendix, in which the slope of the IRT-profile is compared in four model implementations: RS- and CQ-model with (RS^A, CQ^A) and without (RS^0, CQ^0) gradual decay of response suppression. The analyses reveal that the RS-models produce the positive slope of the IRT-function more often than the CQ-models and that this difference between RS- and CQ-models is smaller if the response suppression decays gradually during the retrieval phase.

4.3 Simulation 2: setsize effects

Given that the RS-model captures the basic profile of IRTs, the question arises whether it also shows the critical sensitivity to setsize. Rohrer and colleagues (Rohrer, 1994, 1996, 2002; Rohrer, et al., 1995, 1999; Wixted & Rohrer, 1993) have shown that the distribution of recall latencies reflect the size of the memory set, which could be utilized to identify loci for memory deficits in patient populations. To this end, 1000 simulations of the RS-model were run with 5 or 15 memory units being activated (the 5 highest activated units were used in both setsizes, therefore any effect on first recall latencies can only be attributed to setsize). Inhibition in the selection layer was lowered to $\beta=0.8$ and $W_{ms}=4.0$. As can be seen in Figure 7, the RS-model is sensitive to differences in setsize (average recall: .918 and .307, for setsize 5 and 15, respectively). In particular, the model is slower when the memory set is larger. The reason for this is that with larger setsize, more items activate units in the activation layer and therefore in the selection layer. The overall increase in competing representations leads to a slower rise in activation for each of the units in the selection layer. This continues throughout the recall phase, leading also to longer IRTs. For the first recall latencies, the average latency was 3164 timesteps with size=5 and 3456 timesteps with size=15. For the IRT: 99 timesteps with size=5, 603 time-steps with size=15. The RS-model not only captured the IRT-profile, but is also sensitive to the size of the memory set, thereby providing computational validation of the theoretical analyses of Wixted and Rohrer (1994).

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4.4 Simulation 3: Alzheimer vs. Huntington

Patients with Alzheimer’s dementia suffer from increased loss of neural tissue that represents long-term memory (see e.g., Fleischman & Gabrieli, 1999). This includes aspects of episodic and semantic memory. As in memory retrieval tasks, recall latencies reflect the size of the memory set, AD-patients are faster in retrieving items, but have a lower total recall. Simulation 2 already showed the effect of setsize and will not be repeated here. Huntington’s disease is caused by a loss of striatal neurons, resulting in a decreased

output to the thalamus (see for a review, Alexi, et al., 2000). In the model, HD would affect the selection layer and is approximated by increasing the selection threshold, which slows down the retrieval process without affecting the memory set.

The RS-model with selection $\beta = 1.0$ and $W_{ms} = 2.0$ was used (10 items; 1000 runs) with the difference that the selection threshold was increased from 0.40 to 0.44. As can be seen in Figure 7, the HD-simulation is indeed slower in retrieving items. For the first recall latencies, the average latency was 991 timesteps (HD) compared to 825 timesteps (baseline). For the IRT: 1262 timesteps (HD) compared to 700 time-steps (baseline). This contrasts the results of the AD-patients (setsize effect).

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4.5 Simulation 4: non-mnemonic clustering

During model exploration, an interesting form of clustering was observed. When the weight between the activation and selection layer is high (or the inhibition in the selection layer is low), a number of representations may still be active when a representation is selected. As the selection layer is assumed to receive modulated input (for a model of attentional modulation of response selection see, Usher & Davelaar, 2002), the model links attentional and motivational factors to the speed of retrieval. However, this pattern could only be observed in the distributions if the binsize for the distributions was small enough.

An illustrative simulation of these parameters was conducted. Five items were activated in a simulation with two levels of activation-selection weight, $W_{ms} = [1.5, 2.0]$. Figure 9 presents activation trajectories of a single trial (with noise, $\sigma = 0.1$; the same randomseed was used in both simulations), while Figures 10A and 10B present the recall latency distributions (from 1000 simulation runs) with large (1000 timesteps) and small (100 timesteps) binsize, respectively. It is immediately apparent that the model is able to produce a form of clustering that is independent of the mnemonic structure of the to-be-

retrieved representations. In fact, there is no mnemonic structure. Instead, this type of clustering reflects the pressure that the representations feel in the selection layer combined with the self-recurrency. The simulation also shows that in order to observe this profile, an adequate temporal resolution is required. Therefore it is recommended that in empirical studies, looking at retrieval latencies in free recall tasks, care is taken to obtain precise timing measurements. It remains an open question whether the clustering profile can be observed in neurobiological studies with animals.

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5 Discussion

The aim of the current paper was to compare two commonly used mechanisms of sequential memory retrieval and evaluate their ability to capture the inter-response times in free recall. A generic model in which the two mechanisms were implemented. Simulations revealed that the resampling mechanism provided a better overall qualitative match to the published data on retrieval latencies in a free recall paradigm than the competitive queuing mechanism. A comparative analysis of four model implementations (RS^A , CQ^A , RS^0 , CQ^0 , see section 4.2 and appendix) reveal that the RS-models produce the positive slope of the IRT-function more often than the CQ-models and that this difference between RS- and CQ-models is smaller if the response suppression decays gradually during the retrieval phase. This latter mechanism made the CQ^A -model (CQ with gradual decay of suppression) more similar to the RS-models (RS^0 and RS^A). The resampling mechanism was subsequently tested on its sensitivity to the size of the activated memory set and its success is promising for further research in the specific neural implementation of the mechanism. The use of recall distributions has been shown to provide a better

understanding of the memory deficits in Alzheimer's dementia and Huntington's disease (section 4.4) and resolve theoretical debates that have focused mainly on total recall as the dependent variable. The resampling model captures the differences in recall latency distributions between patients with Alzheimer's dementia or Huntington's disease. The important utility of IRT-analyses in this domain justifies further developments and analyses of the computational architecture to quantitatively account for the neuropsychological data. The implications of the present model comparison follow next.

5.1 Implications for dynamical models of memory

The CQ-mechanism has had great impact on the memory literature, but the simulations show that for profiles of inter-response times in free recall, the mechanism does not fare well compared to the RS-mechanism unless additional assumptions are in place. Even though the evaluation between the two types of models in simulation 1 may imply that CQ-models are inappropriate for free recall, this does not invalidate CQ-models. In fact, given the neurophysiological support for CQ-dynamics, it is conceivable that CQ-dynamics may play a dominant role at the response level and less so at the memory level. Note that the successes of CQ-models are found in tasks that require execution of a well-learned motor program, whether it is drawing geometric shapes (Averbeck, et al., 2002), or pronouncing words (Hartley & Houghton, 1996). As such the use of CQ-dynamics may be more related to the unpacking of chunks, where the content of chunks could be words (as in serial recall), movements (as in typing, spelling; Glasspool & Houghton, 2005; Hartley & Houghton, 1996) or even other chunks (as in planning; Cooper & Shallice, 2000). Within the literature on serial recall, not much emphasis has been placed on retrieval latencies (but see Farrell & Lewandowsky, 2004; Kahana & Jacobs, 2000). Nevertheless, in a production system, Anderson and Matessa (1997) explicitly modeled the inter-response times as the unpacking of chunks, with equal time needed for each item within a chunk and with additional time to move from one to the other chunk. In a follow-up paper (Anderson, et al., 1998) some aspects of free recall were modeled, but not retrieval latencies.

An important assumption of some CQ-models is that after a response it made, the representation leading to an overt response is inhibited. This response suppression decays gradually over time, leading to reselection. Despite this critical feature (i.e., decay of response suppression), the neurophysiological data that supported competitive queuing in general (Averbeck, et al., 2002) does not show this pattern. Although repetitions in movements in making geometric shapes are unlikely, decay of response suppression seems not to be needed to account for repetition errors in serial recall (Botvinick & Plaut, 2006; Farrell & Lewandowsky, 2002) and is even directly contested empirically (Duncan & Lewandowsky, 2005).

