

## Propagation of synchronous spiking activity in feedforward neural networks

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**Summary** — ‘Synfire’ activity has been proposed as a model for the experimentally observed accurate spike patterns in cortical activity. We investigated the structural and dynamical aspects of this theory. To quantify the degree of synchrony in neural activity, we introduced the concept of ‘pulse packets’. This enabled us to derive a novel neural transmission function which was used to assess the role of the single neuron dynamics and to characterize the stability conditions for propagating synfire activity. Thus, we could demonstrate that the cortical network is able to sustain synchronous spiking activity using local feedforward (synfire) connections. This new approach opens the way for a quantitative description of neural network dynamics, and enables us to test the synfire hypothesis on physiological data.

synchrony / cell assembly / synfire chain / pulse packet / propagation / neocortex / neural dynamics

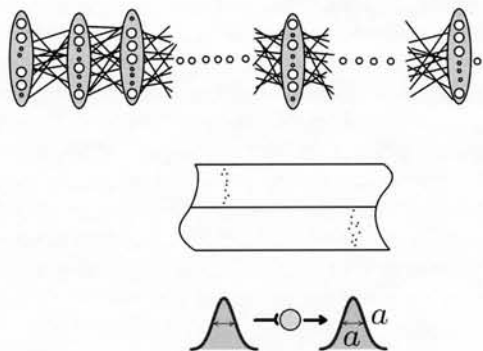
### Introduction

Recently, it was demonstrated that the activity of frontal cortical neurons in the awake behaving monkey comprises excessive occurrences of highly accurate ( $\pm 1$  ms) spike patterns. Interestingly, these patterns can be related to the behavioral state of the animal (Abeles *et al.*, 1993a, b; Grün *et al.*, 1994; Grün, 1996; Riehle *et al.*, 1995, 1996). On the basis of the characteristic anatomy and physiology of the cortex, it was proposed that synfire activity, propagating through the sparsely firing cortical neural network, presents a natural explanation for this phenomenon (Abeles, 1991). In order to test this hypothesis, we studied the dependence of reliable synfire propagation on the structural and the dynamical properties of a model cortical network. We used the concept of pulse packets (Gewaltig *et al.*, 1995; Diesmann *et al.*, 1996) and investigated to what extent this framework can be used to describe propagating synchronous activity in a synfire chain.

