

Neuromodulation of Word Meaning Selection

Gabriele Scheler*

ICSI

1947 Center Street

Berkeley, Ca. 94704

email: scheler@icsi.berkeley.edu

Abstract

Processes of word meaning generation, word association and understanding are known to be impaired in schizophrenia and related diseases. Word meaning selection requires the involvement of prefrontal cortex and processes of working memory and selective attention. Under the dopaminergic hypothesis of schizophrenia, the normal neuromodulatory activation of prefrontal cortex for the performance of working memory-related tasks is disturbed. We present a model of selective attention and its modulation by dopamine and show how abnormal levels of dopamine availability may lead to some of the observed impairments in word meaning selection, namely (a) failure to construct contextually appropriate meanings and (b) intrusions of phonological and episodic associative links within semantic processing.

Introduction

Studies on brain imaging have revealed that the task of word generation, such as in a constrained association task ("name a typical verb for a noun"), reliably produces activity in two distinct brain regions: in parietal cortex, the putative storage area for long-term semantic knowledge, and in areas 44 and 45 in prefrontal cortex (Broca's area) as sites for attentional selection (Thompson-Schill *et al.* 1997).

Attentional selection is a process that is known to underlie neuromodulation, i.e. activation of primarily dopaminergic and noradrenergic receptors on neurons in prefrontal cortex. There are a number of behavioral tests of selective attention and distractibility designed both for animals and humans and a specific enhancement of reaction times and accuracy under conditions of raised dopamine levels or raised D1-receptor activity could be shown.

The processes of active maintenance of representations in working memory and selection of behaviorally relevant information have also been investigated using recordings of neuronal activity of behaving monkeys.

On leave from Department of Computer Science, Technical University of Munich, D-80290 München

During a delayed alternation task, which requires to store the location of an object on a screen during a brief (1–2 s) delay period, a number of neurons show raised activity (i.e. an increased firing rate). This has been interpreted as showing that these neurons provide a representation of the inaccessible stimulus, which requires some internal active maintenance as for instance a resonant state in an attractor network (Zipser *et al.* 1993).

Recently, a further experiment has looked at the selectivity of representations in prefrontal cortex (Rainer, Asaad, & Miller 1998). Monkeys performed a delayed-matching-to-sample task with an array of three objects. After a cue object (the target) had been shown, monkeys had to remember the location of the target object for a delay of 1.5 s. Approximately 50% of the recorded neurons showed a different activity depending on the location of the target, only about 5% showed activity that varied with the location of non-target objects. This effect was present about 140 ms after stimulus onset, and a parallel effect concerning the target object rather than the location, which was unchanged during trial blocks showed persistent activity preferably for target objects.

Similar attentional effects in IT as an area of visual processing (Chelazzi *et al.* 1993) take somewhat longer, 175 ms, and this may suggest that selective representation in prefrontal cortex provides an attentional bias for processing in other parts of the cortex (Miller 1999).

Looking at language processing in the brain, we may note that processes of word meaning selection require the short-term memory storage of several contextual items as well as a selection of relevant information from long-term storage of semantic meanings or features. Selection involves the resolution of competition between retrieved representations.

Neuroimaging studies of verbal working memory (Smith & Jonides 1999) indicate an anatomical separation of maintenance and executive processes such as selection and inhibition.

To provide a model of word meaning selection we therefore need to address three issues:

- a model of selective attention in prefrontal cortex
- a model of long-term storage of semantic information

- a model of retrieval and integration of long-term information with short-term storage

In the following we will provide a model of semantic memory that is based on the notion of semantic features integrated in a self-organizing map-like structure, and that is biologically plausible but not tightly constrained by experimental data of the kind that are available for animal models. We will then propose a model of selective attention and its enhancement and degradation by levels of neuromodulators. Finally we will show how the impairment of processes of selection in prefrontal cortex lead to characteristic disturbances in word meaning processes, such as verb generation, association and semantic priming which can be observed under changed levels of neuromodulators in humans. The problem of retrieval and integration of long-term and short-term information will not be addressed here - we will assume a simple mirroring or pointer-like address system that links these systems together (Collette *et al.* 1999), (Fuster 1998), (Chafee & Goldman-Rakic 1998).