Although the modeling work in this paper highlighted a critical difference in employment of CQ- and RS-mechanisms, the model itself requires extensions in order to account for a variety of other memory-related findings in sequential retrieval. These include semantic (Davelaar, et al., 2006) or episodic clustering, strategic retrieval (idiosyncratic cues: Gronlund & Shiffrin, 1986; output order: Dalezman, 1976) or semantic dementia (Forde & Humphreys, 2002). However, the evaluation presented here was of a qualitative nature and was aimed at providing a means to justify the choice of mechanism used, with analyses of retrieval latencies as the main dependent measure that constraints the modeling choice. Future work may merge the current generic model into other more-specified models of recall memory to address the other findings.

Recent work on recall memory has incorporated new theoretical approaches to working memory (Davelaar, et al., 2005, 2006). In this research, the content of working memory is defined as the activated part of long-term memory (e.g., Cowan, 2001) and the modeling work was focused on the encoding of information in episodic memory. In that work, episodic memory is the matrix of connection weights between a contextual system (related to the medial-temporal lobe) and the cortical long-term memory system. In these models of free recall, the retrieval process was approximated by a selection and recovery phase, akin to that of global memory models. The dynamical model of retrieval presented in this paper provides the back-end to those previous models of encoding. It is noteworthy that the level of inhibition

in the retrieval component produces some form of clustering. A few items are reported in rapid succession, but are not interconnected. The size of this cluster is directly related to the number of items that are active simultaneously in the selection layer (see Figure 9), which could potentially be used in empirical investigations on working memory capacity (reviewed in Cowan, 2001).

5.2 Implications for dynamical models of sequential selection

As mentioned in the introduction, studying free recall may be a more useful paradigm than serial recall to study the properties of sequential retrieval from memory, as serial recall places an external constraint on the inherent selection mechanism. However, under the assumption that this is indeed the case, the question then arises how the inherent selection mechanism is influenced by this external constraint of output order. In other words, assuming that an RS-mechanism underlies all kinds of sequential behavior, how does the need for a particular correct serial order affect the operations of the selection? A partial answer to this is revealed by a closer look at how the slope of the RS-models is affected by the parameters (see Appendix). In free recall, a positive slope of the IRT-function is observed, whereas a negative slope is observed for serial performance such as typing (Salthouse, 1986). To capture a negative slope (i.e., ever faster responding) in the RS^0 -model, the higher self-recurrency would normally lead to more items becoming active, but the also higher lateral inhibition prevents this (together with the lower weight from the activation layer to the selection layer). With every retrieved item (in the selection layer) being inhibited after reaching a threshold, the item next-highest in activation shoots up. As the overall competition within the selection layer decreases during the retrieval phase, the IRT between successive retrievals becomes shorter. The same dynamics happens in the RS^Δ -model where due to the gradual decay of response suppression, the overall selection mechanism needs to be liberal and with a low response threshold. Interestingly, the amount of self-recurrency is lower too.

In a recent computational study of response selection, Usher and Davelaar (2002) proposed that the parameters for self-recurrency and lateral inhibition in a selection layer are modulated by norepinephrine (NE) in a positive manner (both parameters are positively correlated with the level of NE).

Application of that study to the current discussion produces the hypothesis that the instruction to perform in a particular ordered sequence leads to a modulation in NE, which translates into a higher or lower self-recurrency and lateral inhibition in the selection layer and thereby producing an observable negative or positive slope in the IRT-function of actions, respectively. Note that the covariation between self-recurrency and lateral inhibition as function of the IRT-slope is negative for the CQ-models, critically distinguishing the CQ- and RS-models on their reliance on these two parameters. Granted that the analyses in the Appendix are not full-proof and requires further extensions incorporating noise and a consideration of other types of behavior (e.g., error profiles), the current hypothesis is not inconsistent with previous work on response selection (Usher & Davelaar, 2002) and memory for free recall (Davelaar, et al., 2005). Linking the idea of neuromodulation to the different IRT-profiles within a single system may be a useful vehicle for the investigation in the control of selection among competing behavioral alternatives. Recent work has linked NE and the locus coeruleus with conflict monitoring and attentional control (Botvinick, et al, 2001) and with the balance between exploitation-exploration behavior in animals (e.g., Cohen, Aston-Jones & Gilzenrat, 2004).

5.3 Relation to other psychological domains

The evaluation of the memory retrieval dynamics could inform other domains within psychology, such as decision-making, neuropsychological assessment, and language/sequence learning/production. Recent work in the field of decision-making makes increasingly more use of memory theories (e.g., Dougherty, Gettys & Ogden, 1999). For example, when a physician is generating a number of hypotheses about a possible diagnosis, the information about the symptoms is used to cue the memory system and search the activated part of memory to produce a number of likely diagnoses. This type of research could benefit from a deeper understanding of how the retrieval dynamics are affected by such variables as number of possible hypotheses (search set), motivation of the physician (focus of attention for selection), and dual-task situation (affects the retrieval-speed).

In the domain of neuropsychological assessment, a recent study (Scahill, Hodges & Graham, 2005) showed that current episodic memory tasks fail to differentially diagnose patients with Alzheimer's dementia from patients with semantic dementia (SD, a progressive neurodegeneration of the temporal lobe, characterized by loss of semantic memory). Of course, SD-patients can be distinguished from AD-patients using semantic tasks, but it is not certain yet whether episodic memory tasks may contribute in the differential diagnosis. Rohrer and colleagues (1999) argued that recall latencies contain information that separates AD- from HD-patients. The search for alternative (and additional) methods of differentiating between these two groups of patients can be facilitated by neurocomputational models of the kind presented in this paper in which certain components have a clear neurological counterpart. Through simulations of lesions, they can create informed predictions to guide development of more sensitive tests. This type of modeling extends beyond the measures related to sequential retrieval and combined with other dynamical models of memory may prove to be of high value to clinicians.

Finally, Dominey (2005) reviewed his work on sequence learning and grammatical constructions. Whereas the tasks focused more on the learning of sequences, the core component of the modeling comprises the learning of connections between internal states (retrieval cues) and the correct output response. The advantage of his model over standard recurrent networks is that the Dominey-model iterates activation over multiple time-steps and thereby is sensitive to temporal structure of input sequences. In the same vein, the present model could be extended to produce actions (e.g., speech) and thus would require a mechanism to transform the activated abstract message into a sequence of function and content words.

5.4 Limitations and extensions

The current model focused on two proposed inhibition mechanisms involved in memory retrieval. To this end, the inhibition layer and the output layer were oversimplified. This oversimplification was needed in order to reveal the consequences of either implementation. However, two pointers will be given that may be of interest to those involved modeling human behavior. First, adding within-layer inhibition within the

inhibition layer leads the system to exhibit recycling or rehearsal behavior. This could be prevented by having the content of the inhibition layer function as retrieval cues (breaking the cycle), which echoes the use of retrieved cues in subsequent retrieval in global memory models, such as SAM. Second, the pulses in the output layer could be temporally extended through self-connections. These activation profiles could in turn activate subsequent selection mechanisms involved in sequencing actions at a lower level in the action hierarchy, such as speech production (or any other motor sequence), allowing examination of the relation between the information being searched and the speech rate, or speech confusions. These extensions go beyond comparing the two mechanisms and would have obscured the unique differences between them, which are relevant for both the psychological and non-psychological domains. Future work can take the RS-model and investigate the implications of an output buffer to retrieval dynamics.

5.5 Conclusion

This paper compared two mechanisms by which simultaneously activated representations produce actions (here the recall of memoranda) in a sequential manner. Although these two mechanisms have been used in a variety of models, they have not been compared directly to each other before. By examining the dynamics of sequential selection through retrieval latencies, it was shown that sampling-with-replacement captured human memory retrieval better than sampling-without-replacement. Both are further improved by including dynamics of response suppression that gradually fades. This evaluation provides the cognitive modeler with a tool with which to choose the components of a selection mechanism and provide insights in the internal dynamics of a chosen implementation by addressing the patterns it produces given a certain parameter space. Finally, the analyses provide a handle to understand qualitative differences in sequential behavior through global modulation of critical parameters, which require further evaluation from empirical and computational studies in humans and animals.

