

DYNAMIC COOPERATION AND COMPETITION IN A NETWORK OF SPIKING NEURONS

Thomas Trappenberg

Email:thomas@brain.riken.go.jp

Laboratory for Information Synthesis
RIKEN Brain Science Institute
Hirosawa 2-1, Wako-shi, Saitama 351-0198, Japan

ABSTRACT

We discuss recurrent networks with local excitatory and surrounding inhibitory connectivity and their implications as model for the dynamics of sensory awareness and saccade initiation. A version of such a model with spiking neurons is introduced, and its association with simulations of the superior colliculus are reviewed. We also discuss the competition for attention as suggested by Taylor, and present some additional supportive simulations of experiments by Libet and colleagues. Finally we will report on a recent observation in such a model with noisy and spiking neurons without guidance of external input, and show first results of auto- and cross-correlation calculations in the domain of high firing rates.

KEYWORDS: saccades, sensory awareness, spiking neurons, synchronization

1. A PRINCIPAL MECHANISM EMPLOYED BY THE BRAIN?

Neural networks with feedback connectivity of local excitation and surrounding inhibition have been discussed on a conceptual level [1, 2, 3], and in connection with behavior [4, 5, 6], brain functions [7, 8] and applications [9]. Amari [1] has shown that there are several regimes with different asymptotic solutions in such models. Of these regimes there is one with a persistent localized area of neural activity (bubble) even without external input. Once such a bubble becomes established it will enforce itself and will inhibit other areas unless a cooperation of some other neurons win the inhibitory competition and seize the previous active bubble.

This scenario of cooperation and competition is interesting in several respects. Most of all, such a network realizes a dynamic integration of signals from a combination of population coding with a soft winner-takes-all scheme. This form of information integration can, for example, produce a consistent motor command in an environment with sensory information which would otherwise trigger conflicting strategies in an animal or robot. Kopecz and Schönner [4, 5] have speculated that such an information integration mechanism might be employed in primates to integrate endogenous and exogenous information to produce a consistent motor command for saccadic eye movements. On a physiological level converging evidence is pointing towards the intermediate layer of the superior colliculus (SC) as one central station for signal integration within the oculomotor system. These speculations are now fueled by intriguing similarities of simulated saccade initiation with human behavior data [4, 5, 6, 10, 11] and recording data from the monkey's SC [11].

Another interesting area where the dynamics of bubble competition does show striking similarities to experimental data

was found by Taylor [7]. He argued that the bubble dynamic can account for many details of the findings by Libet et al. [12, 13] of sensory experiences after direct stimulation of the somatosensory cortex of awake subjects, which were, until then, still unexplained. Taylor and Alavi [14, 15] made a first step toward finding the neuronal locus of the related competitive mechanism by showing that the thalamus - nucleus reticularis - cortex complex can give rise to an competitive mechanisms.

Our speculation is that the mechanism of dynamic cooperation and competition is employed by the brain in at least two different functional systems. We would like to stress that the detailed neural implementation leading to the necessary effective interaction of neurons can differ, and we are not attempting to model all the details of the brain areas under investigation. Those models have been developed elsewhere (see for example Grossberg et al. [16] for an advanced model of saccade programming in the SC). Instead we will show in this paper how well some brain functions can be related to the principle mechanism of cooperation and competition. Furthermore we will demonstrate that the mechanism of cooperation and competition works also in an implementation with spiking neurons. A further aim of this paper is to outline some additional behavior of the model specific to the version with spiking neurons.

We will introduce our simple implementation in section 2 and review some results in applying this to simulations of saccade reaction times (SRTs) in section 3. In section 4 we report on some additional simulations of Libet's findings. Recent observations of the behavior of the model when driven by some noise without external input are presented in section 5. Finally, in section 6, we will shortly outline some first results of calculations of auto- and cross-correlations in this model.