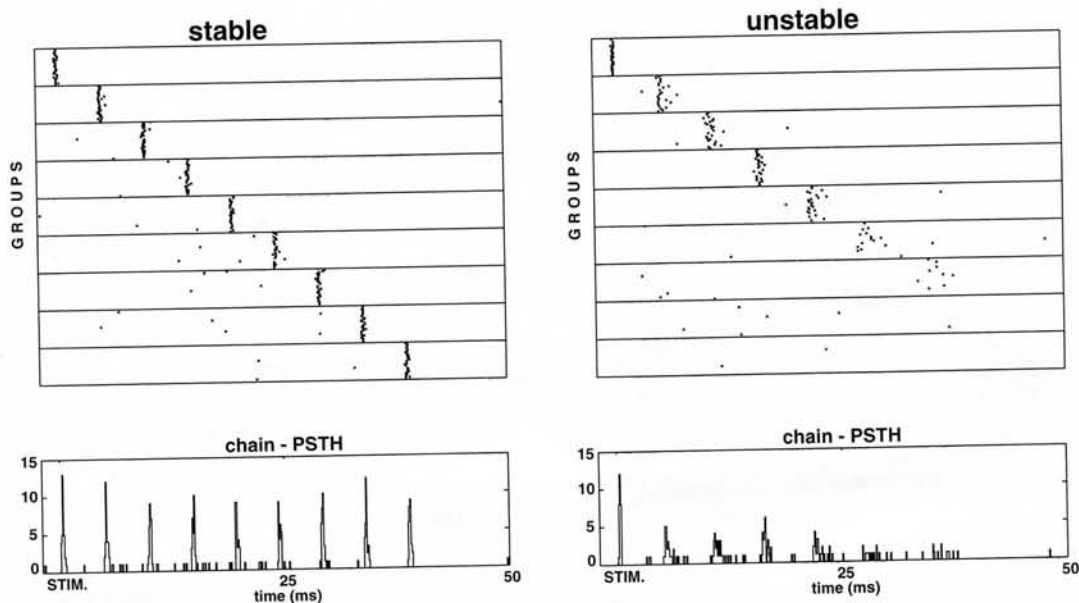
### Synfire chains

Synfire chains consist of diverging/converging links, connecting groups of neurons. A link is characterized by two structural parameters: the width  $w$ , defining the number of neurons in a group and the multiplicity  $m$ , the number of connections from a neuron to the next group. Figure 1 (top row) depicts such a local feedforward chain of neurons. Activity, induced in a group will trigger the neurons in the receiving group. Thus, each group passes the activity on to the next one. The activity, typically observed in such chain-like structures of sparsely firing neurons are volleys of spikes, with

each neuron contributing at most one spike. Figure 2 shows two possible cases of propagating synfire activity: stable (left) and unstable transmission (right). In simulation studies we found that successful transmission from one group to the next depends on the number of activated neurons and on the temporal distribution of their firing (Diesmann *et al.*, 1994). Both parameters exhibit a critical value which determines whether transmission will be stable or not. These critical values depend on the structural parameters  $w$  and  $m$ , as well as on the details of the single neuron dynamics.



**Fig 1.** Synfire chains and pulse packets. The top row shows a sketch of a synfire chain: groups of neurons are connected to form a feedforward chain. The second row illustrates the type of activity that can be found in such a network: volleys of spikes propagate from one group to the next. This situation is further elaborated in the bottom row: a group receives a spike volley, idealized to a probability density function called ‘pulse packet’, and passes it on to the next group. Each pulse packet is characterized by two parameters: the activity  $a$ , defining the number of active neurons in a group and the width  $\sigma$ , defining the temporal dispersion of the group activity.



**Fig 2.** Transmission of synchronous spiking activity in a synfire chain. Each row in the raster displays represents the spiking activity of the neurons in a single synfire group. Below, the total network activity is shown in a PST-histogram. In the stable case (left panels) the neurons of different groups become active at different times, corresponding to their relative position in the chain. In this case the activity is able to propagate through the entire chain, while maintaining its amplitude and temporal dispersion. In contrast, in the unstable case (right panels) the activity deteriorates progressively with each stage. With decreasing activity, the temporal spread of the group response increases and the volley gradually slows down. In the stable case, however, we observe no such widening of the activity and the velocity of propagation remains constant.

In order to characterize the network dynamics, we need to assess the influence of the degree of synchrony on the spike arrival time distribution. Unfortunately, existing measures of neural transmission focus on two limiting cases: full synchrony and random arrival (Abeles, 1982, 1991). Intermediate cases with a finite degree of temporal dispersion are not addressed. Two recent studies (Murthy and Fetz, 1994; Bernander *et al.*, 1994) investigated the influence of input synchrony on the activity of model cortical neurons. However, both these studies described the output activity in terms of firing rate, not as timing of individual spiking events. The concept of pulse packets (Gewaltig *et al.*, 1995; Diesmann *et al.*, 1996) overcomes these restrictions, and enables us to quantify the degree of temporal synchrony in propagating volleys of neural activity.

### Pulse packets

A pulse packet is a probabilistic description of the activity of a group of neurons, represented by a pulse density function  $\rho(t)$ . This pulse density is determined by two parameters: the activity  $a$ , defining the number of active neurons in a group and the width  $\sigma$ , defining

the temporal dispersion of the group's spiking activity (fig 1, bottom). If we assume all neurons to be identical and the chain to be completely connected (*ie* all neurons in a group receive the entire output activity of the previous group), the statistical properties of a group's response are determined by the single neuron parameters. Thus, instead of having to consider all member neurons in a group, we may restrict ourselves to only one neuron, and investigate how its firing probability changes upon dynamic modification of the input. From this description of the single neuron's firing characteristics, we can then extrapolate to the behaviour of the entire group.