Semantic Feature Maps

We start from the assumption that semantic meanings are created out of a set of atomic (unanalyzable) features and that these features are represented by individual neurons or small sets of them. As a matter of fact there are reasons to assume that a distributed representation of atomic features ("microfeatures") by a set of neurons has computational advantages and may be the preferred method of implementation in the brain. In our model, however, we will only deal with the level of features and therefore there is no great difference between the two alternatives.

Feature-representing neurons are linked with other feature neurons by synaptic weights of differing strength (cf. Fig. 1). This means that features are usually activated in clusters, or "structures" with stronger and weaker activated features. Activation within a network means that certain feature neurons receive synaptic input from perceptual (phonological) layers and in turn send action potentials to their projection neurons. Within an interconnected network this leads to reverberations and a general increase of firing rate for the activated neurons, which is proportional to their connectivity pattern (cf. Fig. 2).

If we assume that a certain structure of this kind is represented in prefrontal cortex, i.e. is present in verbal working memory rather than in long-term storage, there is a further process that contributes to activation. In addition to dedicated feature-representing neurons there are a large number of unassigned neurons that maintain weak links to most other neurons and that become "recruited" by strongly activated neurons. There is a competition for the activation of these neurons in that they integrate synaptic input from different sources but will fire in synchrony only with synchronized strong input. This means that a pool of neurons that is tightly

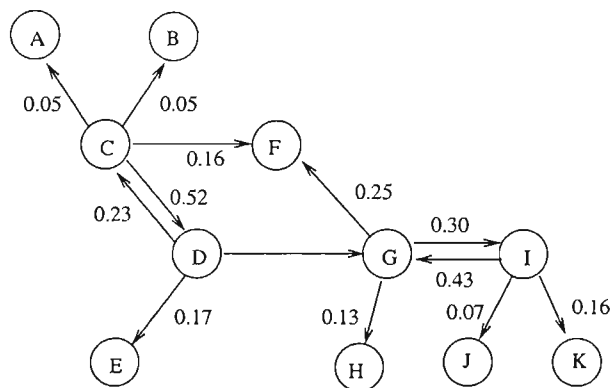


Figure 1: An example of a semantic map with features and links of differing strength. The structure of the maps can be estimated from psychological data. Adapted from a real example in (Spitzer 1997).

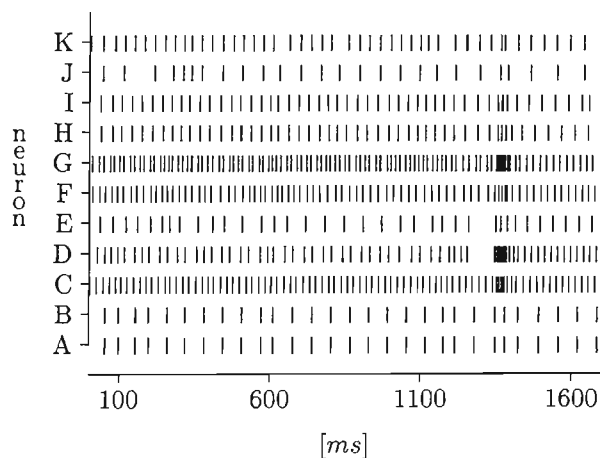


Figure 2: Spiking pattern in a network of integrate-and-fire neurons. Synaptic strengths are taken from Fig. 1. An input is presented to features C and G as an example of a phonological word stimulus. Firing rate of features corresponds to their strength of activation.

correlated will increase its size, while neurons that do not fire together or are less tightly synchronized will remain a low percentage of active neurons. Strong activation of a feature thus leads to an increase in the number of neurons that represent this feature.

A Model of Selective Attention

Capacity limitations of working memory indicate that the active maintenance of representations that is required here is costly and restricted to a few items at a time (Callicott *et al.* 1999). At the same time, "items" may refer to fairly complex constellations of features (Miller 1956), which has also recently been demonstrated in psychophysical experiments for visual working memory (Luck & Vogel 1997).