2. THE RECURRENT MODEL WITH SIMPLE SPIKING NEURONS

In the following we will study a collection of N identical neurons. Each neuron is described by a time dependent 'internal state', $u_i(t)$, which can be associated with the membrane potential of the cell. The time evolution of the membrane potential before a spike and after the refractory period will be described by

$$\tau \frac{du_i}{dt} = -u_i(t) + I_i(t), \quad (1)$$

where τ is a time constant and I_i is sum of synaptic currents into cell i . The neurons influence other neurons proportional to their activity A_j which is associated with the mean firing rate in most standard neural network models. For this type of model we use a standard form of neuron activity, a sigmoidal

function of the inner states of the neurons:

$$A_i = F(u_i) = \frac{1}{1 + \exp(-\beta_a u_i + \Theta_a)}. \quad (2)$$

In the implementation of the model with spiking neurons we use a binary value indicating the occurrence of a spike. We also include noise in the model by defining the firing probability in the interval Δt as

$$P(A_i = \xi | u_i) = \frac{1}{1 + \exp(-\beta_s u_i + \Theta_s)} \Delta t. \quad (3)$$

Furthermore we take into account a finite time, t_{dur} , for the duration of the spike after a spike onset at t_s . The potential is thereby set to zero until after the absolute refractory time t_{ref} ,

$$u_i(t_s < t < t_s + t_{ref}) = 0. \quad (4)$$

Finally, we will specify the sum of synaptic currents I_i into cell i by writing this current in the form

$$I_i(t) = \sum_j \omega_{i,j} A_j(t - t_{del}) + I_i^{in}(t), \quad (5)$$

and chose

$$\omega_{i,j} = a_\omega e^{-(j-i)^2/2\sigma_\omega^2} - a_{\omega,0}. \quad (6)$$

as parameterization of the synaptic efficacy (weight) $\omega_{i,j}$ from neuron i to neuron j . The essence of this formula is that there is an effective excitatory influence for short physical distances between cells, and that there is a long range inhibition effect. We have included a synaptic delay t_{del} in some of the simulations but did not find a strong influence on our results. The external input are chosen as graded inputs around the location l of a model stimulus in the form

$$I_i^{in}(t) = a_{in}(t) e^{-(i-l)^2/2\sigma_{in}^2}. \quad (7)$$

In the simulations discussed below we used a one dimensional layer of $N = 101$ neurons for simplicity. However, as was shown by Taylor [3] (see also [9]), similar results can be expected in higher dimensions.

3. A MODEL OF OCULOMOTOR DYNAMICS

The above model was first employed by Kopecz and Schöner [4, 5] to simulate human saccade data, and was further studied by Trappenberg et al. [6]. Klein et al. [11] have compared the model in several experimental paradigms with human behavior data and cell recordings from the monkey's SC. Due to the limited space we will only give an example of a simulation of basic behavioral data, of which more details can be found in a technical report [10].

In figure 1 we compared model simulations (solid line for the model with average firing rates, and crosses with error bars for the model with spiking neurons) with human behavior data (open circles) analyzed by Taylor and Klein [17] from classical experiments by Saslow [18]. In these experiments human subjects were required to fixate targets presented in various temporal relations to removal of a fixation stimulus (gap/overlap paradigm). These experiments show that the saccade reaction time (SRT), that is the time between target onset and the beginning of the saccade, is longer in an overlap condition compared with a situation of a gap between fixation offset and target onset suggesting a strong disengagement

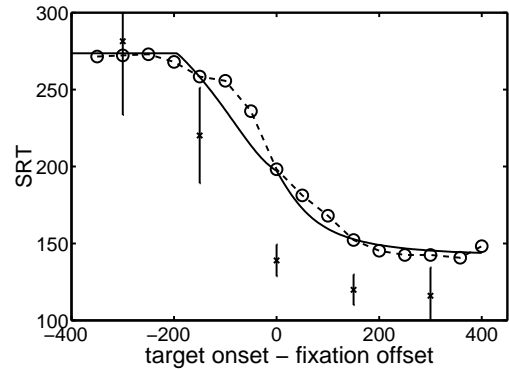


Figure 1: Saccade Reaction Time (SRT) as function of the time between fixation offset and target onset. The open circles are human performance data, the stars are simulation results of the model with average firing rates, and the crosses represent the results from the model with spiking neurons

effect. In the numerical experiments we define the saccade onset as the time when the peripheral activity becomes larger than the central activity (see [10] for more details).

The simulations achieve similar effects, suggesting that the variability of the SRTs could origin (at least partially) in dynamic of competitive mechanisms. However, the question remains if this mechanism is realized in the brain. One obvious candidate is thereby the intermediate layer of the SC as it is thought to be an area of converging exogenous and endogenous signals, and saccade related neurons in this area [19] behave similar to our model neurons [11]. First indirect supportive evidence was reported by Arai et al. [20] who trained a recurrent network with spatial-temporal data from the SC and found a connectivity matrix similar to the one in eq.6. Further evidence is now gathered by Dorris et al. [21] who are recording buildup cells in a distractor paradigm. First raw data have shown an inhibition effect on the buildup of activity for far distractors (relative to the visual field of the recorded neuron), and an enhanced activity for close distractors. These effects are very similar to those seen in simulations [11]. From the size of the effect we hope to gather some quantitative knowledge of the effective connectivity within this layer of the SC. It would also be useful to derive the effective interaction matrix from more detailed models of the SC such as the one of Grossberg et al. [16].