Adopting this approach, we studied the response of a model cortical neuron (Gewaltig *et al.*, 1994) to input activity with varying degrees of synchrony, using the simulation tool SYNOD (Diesmann *et al.*, 1995). The model neuron (membrane time constant 10 ms) was supplied with background noise ('balanced' excitation/inhibition) from a large number (~20 000) of uncorrelated neurons, leading to a high variability of the membrane potential ( $\sigma_{\text{memb}} \cong 4$  mV) and a Poissonian spike interval distribution (rate  $\lambda \cong 2$  Hz). Time course and amplitude of the PSPs were taken from the literature (Fetz *et al.*, 1991), and are assumed to be the same for background and intra-chain connections.

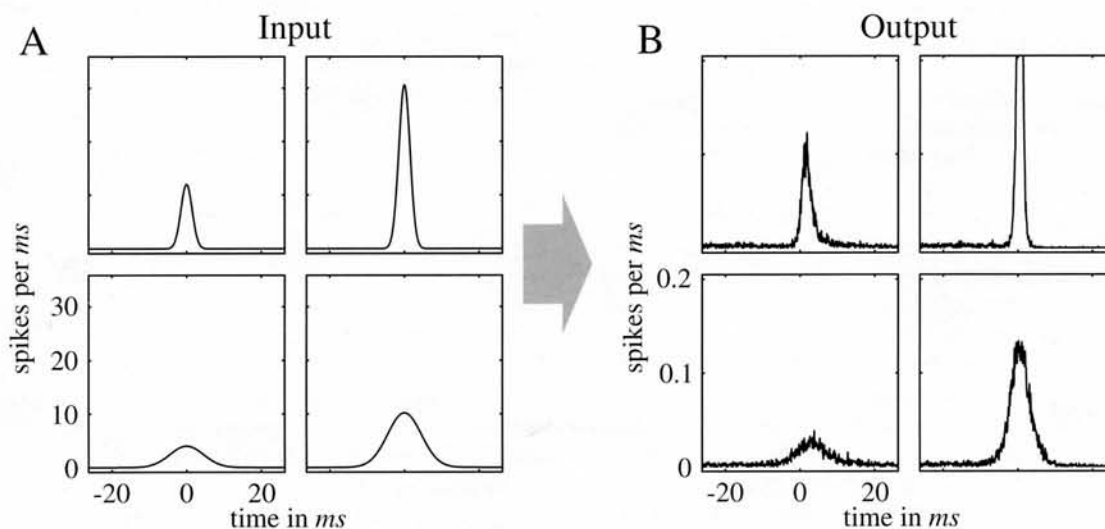
### Neural transmission function

In simulations of this model neuron, we recorded the response (time of first spike) in repeated trials, and collected these in a PST-histogram. After normalization for the number of trials, the resulting output distribution describes the neuron's firing probability density as a function of time. This probability density was similarly described as a pulse packet, and the associated pulse density  $p(t)$ , together with its values of  $a$  and  $\sigma$  were determined. Thus, we could investigate how the output distribution changed, depending on the input distribution (Gewaltig *et al.*, 1995). Figure 3 shows the input (A) and output (B) firing densities for four different input activity distributions. Observe that narrowing the input packet or increasing its size effectively speeds up the transmission: the peak in the output distribution is reached earlier, and also the relative amplitude is enhanced. In order to cover a large section of the input parameter space, the input was varied systematically from a sharp synchronous volley of spikes (small  $\sigma$ , large  $a$ ) to a slow asynchronous rate variation (large  $\sigma$ , small  $a$ ).

Using an appropriate correction for the spontaneous activity of the neuron, we measured for each pair of input parameters ( $a_{in}$ ,  $\sigma_{in}$ ), the corresponding output pair ( $a_{out}$ ,  $\sigma_{out}$ ). The transmission function of the neuron for

dynamic modulations of input synchrony is then given by the mapping of the input pair ( $a_{in}$ ,  $\sigma_{in}$ ) to the output pair ( $a_{out}$ ,  $\sigma_{out}$ ). This mapping yields a compact characterization of the neuron's firing dynamics. In contrast to earlier approaches where the neuron's firing probability is measured quasi-statically as a function of DC-current, this new transmission function takes full account of the dynamic properties of the input distribution.