Oscillation-based models (Lisman & Idiart 1995), (Jensen & Lisman 1998), (Niebur, Koch, & Rosin 1993) of working memory may explain both the severe capacity limitation and the ability to refer to almost arbitrarily complex representations. In these models individual representations consist of groups of neurons with tightly synchronized firing. The content of working memory is a sequence of such representations which are repeated within theta cycles (4–10 Hz). If each item is represented within one gamma cycle (20–80 Hz) (Wehr & Laurent 1996), there are approximately seven distinct items that can repeatedly be activated and thus be active in working memory (Tallon-Baudry *et al.* 1998). At the same time, it becomes clear that memories can be complex, i.e. involve a complete neuronal structure in the above sense.

A model of ongoing activity in working memory may therefore consist of different groups of neurons participating in different functional relationships. At a given time, a number of neurons just show spontaneous, background activity, since they are not activated by a stimulus, and have weak connections to highly active neurons. There will be a number of neurons receiving strong input, which represent a certain item that is active in working memory, and which are connected in the manner of a reverberating attractor (Amit, Brunel, & Tsodyks 1994). There is a pool of inhibitory neurons which will be activated by the current attractor (representation) and suppress activity of the other neuronal groups that receive input activation. By choosing a certain connectivity structure of inhibitory and excitatory groups, a cascade-like activation of neuronal groups can be achieved (Fig. 3, cf. appendix B for a specification of the architecture).

Finally, we assume that there is a set of neurons, which receive some input and which have stronger connections to the active neurons than the background neurons. These neurons are more weakly active (have lower firing rates) than the representational neurons, and they do not follow an oscillatory pattern. We call these neurons "semi-active". In a sense, it is clear that we could have implemented a graded structure of more or less semi-active and inactive neurons, but a categorical structure seemed to be easier to understand and

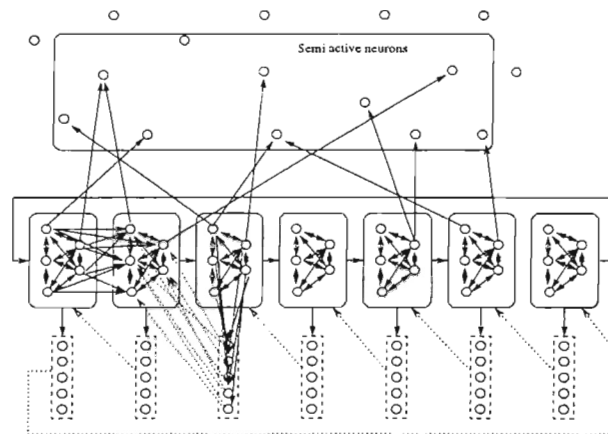


Figure 3: Architecture of oscillatory working memory. Representational neurons form strongly interconnected clusters and activated inhibitory clusters with a k-1 inhibitory pattern. There is a pool of semi-active neurons. Excitatory connections=straight lines, inhibitory connections=dotted lines

analyze. Fig. 4 shows a raster-plot of neuronal activity in such a working memory model.

Representations in working memory are not stable but subject to attentional switches. Items may be rehearsed and accessible for several seconds but normally there are constant switches of content, both voluntary and involuntary. We propose to enhance the basic oscillatory model by a certain amount of background activity, which may spontaneously cluster to small semi-active groups of neurons and which may become entrained to the major oscillations by increased synaptic input, in particular coincident synaptic input. Selective attention may be localized in a different network and can increase or inhibit certain neuronal activations in primary working memory. Selective attention can thus stabilize (focus) representations but also induce switching of representations.

Neuromodulation of Attention

Working on a working-memory related task or under conditions of increased attentional load increases blood flow in specific areas of prefrontal cortex (Cohen *et al.* 1997), (Courtney *et al.* 1997). A dissociation of areas according to modality (spatial working memory, object recognition, verbal working memory) seems to be stable across experiments (Smith & Jonides 1999), a dissociation into short-term storage ("rehearsal") areas and executive function (selective attention, task sequencing, planning), is also suggested, at least for verbal working memory (Smith & Jonides 1999).