4. A COMPETITION FOR CONSCIOUSNESS?

John Taylor asked this question in [7] and demonstrated that the dynamic of competing bubbles does show some of the interesting effects of sensory awareness found by Libet et al. [12, 13]. In these experiments the exposed somatosensory cortex of awake human subjects were stimulated with a pulsed electric current of varying frequency, amplitude and time duration. Libet et al. [12] found that the liminal (i.e. minimal) current, I , necessary to reach sensory awareness, scales with the inverse square root of the stimulus frequency f ,

$$I \sim f^{-1/2}. \quad (8)$$

Furthermore, Taylor [7] extracted the rule

$$I \sim T^{-1/2}. \quad (9)$$

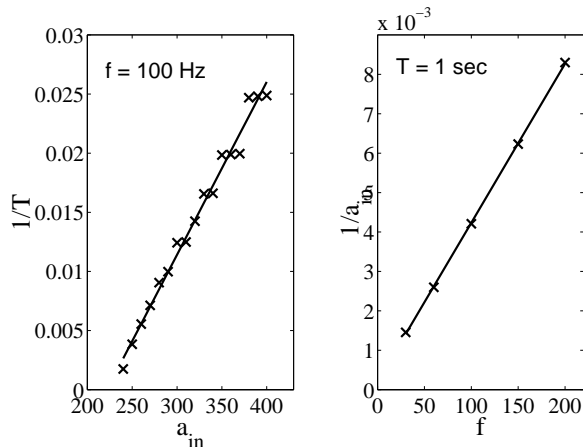


Figure 2: a) Time T for a stimulus at node number 20 to win the competition over a stimulus at node number 80 (with small fixed input) as a function of stimulus amplitude a_{in} . b) Minimal amplitude a_{in} to win the competition within 1000ms for varying frequencies f of the stimulus signal.

for the time T of onset of sensory awareness from the experimental data, and compared this to simulations of the bubble dynamics [7]. In Figure 2a we reproduced these results in the model with average firing rates with an input stimulus similar to that used by Libet, i.e. with a pulse duration of 0.5ms. We show the results for a 100Hz stimulus with varying amplitude a_{in} of the stimulus signal which Taylor argued [7] to be proportional to the square of the current

$$a_{in} \sim I^2 \quad (10)$$

from a current flow analysis. The data agree well with the rule (eq.9) extracted from the experimental data. In Figure 2b we show the frequency dependence of the minimal amplitude necessary to win the competition within 1000ms after stimulus onset and found also a very good agreement with the second rule (eq.8) derived from the human behavior data.

5. BEHAVIOR OF THE NOISY SPIKING NETWORK WITHOUT EXTERNAL INPUT

As shown by Amari [1] there exist a domain in the parameter space of the model with average firing rates which exhibits a finite area of neural activity termed bubble here. We demonstrated in [10] that such a regime also exist in the network with spiking neurons, even in the presents of noise if the noise level is not to high. However, compared to the model with average firing rates, the stability of the bubble could be reduced because the membrane potential is reset to zero after a spike occurred. The firing current for each neuron must therefore be relative high compared to the firing threshold to maintain an ongoing firing in the bubble.

We discussed in the previous sections how the competitive model can integrate different inputs and drew our attention to the superior colliculus and the thalamo-cortical loop as possible sites were such mechanisms are used in the brain. If such a mechanism is used it becomes obvious to ask how such a system behaves without external input, which should

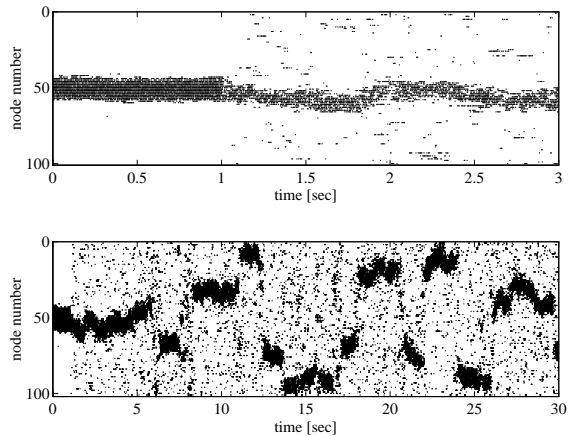


Figure 3: Spike train in the model with spiking neurons including strong noise. An external input in the center of the neuron layer was removed after 1sec.