References

- Alexi, T., Borlongan, C. V., Faull, R. L. M., Williams, C. E., Clark, R. G., Gluckman, P. D., & Hughes, P. E. (2000). Neuroprotective strategies for basal ganglia degeneration: Parkinson's and Huntington's diseases. *Progress in Neurobiology*, *60*, 409-470.
- Anderson, J. R., Bothell, D., Lebiere, C., & Matessa, M. (1998). An integrated theory of list memory. *Journal of Memory and Language*, *38*, 341-380.
- Anderson, J. R., & Matessa, M. (1997). A production system theory of serial memory. *Psychological Review*, *104*, 728-748.
- Averbeck, B. B., Chafee, M. V., Crowe, D. A., & Georgopoulos, A. P. (2002). Parallel processing of serial movements in prefrontal cortex. *Proceedings of the National Academy of Sciences*, *99*, 13172-13177.
- Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*, 907-918.
- Botvinick, M. M., Braver, T. S., Carter, C. S., Barch, D. M., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*, 624-652.
- Botvinick, M. M., & Plaut, D. C. (2006). Short-term memory for serial order: a recurrent neural network model. *Psychological Review*, *113*, 201-233.
- Brown, G. D. A., Preece, T., & Hulme, C. (2000). Oscillator-based memory for serial order. *Psychological Review*, *107*, 127-181.
- Burgess, N., & Hitch, G. J. (1992). Towards a network model of the articulatory loop. *Journal of Memory and Language*, *31*, 429-460.
- Burgess, N., & Hitch, G. J. (1999). Memory for serial order: a network model of the phonological loop and its timing. *Psychological Review*, *106*, 551-581.

- Cohen, J. D., Aston-Jones, G., & Gilzenrat, M. S. (2004). A systems-level perspective on attention and cognitive control: guided activation, adaptive gating, conflict monitoring, and exploitation versus exploration. In M. I. Posner (Ed.), *Cognitive neuroscience of attention*. New York: Guilford Press.
- Cooper, R., & Shallice, T. (2000). Contention scheduling and the control of routine activities. *Cognitive Neuropsychology*, *17*, 297-338.
- Cowan, N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*, 87-185.
- Davelaar, E. J., Goshen-Gottstein, Y., Ashkenazi, A., Haarmann, H. J., & Usher, M. (2005). The demise of short-term memory revisited: empirical and computational investigations of recency effects. *Psychological Review*, *112*, 3-42.
- Davelaar, E. J., Haarmann, H. J., Goshen-Gottstein, Y. & Usher, M. (2006). Semantic similarity dissociates short- from long-term recency: testing a neurocomputational model of list memory. *Memory & Cognition*, *34*, 323-334.
- Dominey, P. F. (2005). From sensorimotor sequence to grammatical construction: evidence from simulation and neurophysiology. *Adaptive Behavior*, *13*, 347-361.
- Dougherty, M. R. P., Gettys, C. F., & Ogden, E. E. (1999). MINERVA-DM: A memory processes model for judgments of likelihood. *Psychological Review*, *106*, 180-209.
- Duncan, M., & Lewandowsky, S. (2005). The time course of response suppression: no evidence for a gradual release from inhibition. *Memory*, *13*, 236-246.
- Farrell, S., & Lewandowsky, S. (2002). An endogenous distributed model of ordering in serial recall. *Psychonomic Bulletin & Review*, *9*, 59-79.
- Farrell, S., & Lewandowsky, S. (2004). Modelling transposition latencies: constraints for theories of serial order memory. *Journal of Memory and Language*, *51*, 115-135.
- Fleischman, D. A., & Gabrieli, J. (1999). Long-term memory in Alzheimer's disease. *Current Opinion in Neurobiology*, *9*, 240-244.

- Forde, E. M. E., & Humphreys, G. W. (2002). The role of semantic knowledge in short-term memory. *Neurocase*, 8, 13-27.
- Frank, M. J. (in press). Hold your horses: a dynamic computational model for the subthalamic nucleus in decision making. *Neural Networks*.
- Frank, M. J., Sherman, S. J., & Scheres, A. (in press). Understanding decision making deficits in neurological conditions: insights from models of natural action selection. *Philosophical Transactions of the Royal Society, B*.
- Glasspool, D. W. (2005). Modelling serial order in behaviour: Evidence from performance slips. In G. Houghton (Ed.). *Connectionist model in cognitive psychology*. Hove: Psychology Press.
- Glasspool, D. W., & Houghton, G. (2005). Serial order and consonant-vowel structure in a graphemic output buffer model. *Brain and Language*, 94, 304-330.
- Gronlund, S. D., & Shiffrin, R. M. (1986). Retrieval strategies in recall of natural categories and categorized lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 12, 550-561.
- Grossberg, S. (1978a). Behavioral contrast in short-term memory: serial binary memory models or parallel continuous memory models? *Journal of Mathematical Psychology*, 17, 199-219.
- Grossberg, S. (1978b). A theory of human memory: self-organization and performance of sensory-motor codes, maps, and plans. In R. Rosen & F. Snell (Eds.), *Progress in theoretical biology. Vol. 5*. New York: Academic Press.
- Gurney, K., Prescott, T. J., & Redgrave, P. (2001). A computational model of action selection in the basal ganglia. I. A new functional anatomy. *Biological Cybernetics*, 84, 401-410.
- Hartley, T., & Houghton, G. (1996). A linguistically constrained model of short-term memory for words and nonwords. *Journal of Memory and Language*, 35, 1-31.
- Henson, R. N. A. (1998). Short-term memory for serial order: the start-end model. *Cognitive Psychology*, 36, 73-137.

- Henson, R. N. A., Norris, D. G., Page, M. P. A., & Baddeley, A. D. (1996). Unchained memory: error patterns rule out chaining model of immediate serial recall. *Quarterly Journal of Experimental Psychology*, *49*, 80-115.
- Hintzman, D. L. (1984). MINERVA 2: A simulation model of human memory. *Behavior, Research Methods, Instruments, & Computers*, *16*, 96-101.
- Houghton, G. (1990). The problem of serial order: a neural network model of sequence learning and recall. In R. Dale, C. Mellish, & M. Zock (Eds.), *Current research in natural language generation*. London: Academic Press.
- Kahana, M. J., & Jacobs, J. (2000). Interresponse times in serial recall: effects of intraserial repetition. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *26*, 1188-1197.
- Murdock, B. B. (1982). A theory for the storage and retrieval of item and associative information. *Psychological Review*, *89*, 609-626.
- Murdock, B. B., & Okada, R. (1970). Interresponse times in single-trial free recall. *Journal of Experimental Psychology*, *86*, 263-267.
- Page, M. P. A., & Henson, R. N. A. (2001). Computational models of short-term memory: modeling serial recall of verbal material. In J. Andrade (Ed.), *Working memory in perspective*. Hove, UK: Psychology Press.
- Page, M. P. A., & Norris, D. (1998). The primacy model: a new model of immediate serial recall. *Psychological Review*, *105*, 761-781.
- Patterson, K. E., Meltzer, R. H., & Mandler, G. (1971). Inter-response times in categorized free recall. *Journal of Verbal Learning and Verbal Behavior*, *10*, 417-426.
- Pitt, M. A., Kim, W., Navarro, D. J., & Myung, J. I. (2006). Global model analysis by parameter space partitioning. *Psychological Review*, *113*, 57-83.

- Raaijmakers, J. G. W., & Shiffrin, R. M. (1980). SAM: a theory of probabilistic search of associative memory. In G. Bower (Ed.), *The psychology of learning and motivation, Vol 14*. New York: Academic Press.
- Raaijmakers, J. G. W., & Shiffrin, R. M. (1981). Search of associative memory. *Psychological Review*, *88*, 93-134.
- Ranganath, C., & Blumenfeld, R. (in preparation). Prefrontal cortex and human memory: an integrated account of results from neurophysiological and neuroimaging studies of working- and long-term memory.
- Rohrer, D. (1996). On the relative and absolute strength of a memory trace. *Memory & Cognition*, *24*, 188-202.
- Rohrer, D. (2002). The breadth of memory search. *Memory*, *10*, 291-301.
- Rohrer, D., & Wixted, J. T. (1994). An analysis of latency and interresponse time in free recall. *Memory & Cognition*, *22*, 511-524.
- Rohrer, D., Salmon, D. P., Wixted, J. T., & Paulsen, J. S. (1999). The disparate effects of Alzheimer's disease and Huntington's disease on semantic memory. *Neuropsychology*, *13*, 381-388.
- Rohrer, D., Wixted, J. T., Salmon, D. P., & Butters, N. (1995). Retrieval from semantic memory and its implications for Alzheimer's disease. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 1127-1139.
- Salthouse, T. A. (1986). Perceptual, cognitive, and motoric aspects of transcription typing. *Psychological Bulletin*, *99*, 303-319.
- Scahill, V. L., Hodges, J. R., & Graham, K.S. (2005). Can episodic memory tasks differentiate semantic dementia from Alzheimer's disease? *Neurocase*, *11*, 441-451.
- Usher, M., & Davelaar, E. J. (2002). Neuromodulation of decision and response selection. *Neural Networks*, *15*, 635-645.

Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: the leaky, competing accumulator model. *Psychological Review*, *108*, 550-592.

Wixted, J. T., & Rohrer, D. (1993). Proactive interference and the dynamics of free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *19*, 1024-1039.

Wixted, J. T., & Rohrer, D. (1994). Analyzing the dynamics of free recall: an integrative review of the empirical literature. *Psychonomic Bulletin & Review*, *1*, 89-106.

Appendix

This appendix presents an analysis of four model implementations: the RS-model and the CQ-model that differ in the locus of the post-response suppression and within each model, this suppression remains throughout the remainder of the retrieval phase or gradually decays. A qualitative analysis addresses the question of how central a particular pattern, in this case the slope of the IRT-profile, is to a particular model and thereby provides a general answer to what type of implementation of sequential retrieval captures existing data on IRT-profiles in a free recall paradigm best. Note that all four implementations exhibit sequential behavior and are compared to data from memory experiments. Different results may be obtained if the models are compared against data from motor planning. After a brief description on the computational method used, the results will be presented and the appendix closes with some evaluation of this method.

The analysis takes its inspiration from a recent paper by Pitt, Kim, Navarro and Myung (2006) in which they presented a procedure called Parameter Space Partitioning (PSP) that allows a computational modeler to analyze the parameter space of a given model. The procedure involves the modeler to identify a particular set of patterns and to go through the multidimensional parameter space in search of those patterns. The full procedure was not used in this study and the reader is referred to the paper by Pitt and colleagues for details on the procedure and how to use it. Briefly, the PSP-procedure selects a set of parameters and evaluates the model's prediction (or pattern). The algorithm works such that it samples from each pattern at least once and uniformly. An interesting feature of this procedure is that it provides an estimate of the size of the parameter space that is occupied by a particular pattern. In other words, the procedure is able to address the question how central a particular data pattern is to a given model, which is exactly what is needed in comparing CQ- and RS-models.

The inspiration from the PSP procedure was to go through the parameter space of the four models (CQ and RS, with and without gradual decay of inhibition) and address whether and how much the slope of the inter-response time function is influenced by (1) the structural differences between the models, (2)

the presence/absence of decaying inhibition, and (3) the four chosen parameters. These parameters were chosen because initial explorations by hand showed that these parameters mattered most in the simulations in section 4. These parameters were, the connection weight between the activation layer and the selection layer, W_{ms} , the self-recurrency of the unit in the selection layer, α , the lateral inhibition between all pairs in the selection layer, β , and the threshold, θ , above which a response is made. In the models with decaying inhibition, the self-recurrency of the units in the inhibition layer was reduced to 1.2, which was shown to be a compromise between obtaining noticeable reactivation while preventing too many repetitions (perseverations). The models are named RS^0 and CQ^0 for those without decaying inhibition, and RS^Δ and CQ^Δ for those with decaying inhibition.

Procedure

Step 0: Explore all models by hand and define a parameter boundary and an initial set of parameters. The parameter vector used for the initial parameters was $P_0 = [W_{ms}; \alpha; \beta; \theta] = [2.0; 1.0; 1.0; 0.4]$. The boundaries were set to $W_{ms} = [1.2 : 2.2]$, $\alpha = [0.8 : 2.0]$, $\beta = [0.2 : 2.0]$, and $\theta = [0.3 : 0.5]$.

Step 1: Patterns were defined by the slope of the IRT-function and the number of items reported within a simulation run of 6000 iterations. This yields 2 (slope > 0, slope <= 0) x 8 (3 through 10 outputs) + (no output or less than 3 outputs) = 17 patterns. The PSP-program from Pitt et al was used on the noiseless models with the initial set of parameters, P_0 , and default values. All models produced all 17 patterns. The PSP program produced values that indicate the volume of the region of all possible patterns occupied by a certain pattern (see for details, Pitt, et al, 2006). Although the log(volume) favored the RS-models, as measured with the number of times that the log(volume) is greater for the positive slope for a given total output ($RS^0 - 8/8$; $CQ^0 - 4/8$; $RS^\Delta - 8/8$; $CQ^\Delta - 3/8$), this result is not optimal as the models were run without noise (and the procedure is limited to nonstochastic simulation runs). This step also produced additional parameter sets (in matrix xm_{cv} from the program), one for each of the 17 patterns, P_{psp1} .

Step 2: Parameter sets that were obtained under step 1 were used as initial parameters in a further search through parameter/pattern space. This guarantees that all regions will be sampled from. To speed up the simulations (each of the 4 simulations under step 1 took 2.5 hours of computing time) the number of patterns was reduced to 3 (slope>0, slope<=0, no output or less than 3 outputs). The program was also modified to store all unique combinations of parameters and the corresponding pattern.

As 17 PSP-runs were done on each (noiseless) model, the averaged log(volume) was informative. The results are shown in Table A1, showing great consistency across the two steps. The RS-models do generally better than the CQ-models, but this difference is greatly attenuated when a decaying of response suppression is implemented (for all comparisons, $p < .001$).

Volume estimates support the central thesis of this paper that when it comes to modeling inter-response times, resampling is preferred over competitive queuing. However, as all models are able to produce all possible patterns, caution should be taken to prevent over-interpretation. As mentioned, all points that were being evaluated in the PSP-algorithm were stored together with the results. This yielded more than 100,000 parameter sets for each model. Table A2 shows the number of parameter sets for each model against each pattern. Again it can be observed that a positive slope is more central to the RS- than to the CQ-model, and that with decay of response suppression implemented this difference decreases.

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INSERT TABLE A2 ABOUT HERE

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INSERT FIGURE A1 ABOUT HERE

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Figure A1 shows the normalized distributions of relative frequencies for each model, for the valid patterns and for each of the four parameters. A uniform distribution would be centered on 0.05. This means that for all models the strength between the activation and selection layers does not affect the slope of the IRT-function. Only the RS^0 -model tends to be somewhat affected by this parameter. Note however, that W_{ms} does seem to be relevant when it comes to clustering behavior in the output (see simulation 4). The same holds for the parameter for the response threshold. The self-recurrency and the lateral inhibition in the selection layer greatly affect the slope of the IRT-function, depending on the model. For RS^0 , positively sloped IRT-functions have intermediate values of α and β , whereas for negatively sloped IRT-functions the values of α and β are large. For CQ^0 , positively sloped IRT-functions have high α and low β (suggesting low selection), whereas for negatively sloped IRT-functions α is low and β is large (suggesting high selection). For RS^Δ , positively sloped IRT-functions have undetermined values of α and β , whereas for negatively sloped IRT-functions the values of α and β are small. Finally, for CQ^Δ , positively sloped IRT-functions have undetermined values of α and β , whereas for negatively sloped IRT-functions have low values of α and high values for β (suggesting high selection).

In summary, the values for α and β seem to suggest that the CQ-models tend to settle into high or low mode of selection producing negatively or positively sloped IRT-functions, respectively, whereas RS-models are consistently keeping the same mode of selection. These mode preferences are attenuated with decaying response suppression.

Limitations

Although this new procedure may prove to be a very useful addition to the modeler's toolbox, a number of simplifications have been applied here that should be noted. First, the models are stochastic models and the PSP assumes a stationary pattern space. To this end the models were run without noise, which reduces

the full model potential, but does allow for addressing the slope of the IRT-function. Second, the number of patterns was greatly reduced compared to what the models can do. Besides having distributions of total recalls, the models are also able to show clustering behavior. This feature was not part of the pattern-definitions, but was instead addressed in a full stochastic version in simulation 4. Third, default parameter for the PSP algorithm was used and it can be argued that more optimal values are possible that allow better estimates of volume. Nevertheless, the volume results from steps 1 and 2 were consistent and the algorithm produced a massive amount of data used in distributions of the parameters. Finally, only a subset of parameters was varied, limiting the size of parameter space. This should not be an issue, as the aim of this exercise was to compare models given the same 4 parameters that were found to be greatly affecting performance, some of which could be linked to brain damage.