The neural transmission function can be visualized using iso- $a_{in}$  and iso- $\sigma_{in}$  plots (fig 4), each one emphasizing a specific aspect of the synchronous transmission. For example, panel D shows the output width  $\sigma_{out}$  versus the input width  $\sigma_{in}$  for constant  $a_{in}$ . Observe that for  $a_{in} = 45$  the outgoing pulse packet is always wider than the incoming one. Synchronous input is thereby dispersed in time. However, when the input packet contains more spikes (here:  $a_{in} = 115$ ) the curve crosses the diagonal at some critical value for  $\sigma_{in}$ . Beyond this intersection the curve remains below the diagonal, implying that the neuron exhibits a synchronizing behavior. Panel A is comparable to the traditional sigmoid transfer function, used in many neural network models. Note however, that the temporal dispersion of the input (*ie*  $\sigma_{in}$ ) strongly influences the magnitude  $a_{out}$  of the response. Also the remaining two panels (B, C) demonstrate that the parameters size and width cannot be treated separately. Each of these two



**Fig 3.** Single neuron response to pulse packet input. The model neuron's response to Gaussian shaped input pulse packets, for four different choices of parameters: input packet widths are  $\sigma = 1.5$  ms (top) and  $\sigma = 4.5$  ms (bottom), the numbers of spikes in the input packets are  $a = 45$  (left) and  $a = 115$  (right). Note the different scaling of the ordinate in panel B. The upper right distribution in panel B is clipped; the actual peak value is  $0.52 \text{ ms}^{-1}$ .

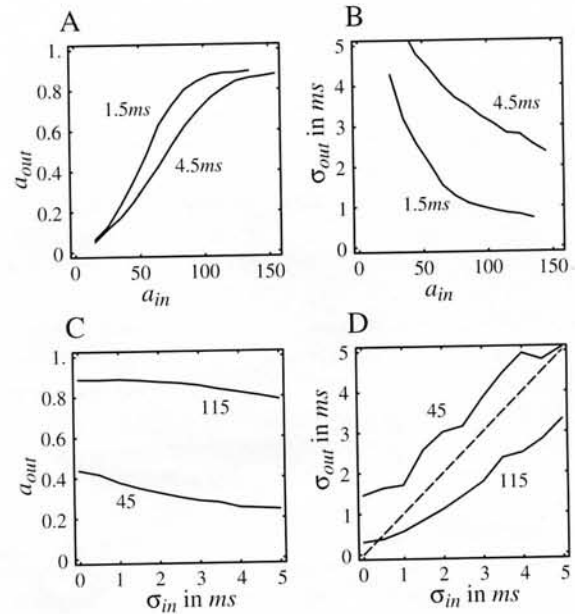
input parameters influences both parameters of the output distribution, with especially the output width  $\sigma_{out}$  critically depending on the input size  $a_{in}$ .

### Activity propagation in synfire chains

Under certain assumptions, these single neuron dynamics can be carried over to describe the behavior of groups of neurons in a synfire chain. In the simplest case we assumed that the chain is completely connected and that all neurons in the chain are identical. The transmission function for a group can then be interpreted as a linear superposition of the single neuron transmission functions. If the width of the neural groups is sufficiently large, the propagation of activity through the chain can directly be described by pulse packets: scaling the ordinate of figure 4A with the number of neurons in the group yields the transformation of packet size from one group to the next. Thus, the pair (A, D) can be interpreted as an iterative map, describing the evolution of synchronization along the chain. The diagonal intersection in figure 4D corresponds to an invariant pulse packet, defining the stable state of the system. In this context we note that multiplying the ordinates in figure 3B by a factor of about 100, we arrive at the same order of magnitude as in figure 3A. Given the neuron properties and the weight of the synaptic connections, this is indeed the number of neurons required for stable transmission of synfire activity.

However, since the width of a synfire group is finite, there will be a deviation of the actual input a neuron receives from the theoretical pulse density function  $p(t)$ . Thus, the width of a group also determines its synchronization properties. In the case of incompletely connected chains, *ie*  $m < w$ , another problem arises. Each neuron in a group receives a different fraction of the propagating pulse packet. As a result of the non-identical inputs, the neurons will also have non-identical response properties, introducing a further deviation from the idealized transmission function as given by the pulse packet approach. Both these effects, finite width and incomplete connectivity, introduce 'errors' in the neuron groups' 'estimate' of the incoming pulse packet. As a result, the same synfire chain will not behave exactly identical in different trials. Pulse packets activated simultaneously in two identical synfire chains will develop a time lag with respect to each other that may become successively larger with each group it has passed, comparable to a random walk (see also Bienenstock, 1995).