occur, at least partially, during sleep¹. Without noise the locus of activity is stable. However, even some small noise can at least shift the location of the bubble. An example is given in figure 3a which shows simulated spike trains. The external input, which stabilizes a bubble in the center of the neuron layer, was removed at 1sec. This results in a drifting bubble of reduced size which in turn allows for more random spikes in the periphery due to the reduced inhibition.

It is very interesting to observe the same simulation on a larger time scale as shown in figure 3b. As can be seen there is still a unique area of enhanced neural activity (bubble), but this area jumps around on a time scale of about 2sec in this simulation. It is so far unknown how large the domain of this behavior is and if such jumping loci can be observed in the brain. It could very well be a source of rapid eye movements during REM sleep originating in the superior colliculus, or the source of jumping attention during dreaming from the thalamo-cortical loop. The time scale of rapid eye movement was observed to be around 1sec which is not too far from the scale found in the simulation. It is also intriguing to ask if there is some relations to switching perception such as in the visual perception of the Necker cube.

6. AUTO- AND CROSS CORRELATIONS

Cross-correlation (CC) analysis of spike patterns between pairs of neurons have long been used by physiologist to identify possible synaptic connectivity of neurons in the nervous system. Usher et al. [8] have calculated auto- and cross-correlations in a similar model of the visual cortex and found some signals of cross-correlations for small distances of neurons as can be expected from the pattern of synaptic efficacies. In contrast to our simulations, they examined the model in a regime of low firing rates. In this regime the probability that neighboring neurons will be active while a neuron spikes is low, so that the probability that this neuron will initiate a spike of neighboring neurons can be high and should lead to some cross-correlations within the cooperative bubble.

¹There might still be internal activity from other brain areas driving those systems. However, we will explore the extreme case of no input to the competitive system.

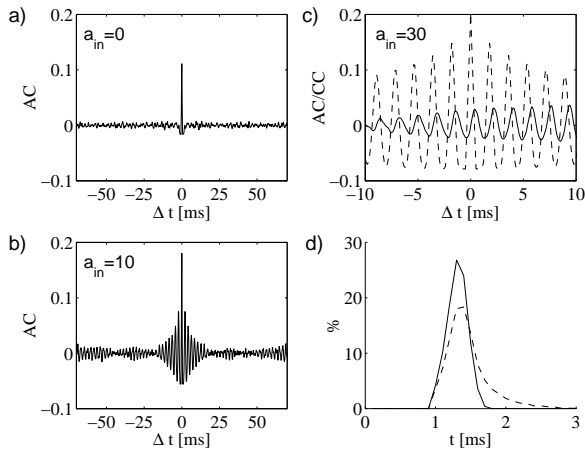


Figure 4: a) b) c) Auto-correlations (ACs) and c) cross-correlations (CCs) with different magnitude of external input a_{in} . d) Histograms of inter-spike intervals averaged over a small (solid line) and large (dashed line) area within the bubble of activity.

This is in contrast to our simulations in the domain of large firing rates where we found synchronization only for extremely large external input as demonstrated in Figure 4. Figure 4a displays the results for the auto-correlation function within the center of the active bubble without external input, but only the auto-correlation with a strong external input of $a_{in} = 10$ as shown in Figure 4b shows some oscillations. Also, even with this strong synchronizing external input we do not get strong cross-correlations as shown in figure 4c where we compared the auto-correlation (dashed line) to the cross-correlation of neighboring nodes (solid line) in a simulation with even larger external input ($a_{in} = 30$). This shows that the relative long refractory time in our model together with the large firing rate results in a more independent firing pattern in this domain of the model. This can also be seen in the histograms of inter-spike intervals (ISIs) shown in Figure 4d. The solid line represents histograms of ISIs averaged over 9 central nodes which display a Gaussian shape. We only observe a long tail in the distribution if we average over more nodes (dashed line for 23 nodes) because it included nodes at the edge of the bubble which are influenced by fluctuations of the bubble location. This might be one source of the long tail in the ISIs not mentioned in [8].