These limitations aside, the procedure has given much more than an analysis by hand could have given. Future work may address the above problems more directly and give more principled answers to questions of how central the full (stochastic) pattern of IRT-functions is to a given model.

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Footnotes

1. The literature seems somewhat inconsistent in its definition of which post-Houghton (1990) models can be called CQ-models. Here, the definition is used that a CQ-model is a model in which given the same context, the layer immediately preceding the selection (or sampling) layer, (1) drives the selection, (2) has multiple representations active, and (3) has its activation profile altered as a consequence of the selection layer. This captures the notion of a queue that is altered with subsequent selection. Within this definition, models like the Primacy model (Page & Norris, 1998) and the Start-End model (Henson, 1998), but also Grossberg's (1978) models are CQ-models. Models of free recall, such as SAM (Raaijmakers & Shiffrin, 1980, 1981) do not alter the activation profile given the same context, and thus are not considered CQ-models, but instead are here referred to as resampling (RS) models.

2. The reader may also have noted that the timing signal itself could be implemented using a simple chaining mechanism. Whereas the strong arguments have been raised against item-to-item chaining (Henson, et al, 1996), all the models converged on using a temporal context signal that can be implemented using a simple chaining sub-model (for an early CQ-model of serial recall with random context change, see Burgess & Hitch, 1992). This issue has not been clarified in the CQ-literature and with the development of recurrent network models of serial recall that capture the error patterns (Botvinick & Plaut, 2006), a closer look at mechanisms of serial order seems warranted.

Tables

Table A1. Result of the PSP-algorithm under steps 1 and 2. The percentages indicate the amount of the valid space (where the model produces slopes for the IRT-function) and the percentage of that space that contains the pattern of positive slopes. Step 1 results are taken over all total output (8 datapoints). Step 2 results are averaged across 17 PSP runs with standard deviations in brackets.

PSP-run		Model			
		Without decay		With decay	
		RS ⁰	CQ ⁰	RS ^Δ	CQ ^Δ
Step 1	Valid	54.9%	32.2%	17.2%	28.7%
	Slope>0	85.0%	38.0%	83.9%	78.9%
Step 2	Valid	56.2% (3.6%)	37.8% (3.3%)	25.9% (2.6%)	34.2% (3.8%)
	Slope>0	89.1% (5.8%)	42.5% (5.9%)	91.4% (7.4%)	77.3% (5.7%)

Table A2. Total number of parameter sets obtained in step 2 for each model against each possible pattern.

		Model			
		Without decay		With decay	
		RS ⁰	CQ ⁰	RS ^Δ	CQ ^Δ
Invalid	34357	43409	49980	43878	
Valid (slope≤0)	22498	36861	16377	17966	
Valid (slope>0)	43640	37567	51989	44676	

Figure captions

Figure 1. Architecture of the model used in Grossberg (1978). Each unit in the activation layer has self-recurrent excitatory connection and inhibits all other units in the same layer. The feedforward one-to-one connections from the activation layer to the selection layer are excitatory, whereas the feedback one-to-one connections are inhibitory. At the lower end is a snapshot of the activation gradient in the activation layer. On the left, the left-most unit is the most active and leads to a response. After that, the feedback inhibition causes that unit to be lowered in activation. Due to decrease in the amount of inhibition in the activation layer, the unit with the next-highest activation level can increase in activation and will lead to the next response. This cycle continues until all units who received activation have produced an output.

Figure 2. Mean interresponse time (IRT) as a function of ordinal position in output. The list had twenty items and because participants successfully report a variable number of items, the data is partitioned according to total number of words recalled (4-9). Note that independent of the total number of items reported from a 20-word list, the interresponse times increases with the number of words reported so far. From Murdock, B. B., & Okada, R. (1970). Interresponse times in single-trial free recall. *Journal of Experimental Psychology*, 86, 263-267. Published by APA. Reprinted with permission.

Figure 3. Model architecture. The model consists of 4 interconnected layers. The arrows ending in pointed heads and circled heads are excitatory and inhibitory connections, respectively. A number of representations are activated at the activation layer which feeds activation to the selection layer. When a unit in the selection layer reaches a selection threshold, the input to the inhibition and response layers receive a sharp pulse. Depending on the employed mechanism, the output of the inhibition layer inhibits the selection (in the RS-model) or the activation (in the CQ-model) layer.

Figure 4. Profiles of the influence of the self-recurrency and lateral inhibition parameters on the activation of 10 activated units. A: two-dimensional contour map of the number of activated units (at 2000 iteration time-steps). Note that the values for the lateral inhibition are on a logarithmic scale. The three dots are parameter combinations that were used to illustrate activation trajectories. B: Activation trajectories for

high selection. Note that at first two (out of 10) units are most active, followed by one unit increasing in activation; a selection has taken place. C: Activation trajectories with low inhibition, but high activation leading to no selection, but all units being above a 0.2 threshold. D: Activation trajectories with low inhibition and low activation, leading to no selection and all units being below a 0.2 threshold.

Figure 5. Activation trajectories of the RS- and CQ-model. Activation between layers goes from “memory” to “selection” to “output”, with “inhibition” suppressing the activation at either the “memory” (CQ-model) or the “selection” (RS-model) layer. Note that the RS-model does not produce all responses (8 spikes in the output layer), whereas the CQ-model does. Note also that the activation in the memory layer for the CQ-model shows the signature of the CQ-mechanism (after an output the corresponding trace is inhibited, which causes increase in activation for the remaining traces).

Figure 6. Results of simulation 1. A. First recall latencies and inter-response times for the noise-less RS- and CQ-models. Note the increase in IRT for the RS-model and the decrease in IRT for the CQ-model. B. IRTs as a function of total recall and recall interval for the RS-model. C. IRTs as a function of total recall and recall interval for the CQ-model.

Figure 7. Results of simulation 2. Comparison of small (thin line) and large (thick line) memory set sizes. A. First recall latency distributions. The two distributions overlap considerably. B. IRT distributions.

Figure 8. Results of simulation 3. Comparison of normal selection threshold (thin line) and high selection threshold (representing Huntington disease; thick line). A. First recall latency distributions. The mean recall latency is slower for the HD-simulation. B. IRT distributions for normal and HD-simulation.

Figure 9. Activation trajectories of the RS-model, with strong connection weight between memory and selection layer (left) compared to a baseline (right). Note the bursting behavior of the model despite equivalent mnemonic structure, which is due to not having a full selection in the selection layer (2 units are active simultaneously before the first response is made).

Figure 10. Results of simulation 4. Recall latency distributions for weak (solid line) and strong (dotted line) W_{ms} . A. course-grained binsize (1000 time-steps), and B. fine-grained binsize (100 time-steps). Note the faster latencies with increased strength and the appearance of clustering with small binsize.

Figure A1. Normalized relative frequency distributions for each of the four parameters and for each of the four models. From top to bottom: W_{ms} , α , β , and threshold. The thick lines represent the distribution of the parameter values (shown on the x-axes) for which the corresponding model produced an IRT-function with slope >0 . The thin lines represent the distribution of the parameter values for which the corresponding model produced an IRT-function with slope ≤ 0 . A uniform distribution would be $y=0.05$. Note the strong influence of the self-recurrency (alpha) and lateral inhibition (beta) parameters. Note also that models implementing decaying response suppression (the two right columns) are less sensitive (flat line) to the values of the alpha and beta parameters than the models that do not implement a decaying response suppression (two left columns).