Working memory tasks also increase extracellular dopamine in healthy monkeys. Experiments with amphetamine in both humans (Fleming *et al.* 1995) and monkeys (with low or high dopamine availability) have shown that there is a narrow range of optimal dopamine availability - both low and high dopamine levels im-

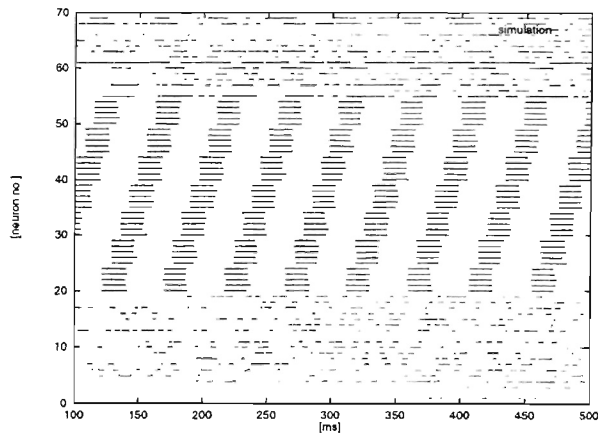


Figure 4: Oscillatory model of working memory. The bottom row shows the spontaneous activity of weakly (link density(ld)=0.01, synaptic weights(sw)=0.05) connected neurons. The top row shows the activity of more strongly connected neurons (ld=0.02, sw=0.2). The center part shows the sequential activation of seven attractors. Input is received only during the first 50 ms. The activity of inhibitory neurons is not shown.

pair tasks involving delayed decisions (working memory) and inhibition of alternatives (attention). It seems that a specific level of dopamine receptor activity is optimal in maintaining and stabilizing representations and in directing attention.

Dopamine acts on single neurons in prefrontal cortex primarily via D1-receptors on excitatory (pyramidal) cells and D2-receptors on inhibitory cells (Goldman-Rakic, Lidow, & Gallagher 1990), (Goldman-Rakic *et al.* 1992). D1-receptor activation changes the efficacy of calcium-activated afterhyperpolarizing potassium channels (Vergara *et al.* 1998), which leads to an altered signal transmission compared to unmodulated neurons. Basically, a modulated neuron resets quickly, and can process many signals in quick succession faithfully, while the unmodulated neuron shows signal dampening effects over a period of up to 400 ms. In the latter case, we have signal masking effects, where the strength of a synaptic input that is needed to induce firing diminishes with the interval to the previous spike, while this "relative refractory period" is reduced for a modulated neuron (Scheler & Fellous 1999). The detailed single-neuron models used in this work and their physiologically motivated parameters are given in appendix A.

The effects of D2-receptors have been less clearly characterized. Their main effects are a reduction of the size of excitatory postsynaptic potentials by limiting glutamate efflux and a depolarization of inhibitory neurons, i.e. an increase in the amount of inhibition. There are considerably more D1-receptors in rat and monkey prefrontal cortex than D2-receptors, and D2-receptors need a much higher level of dopamine to become active (Goldman-Rakic *et al.* 1995). In our model D2 acti-

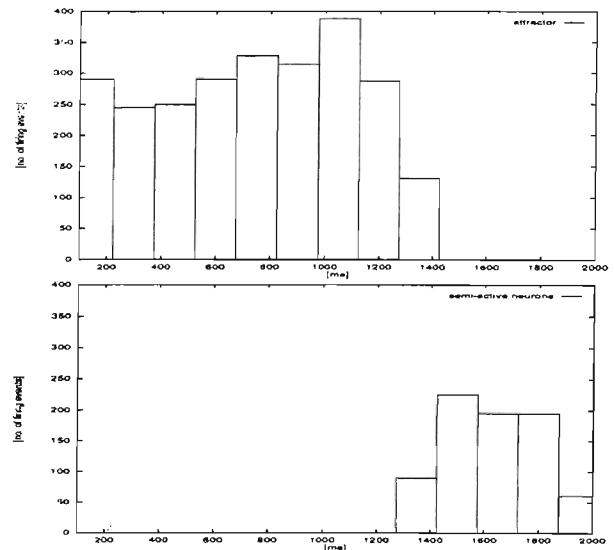


Figure 5: Attention switch with D1-modulated neurons. Shown are the number of firing events within a representational attractor in 150-ms bins. Panel A shows the "old" representation that is activated by attentional module A, Panel B show the a new semi-active group that is activated by attentional module B. The change in input to the attentional module occurs at about 1500 ms.

vation is mainly needed to stabilize network activity at higher levels of D1-activation.