7. OUTLOOK

In the search for the principles of brain processing, dynamic cooperation and competition might be a prime candidate. Converging evidence is suggesting that this mechanism might be realized in the brain. It is fascinating how many details of various brain functions, as found by behavioral and physiological experiments, can be simulated by the simple model discussed in this paper. It might teach us the lesson that a competitive integration of sensory signals is a way to archive goal directed control of a large system which has to function in a changing environment. Research into neural correlates of this mechanism as well as towards technical applications are promising.

This research was supported by an NSERC (Canada) Collaborative Project Grant.

References

- [1] Amari, S.-I., "Dynamics of Pattern Formation in Lateral-Inhibition Type Neural Fields," *Biol. Cybern.*, **Vol.27**, pp.77–87 (1977).
- [2] Grossberg, S., *Stud. Appl. Math.* **Vol.LII**, pp.213–(1973).
- [3] Taylor, J.G., "Neural Bubble Dynamics in Two Dimensions I: Foundations," *Biol. Cyb.*, to appear (1998).
- [4] Kopecz, K., "Saccadic Reaction Time in Gap/Overlap Paradigm: a Model Based on Integration of Intentional and Visual Information on Neural, Dynamic Fields," *Vis. Res.*, **Vol.35**, pp.2911–2925 (1995).
- [5] Kopecz, K., Schöner, G., "Saccadic motor planning by integrating visual information and expectation on neural dynamic fields," *Biol. Cybern.*, **Vol.73**, pp.49–60 (1995).
- [6] Trappenberg, T., Simpson, S., Klein, R.M., McMullen, P., Munoz, D.P., Dorris, M.C., "Neural Field model of oculomotor preparation and disengagement," *Proceedings of WCNN'97 in Huston*, **Vol.1**, pp.591–596 (1997).
- [7] Taylor, J.G., "A competition for consciousness?," *Neurocomputing*, **Vol.11**, pp.271–292 (1996).
- [8] Usher, M., Stemmler, M., Koch, Ch., Olami, Z., "Network Amplification of Fluctuations Causes High Spike Rate Variability, Fractal Firing Patterns and Oscillatory Local Field Potentials" *Neural Computation*, **Vol.6**, pp.795–836 (1996).
- [9] Konen, W.K., Maurer, T., von der Malsburg, Ch., "A Fast Dynamic Link Matching Algorithm for Invariant Pattern Recognition," *Neural Networks*, **Vol.7**, pp.1019–1030 (1994).
- [10] Trappenberg, T., "A Model of the Superior Colliculus with Competing and Spiking Neurons," *BSIS Technical Report*, **No.98-3**, (1998).
- [11] Simpson, S., Klein, R.M., Trappenberg, T., work in progress.
- [12] Libet, B., Alberts, W.W., Wright, E.W., DeLattre, L.D., Feinstein, B., "Production of threshold levels of conscious sensation by electrical stimulation of human somatosensory cortex," *J. Neurophys.*, **Vol.27**, pp.546–578 (1964).
- [13] Libet, B., "Brain stimulations in the study of neuronal functions for conscious sensory experience," *Human Neurobiology*, **Vol.1**, pp.235–242 (1982).
- [14] Taylor, J.G., Alavi, F.N., "A global competitive model for attention," *Neural Network World*, **Vol.5**, pp.477–502 (1967).
- [15] Taylor, J.G., Alavi, F.N., "A global competitive neural network," *Biol. Cybern.*, **Vol.72**, pp.233–248 (1995).
- [16] Grossberg, S., Roberts, K., Aguilar, M., Bullock, D., "A Neural Model of Multimodal Adaptive Saccadic Eye Movement Control by Superior Colliculus," *J. of Neuroscience*, **Vol.17**, pp.9706–9725 (1997).
- [17] Taylor, T.L., Klein, R.M., pers. comm. (1997).
- [18] Saslow, M.G., "Saccade latency and warning signals: Stimulus onset, offset and change as warning events," *J. of Opt. Soc. of Am.*, **Vol.57**, pp.1024–1029 (1967).
- [19] Munoz, D.P., Wurtz, R., "Saccade related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells," *J. Neurophys.*, **Vol.73**, pp.2313–2333 (1995).
- [20] Arai, K., Keller, E.L., Edelman, J.A., "Two-Dimensional Neural Network Model of the Primate Saccade System," *Neural networks*, **Vol.7**, pp.1115–1135 (1995).
- [21] Dorris, M.C., Munoz, D.P., Everling, S., pers. commun.