Figure 1

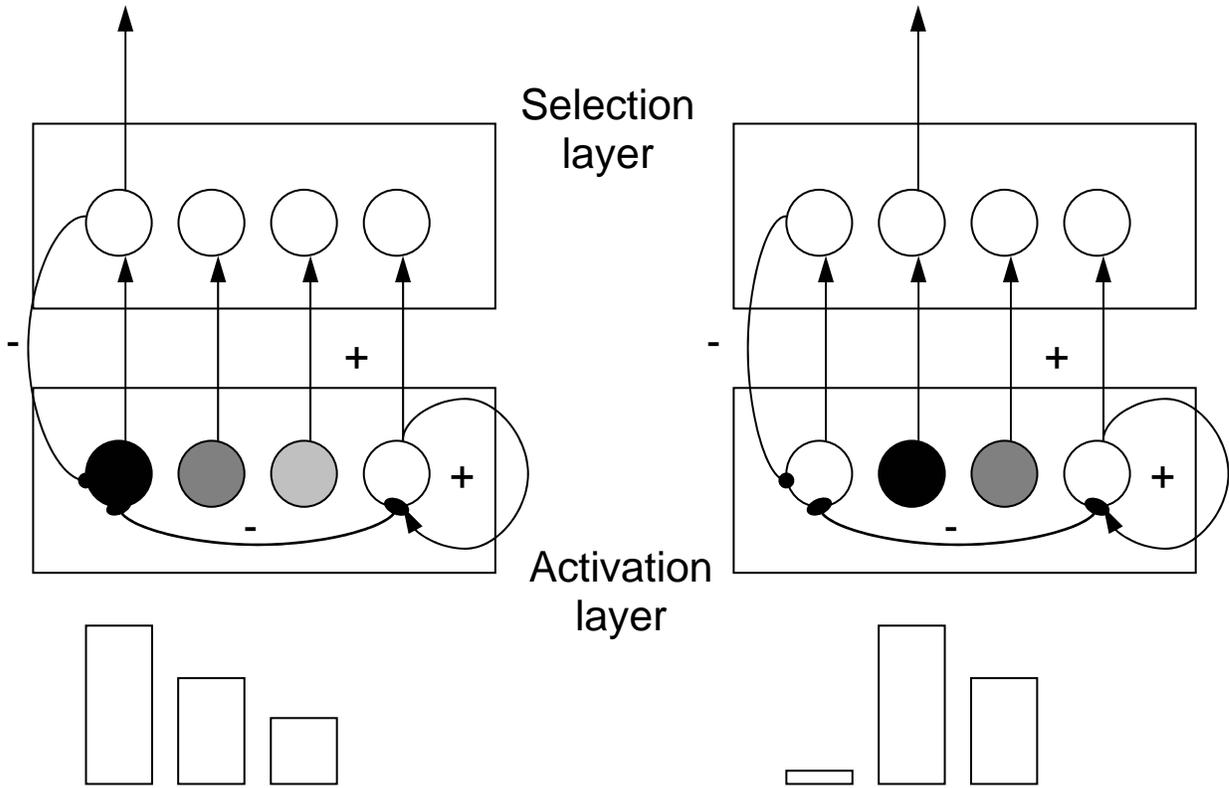


Figure 2

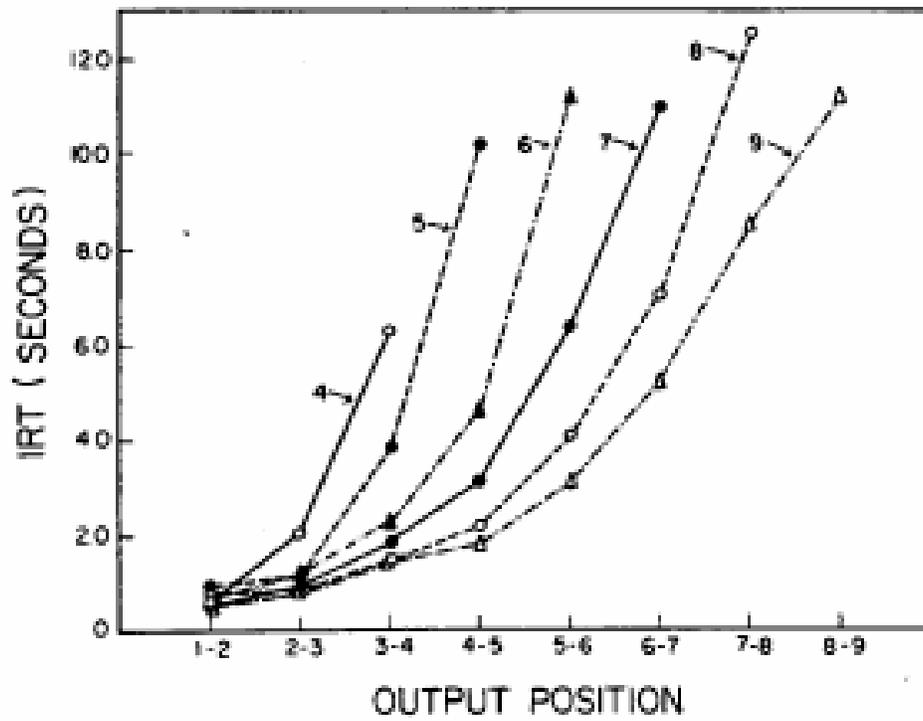


Figure 3

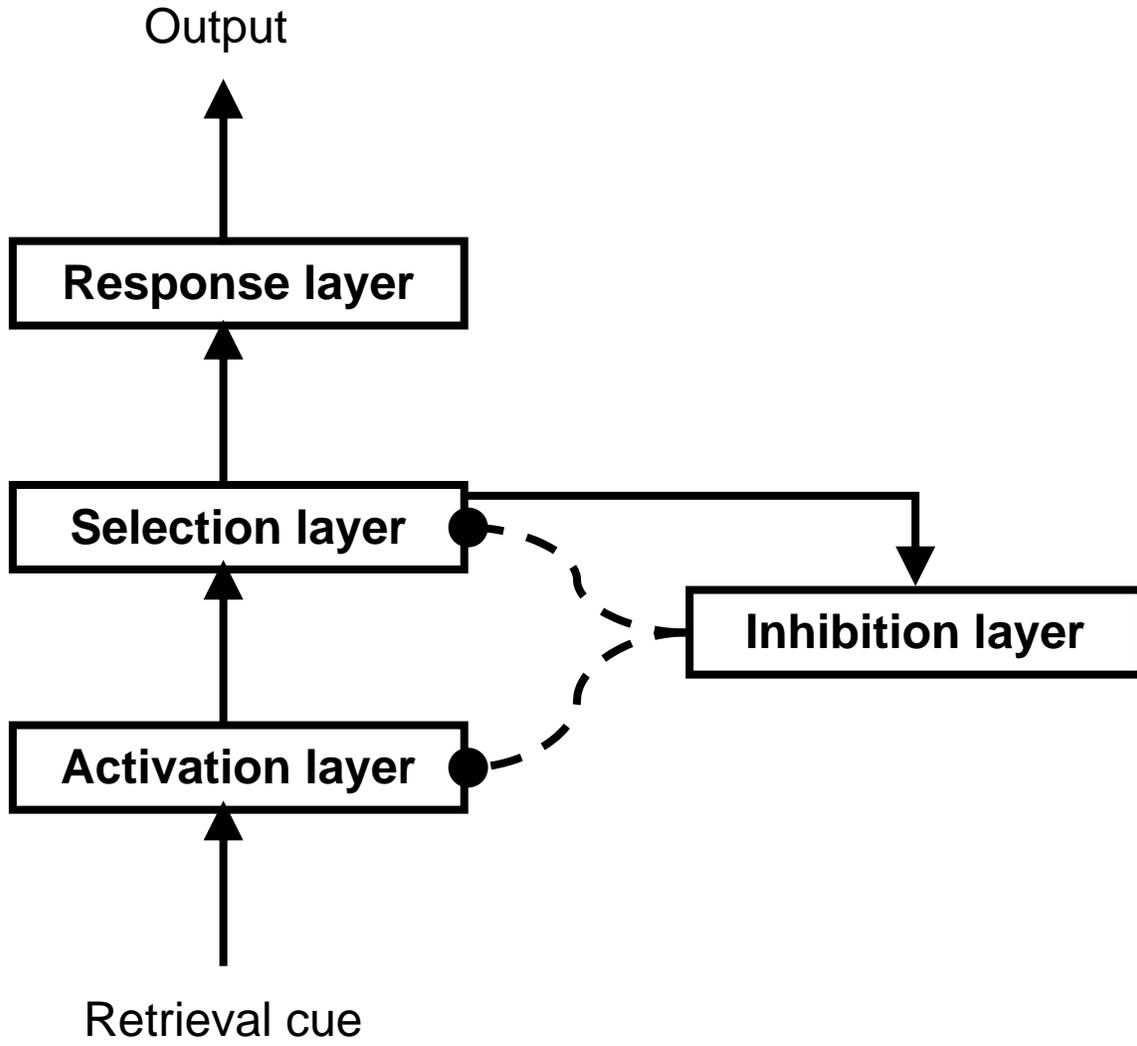


Figure 4

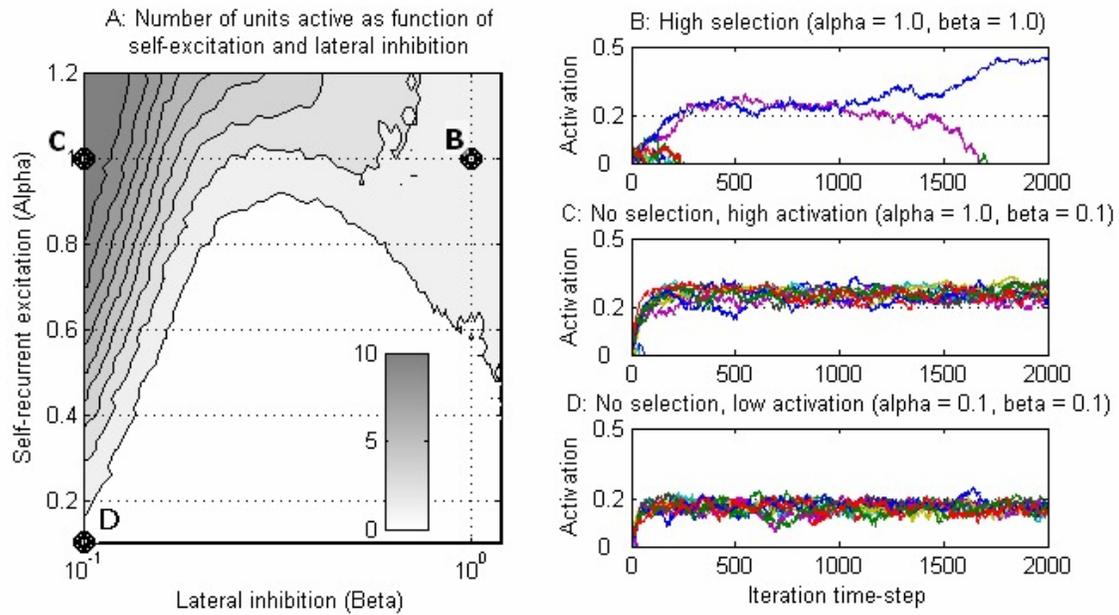


Figure 5

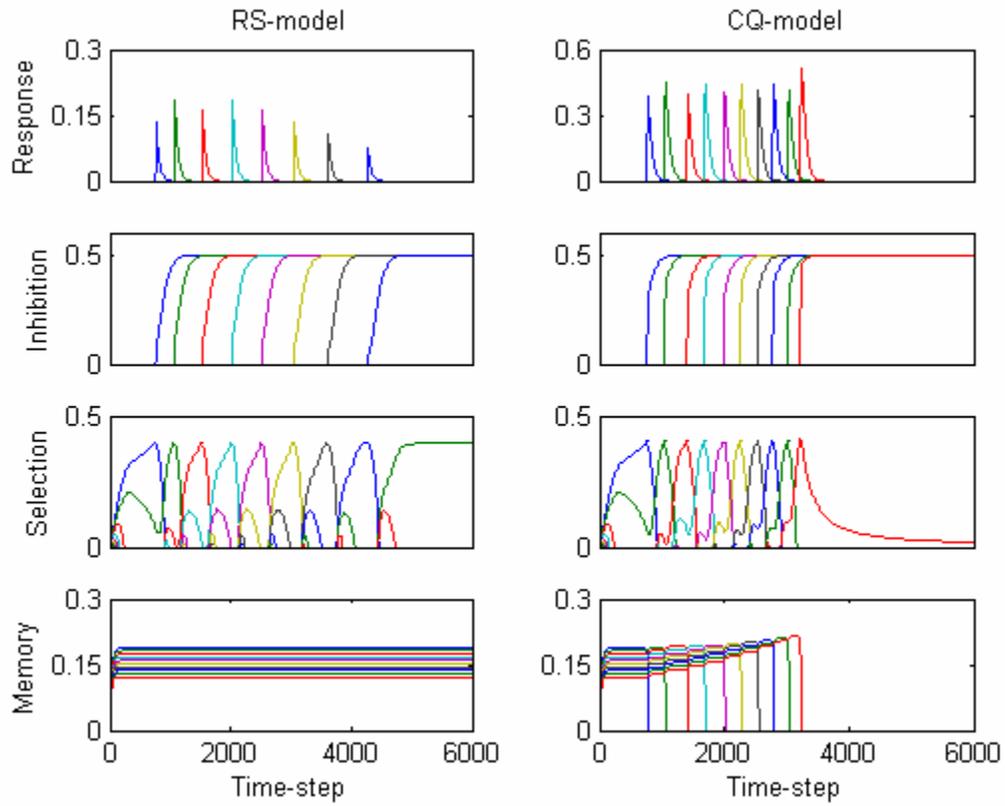


Figure 7

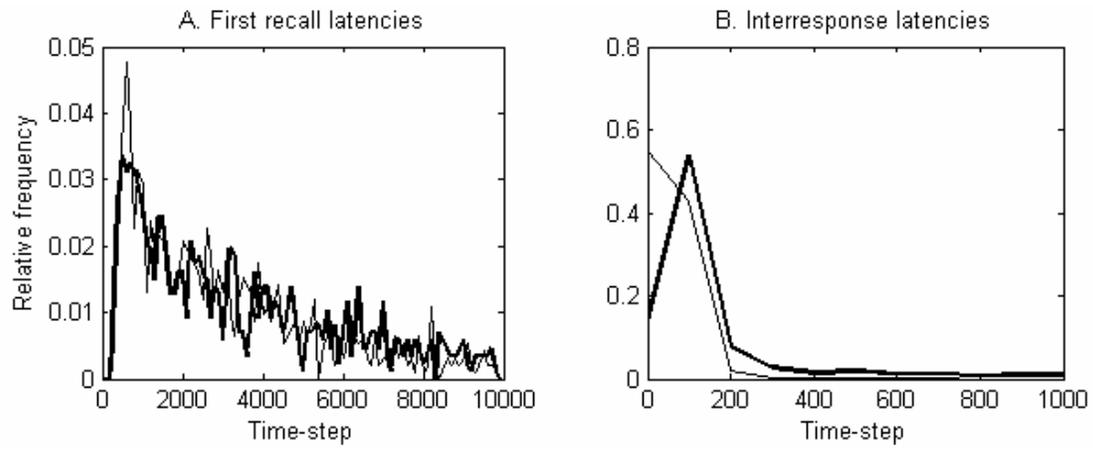


Figure 8