When we look at the oscillatory memory buffer that represents the set of active memory items, we note that they are tightly synchronized and have comparatively small delays. As long as single neurons in the attention module and in the working memory module have the temporal properties of modulated neurons, the network is stable and inputs from the attention module can be directed either at active items or at semi-active groups. (cf. Fig. 5).

With neurons that have temporal dependencies in their signal processing, the precise coincident timing of individual spikes within the oscillatory cycle is lost. This leads to a "sprinkler-like" activation of memory items by the attentional module with a consequent loss of either attentional boosting and stabilizing of memories or of fast and reliable switches. Instead, at a low dopamine level, we would expect a reduced focus with consequent impaired performance on delayed decision tasks, and an increased (involuntary) distractability, such as performance on the Stroop or Eriksen tasks (Cohen, Dunbar, & McClelland 1990), (Servan-Schreiber *et al.* 1998) (cf. Fig. 6).

Neuromodulation of Word Meaning Access

Concerning the neuromodulation of word meaning processes, data have been primarily collected from the ob-

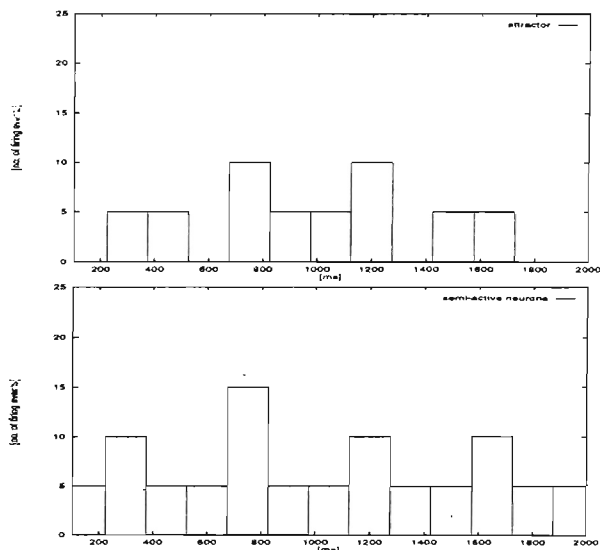


Figure 6: Attention switch with non-modulated neurons. With respect to Fig. 5 all parameters were kept constant, except the single-neuron model. We can see a failure of a rapid and reliable attentional switch.

ervation and testing of schizophrenics. The revised dopaminergic theory of schizophrenia states that there is a lack of dopaminergic tone in prefrontal cortex throughout the disease (Friedman, Temporini, & Davis 1999), however acute psychotic states have also been associated with a high level of dopamine turnover in prefrontal cortex

Schizophrenic impairment in word meaning generation can be traced in part to a failure to construct contextually appropriate feature constellations: instead of a less frequent, contextually appropriate meaning often the more frequent, dominant meaning is retrieved. This "literalism" of understanding also occurs in the interpretation of metaphors and other indirect uses of speech. We may interpret this impairment as a failure to inhibit dominant feature associations and to select relevant associations in the activation of a meaning structure in working memory. This is essentially the same task as verb generation, i.e. the generation of a certain type of word association.

It must be noted however that word meaning selection in general is an automatic task, which is not under the control of voluntary attention, and which does not require conscious effort. It is certainly not part of the 7+2 restriction of conscious on-line storage of separate items. On the other hand the processes underlying selection in processing of verbal feature structures are probably similar to effortful processing, which may simply require the contribution of a greater number of cortical neurons (Dehaene, Kerszberg, & Changeux 1998).

Thus the processes observed in conscious working memory may underlie automatic processes as well (for a similar view see (Cohen, Dunbar, & McClelland 1990)).

We may assume that a whole activated structure from

long-term memory is "loaded into" working memory, i.e. that it is activated and attentionally controlled from working memory. This would involve a change of representation to an oscillatory attractor type network (cf. (Cohen & Knudsen 1999) for analogous representational changes in auditory perception).

This change of representation could be brought about by the activation of a specialized architecture as shown above, and the recruitment of neurons to support that representational format. In that sense, strongly activated neurons will become oscillators, while weakly activated neurons will become semi-active neurons. The LTM structure shown in Fig. 2 can thus be transformed into a representation as in Fig. 4.

The representation of tasks that guide attentional processes is replaced by a contextual representation of cues that guide the meaning selection process. These may now boost certain weak aspects of the representation and automatically suppress certain strong features. A compromised attentional system, which has non-modulated neurons, i.e. a lack of dopamine in the prefrontal cortex, will fail to provide this attentional switch fast and effortlessly in all cases.

A certain difficulty with this system is of a theoretical nature. With the current separation of attentional selection module and working memory rehearsal ("storage") system, it does not become clear why there should be a change in representation at all. The specific nature of working memory representations probably reflects a more integrated function of storage and selection than described here.

We have assumed that an activated meaning structure consists only of semantic features so far, yet word meaning activation under conditions of altered catecholaminergic activity also shows patterns of interference from phonological storage and episodic memory. Presumably a spatial segregation of processing areas for different types of information is compromised by a lack of attentional selection of relevant information. This closeness of different types of associational relations actually resembles an earlier developmental stage, when a more effortful, attention-intensive processing with a greater prefrontal contribution is present (Krasnegor, Lyon, & Goldman-Rakic 1997). We may assume that the failure to distinguish between e.g. phonological and semantic associations in schizophrenia is due to the involvement of larger areas in prefrontal cortex and at the same time their comparatively compact representations (with respect to parietal cortex). Then the selection mechanisms for semantic information, which we have shown to produce only weak preferences at a low dopaminergic tone may be overridden by an equally weak preference for a phonologically associated representation.

Conclusion

We have presented a neural network model of selective attention and semantic memory that employs single neurons with the basic characteristics of integrate-

and-fire neurons, but adaptable to different levels of dopaminergic activation.

Using this type of model neuron, we have built a two-module network consisting of a short-term storage device and a central executive function network which implements the function of directing attention. The short-term storage function was realized by an oscillatory buffer consisting of sequences of activation of tightly synchronized groups of neurons. We propose that activated meaning structures from long-term memory are present in short-term memory during the tasks of word meaning understanding and generation. The functioning of working memory depends on a specific dopaminergic tone that corresponds to an optimal activation of D1-receptors and their counterbalance by D2-receptors. This dopaminergic tone is reflected as certain temporal signal processing characteristics of single neurons. We could show that the functions of stability of representation, selectivity and inhibition of interference effects depend on these neuronal properties. Specific impairments in word meaning access observed in schizophrenics and attributed to the general low dopaminergic tone in prefrontal cortex can thus be explained by the given model.

Appendix A: Single-Neuron Models

The basic single-neuron model adopted in this work is that of an integrate-and-fire unit, i.e. a model without dendritic structure. Temporal varying properties are rendered by parameters for resistance (R) and driving force (E) (cf. (Stevens & Zador 1998)).

$$V = \Delta V \times \exp\left(\frac{t - t_0}{\tau \times R(t) \times (1 + E_2(t))}\right) - E(t)$$

$$E(t) = E_0 \times \exp\left(\frac{t - t_0}{\tau_E}\right)$$

$$R(t) = R_0 \times \exp\left(\frac{t - t_0}{\tau_R}\right).$$

$$E_2(t) = E_2^0 \times \exp\left(\frac{t - t_f}{\tau_{E_2}}\right)$$

E_2^0 is initially set to 0. Immediately after each firing event, E_2^0 is increased by Δ_{E_2} until a limit of E_2^{max} is reached. Several different variants of the basic model are used in the simulations:

- For inhibitory neurons, a basic, non-temporal formulation of the model was used. Inhibitory neurons show low accommodation effects and are presumably not modulated by D1-receptors.
- Excitatory (pyramidal) cells were modeled using measurements from rat prefrontal slices. We distinguish between a baseline condition (no dopamine receptor activity) and a modulated condition (D1-receptor activity). Furthermore certain intermediate values have been chosen, which may be indicative of partial receptor activity.

- the single-neuron model used in Fig. 2:

$\tau = 20 \text{ ms}$, $\tau_R = 450 \text{ ms}$, $\tau_E = 125 \text{ ms}$, $R_0 = 1.8$, $E_0 = -8 \text{ mV}$, $\Delta_{E_2} = 0.9$, $\tau_{E_2} = 12.5 \text{ ms}$, $E_2^{max} = 2.0$, $\theta = -44 \text{ mV}$, synaptic delay = 2 ms. In comparison to the measured baseline condition, this has a lower accommodation effect (τ_R is longer, τ_E , τ_{E_2} are shorter, and E_{max} is lower), which serves to keep up activity in the chosen network structure.