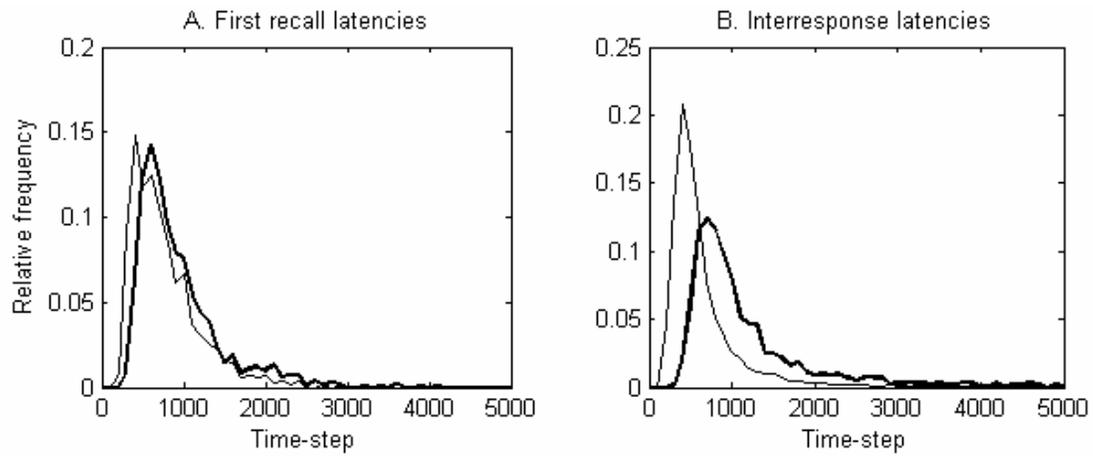


Figure 9

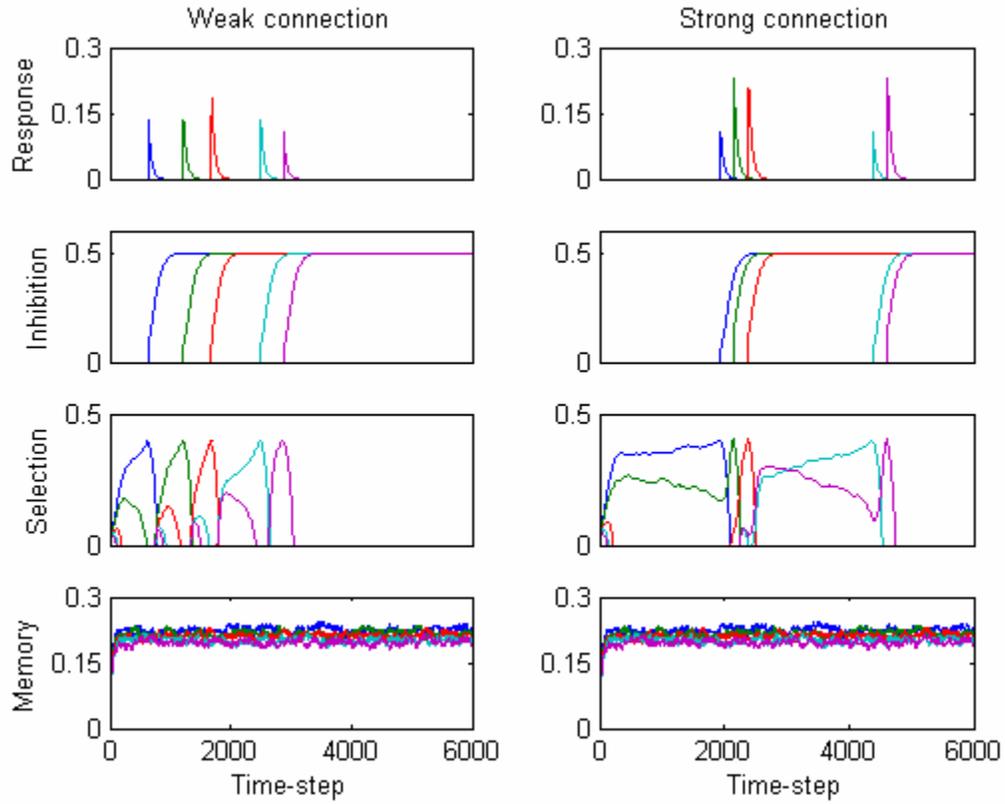


Figure 10

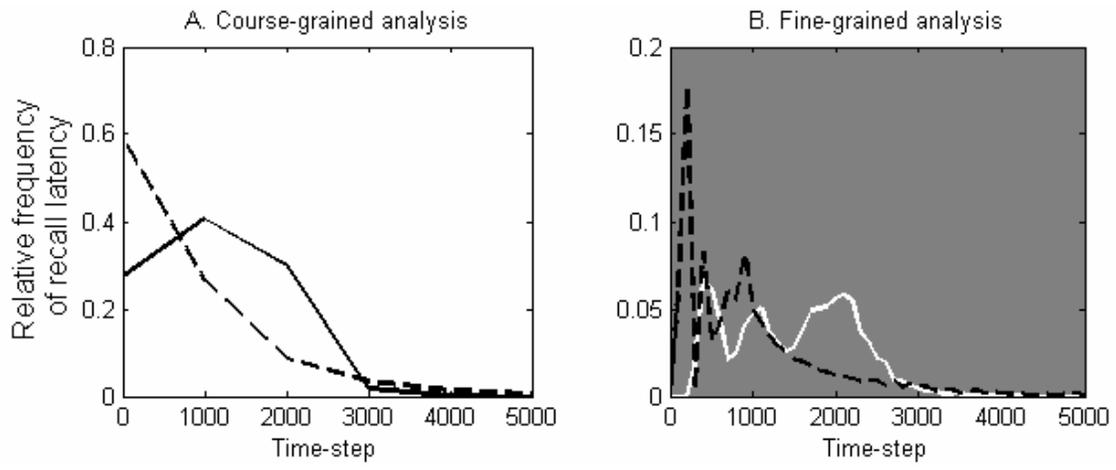
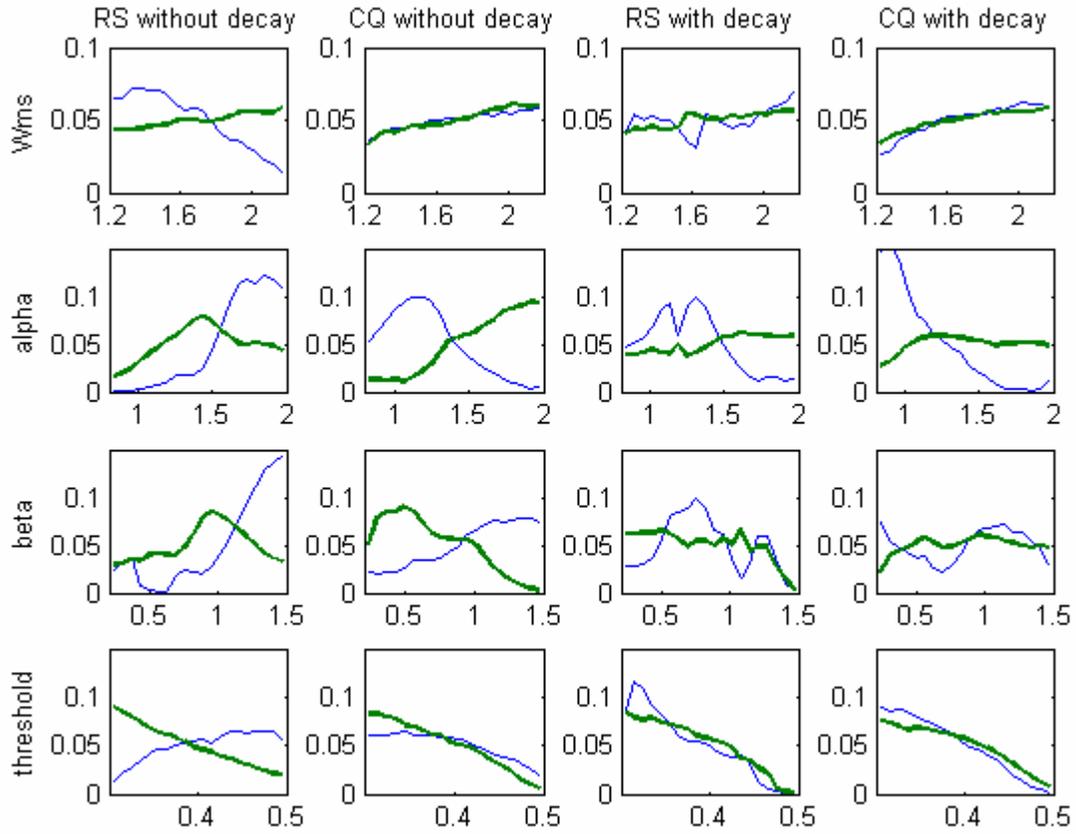


Figure A1



Biography

Eddy J. Davelaar holds M.Sc.s in Biological Health Sciences and in Psychology, both from Maastricht University in 1999. He holds a Ph.D. in Psychology from Birkbeck, University of London. His main research interest is the control of memory and attention, using a variety of experimental and computational methods. Current location: School of Psychology, Birkbeck, University of London, Malet Street, WC1E 7HX, London, United Kingdom (e.davelaar@bbk.ac.uk).