- the single-neuron model used in Fig. 4:

$\tau = 22.5 \text{ ms}$, $\tau_R = 37.5 \text{ ms}$, $\tau_E = 135 \text{ ms}$, $R_0 = 8$, $E_0 = -1.1 \text{ mV}$, $\Delta_{E_2} = 0.0$, $\tau_{E_2} = 250 \text{ ms}$, $E_2^{max} = 0.0$, $\theta = -46 \text{ mV}$, and synaptic delay = 2 ms.

These are the parameter settings that provide a good fit with the measured input-output function of a D1-modulated neuron.

Appendix B: Architecture of the working memory model

For the model used in Fig. 3 and Fig. 4 the following link densities (ld) and synaptic weights (sw) for functional groups of neurons were used: neurons within a representational attractor: ld=1.0 sw=0.8, between attractors: ld=1.0 sw=1.0, between attractors and semi-active neurons: ld=0.02 sw=0.2, from inhibitory neurons to attractors: ld=1.0 sw=-2.0, from attractors to inhibitory neurons: ld=1.0 sw=2.0, between attractors and background neurons: ld=0.01 sw=0.05.

For the attentional model (Fig. 5 and 6) the following additional architectural parameters have been used: between attentional neurons and semi-active neurons: ld=1.0 sw=0.2, from inhibitory neurons to attractors: ld=1.0 sw=-2.0D/-0.7BL, from attentional neurons to attentional inhibitory neurons: ld=1.0 sw=0.6, from attentional inhibitory neurons to representational neurons (semi-active and attractors): ld=1.0 sw=-1.5D/-0.4BL, from representational neurons to representational inhibitory neurons: ld=1.0 sw=0.6, from representational inhibitory neurons to representational neurons: ld=1.0 sw=-1.5D/-0.4BL.

For simplicity the increase of inhibitory activity due to D2-receptor activation has been modelled (incorrectly) by a greater synaptic strength (indicated by BL for the baseline, non-modulated case and D for the dopamine-modulated case). The net result of more inhibition in the network for the modulated condition, however, is the same.

References

- Amit, D.; Brunel, N.; and Tsodyks, M. 1994. Correlations of cortical Hebbian reverberations: Theory and experiment. *Journal of Neuroscience* 14(11):6435-6445.
- Callicott, J.; Mattay, V.; Bertolino, A.; Finn, K.; Coppola, R.; Frank, J.; Goldberg, T.; and Weinberger, D. 1999. Physiological characteristics of capacity constraints in working memory as revealed by fMRI. *Cerebral Cortex* 9:20-26.

- Chafee, M., and Goldman-Rakic, P. 1998. Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *Journal of Neurophysiology* 79(6):2919-2940.
- Chelazzi, L.; Miller, E.; Duncan, J.; and Desimone, R. 1993. A neural basis for visual search in inferior temporal (IT) cortex. *Nature* 363:345-347.
- Cohen, Y., and Knudsen, E. 1999. Maps versus cluster: different representations of auditory space in the midbrain and forebrain. *Trends in Neurosciences* 22:128-135.
- Cohen, J.; Perlstein, W.; Braver, T.; Nystrom, L.; Noll, D.; Jonides, J.; and Smith, E. 1997. Temporal dynamics of brain activation during a working memory task. *Nature* 386:604-608.
- Cohen, J.; Dunbar, K.; and McClelland, J. 1990. On the control of automatic processes: a parallel distributed processing account of the Stroop effect. *Psychological Review* 97(3):332-361.
- Collette, F.; Sahnon, E.; van der Linden, M.; Chicerio, C.; Belleville, S.; Degueldre, C.; Delfiore, G.; and Franck, G. 1999. Regional brain activity during tasks devoted to the central executive of working memory. *Cognitive Brain Research* 7(3):411-417.
- Courtney, S.; Ungerleider, L.; Keil, K.; and Haxby, J. 1997. Transient and sustained activity: a distributed neural system for human working memory. *Nature* 386:608-611.
- Dehaene, S.; Kerszberg, M.; and Changeux, J. 1998. A neuronal model of a global workspace in effortful cognitive tasks. *Proc Natl Acad Sci USA* 95(24):14529-34.
- Fleming, K.; Bigelow, L.; Weinberger, D.; and Goldberg, T. 1995. Neuropsychological effects of amphetamine may correlate with personality characteristics. *Psychopharmacology Bulletin* 31(2):357-362.
- Friedman, J.; Temporini, H.; and Davis, K. 1999. Pharmacologic strategies for augmenting cognitive performance in schizophrenia. *Biological Psychiatry* 45:1-16.
- Fuster, J. 1998. Distributed memory for both short and long term. *Neurobiology of Learning and Memory* 70(1-2):268-274.
- Goldman-Rakic, P.; Lidow, M.; J.F.Smiley; and M.S.Williams. 1992. The anatomy of dopamine in monkey and human prefrontal cortex. *Journal of Neural Transmission Supplement* 36:163-177.
- Goldman-Rakic, P.; C.Bergson; Mrzljak, L.; and Williams, G. 1995. Dopamine receptors and cognitive function in nonhuman primates. In K.A.Neve, and R.L.Neve., eds., *The Dopamine Receptors*. Totowa, NJ.: Humana Press. 499-522.
- Goldman-Rakic, P.; Lidow, M.; and Gallagher, D. 1990. Overlap of dopaminergic, adrenergic and serotonergic receptors and complementarity of their subtypes in primate prefrontal cortex. *Journal of Neuroscience* 10:2125-2138.
- Jensen, O., and Lisman, J. E. 1998. An oscillatory short-term memory buffer model can account for data on the Sternberg task. *Journal of Neuroscience* 18(24):10688-10699.
- Krasnegor, N.; Lyon, G. R.; and Goldman-Rakic, P., eds. 1997. *Development of the Prefrontal Cortex*. Brookes.
- Lisman, J., and Idiart, M. 1995. Storage of 7+-2 short-term memories in oscillatory subcycles. *Science* 267:1512-1514.
- Luck, S., and Vogel, E. 1997. The capacity of visual working memory for features and conjunctions. *Nature* 390:279-281.
- Miller, G. A. 1956. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review* 63:81-97.
- Miller, E. K. 1999. The prefrontal cortex: Complex neural properties for complex behavior. *Neuron* 22:15-17.
- Niebur, E.; Koch, C.; and Rosin, C. 1993. An oscillation-based model for the neuronal basis of attention. *Vision Research* 33:2789-2802.
- Rainer, G.; Asaad, W.; and Miller, E. 1998. Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 577-579.
- Scheler, G., and Fellous, J. 1999. Dopaminergic modulation of the signal-to-noise ratio of spiking neurons. (*in preparation*).
- Servan-Schreiber, D.; R.M.Bruno; Carter, C.; and J.D.Cohen. 1998. Dopamine and the mechanisms of cognition: Part I. a neural network model predicting dopamine effects on selective attention. *Biological Psychiatry* 43:713-722.
- Smith, E., and Jonides, J. 1999. Storage and executive processes in the frontal lobes. *Science* 283:1657-1661.
- Spitzer, M. 1997. A cognitive neuroscience view of schizophrenic thought disorder. *Schizophrenia Bulletin* 23(1). 29-50.
- Stevens, C., and Zador, A. 1998. Novel integrate-and-fire-like model of repetitive firing in cortical neurons. In *Proceedings of the 5th Joint Symposium on Neural Computation, UCSD, La Jolla, CA*.
- Tallon-Baudry, C.; Bertrand, O.; Peronnet, F.; and Pernier, J. 1998. Induced gamma-band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience* 18(11):4244-4254.
- Thompson-Schill, S.; D'Esposito, M.; Aguirre, G.; and Farah, M. 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences USA* 94:14792-14797.
- Vergara, C.; Latorre, R.; Marrion, N.; and

- J.P. Adelman. 1998. Calcium-activated potassium channels. *Current Opinion in Neurobiology* 8:321-329.
- Wehr, M., and Laurent, G. 1996. Odor encoding by temporal sequences of firing in oscillating neural assemblies. *Nature* 384:162-166.
- Zipser, D.; Kehoe, B.; Littlewort, G.; and Fuster, J. 1993. A spiking network model of short-term active memory. *Journal of Neuroscience* 13(8):3406-3420.