Another, though unrelated, effect is caused by the embedding of the local feedforward synfire chain struc-



**Fig 4.** Different views of the neural transmission function. The four panels show the dependence of the size  $a_{out}$  (left) and the width  $\sigma_{out}$  (right) of the output packet on the size  $a_{in}$  (top) and the width  $\sigma_{in}$  (bottom) of the input packet, for two different choices of the parameter held constant. These values (indicated in the graphs) correspond to the parameter values used in figure 3.

ture in the network environment. In our simulations, each neuron received independent background activity. Accordingly, for the pulse packet theory, we considered the neurons within a group as being independent with respect to their stochastic properties. In a more realistic situation, however, it is likely that neighbouring neurons have considerable correlations in their background inputs. This will result in correlations of their firing behaviour. Hence, the neurons in a group are not necessarily independent. Furthermore, these correlations will depend on the actual embedding in the cortical network.

### Discussion

The approach outlined here opens the way for a quantitative description of network dynamics beyond the single neuron level. It provides a parametric language to describe the propagation of synchronous activity in networks that can be characterized as 'local feedforward', *ie* locally composed of chains of groups of neurons. The formalism of pulse packets presents a conceptual bridge to link the single neuron dynamics to the mechanisms involved in stable transmission of



information in such networks. Using this approach we have shown that a moderately realistic model of a cortical pyramidal neuron is capable of sustaining highly precise ( $\pm 1$  ms) synchronous firing in concert with other neurons, provided the network allows for sufficient convergence. Our simulations indicate that for the synaptic efficacies used, packets with about 100 spikes are needed to ascertain stable transmission.

The formalism of pulse packets provides the appropriate framework to clarify the notion of 'coincident' firing (Aertsen *et al.*, 1995). This yields a natural solution to the question whether the cortical neuron acts as an 'integrator' or as a 'coincidence detector' — a question which was raised many years ago (Abeles, 1982), and was revived recently (eg Bernander *et al.*, 1994; Shadlen and Newsome, 1994). The notion of pulse packets conveniently embeds these two different modes into one unified concept. Our investigation shows that the neuron may behave as either of the two, depending on the degree of synchrony of the input activity. The temporal structure of the input determines which of the two aspects is emphasized.

The results of our simulations indicate that this framework can be extended to the case of incompletely connected chains with finite width. Current work focuses on the validity of the pulse packet approach in the setting of more realistic assumptions regarding cortical anatomy and correlations in background activity. Finally, and most interestingly from the experimental point of view, the spike time distributions obtained in our simulations can be compared to the temporal statistics in recurring spike patterns in physiological data, and thus be used to test the synfire hypothesis for activity in the working brain (Aertsen *et al.*, 1995).

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## References

Abeles M (1982) The role of cortical neuron: Integrator or coincidence detector. *Isr J Med Sci* 18, 83–92

- Abeles M (1991) *Corticonics. Neural circuits in the cerebral cortex*. Cambridge University Press, Cambridge, UK
- Abeles M, Bergman H, Margalit E, Vaadia E (1993a) Spatio-temporal firing patterns in the frontal cortex of behaving monkeys. *J Neurophysiol* 70, 1629–1643
- Abeles M, Prut Y, Bergman H, Vaadia E, Aertsen A (1993b) Integration, synchronicity and periodicity. In: *Brain Theory: Spatio-temporal aspects of brain function* (Aertsen A, ed) Elsevier Science Publ, Amsterdam, 149–181
- Aertsen A, Diesmann M, Grün S, Arndt M, Gewaltig M-O (1995) Coupling dynamics and coincident spiking in cortical neural networks. In: *Supercomputers in Brain Research: From Tomography to Neural Networks* (Herrmann H *et al.*, eds) World Sci Publ, 213–223
- Bernander O, Koch C, Usher M (1994) The effect of synchronized inputs at the single neuron level. *Neural Comp* 6, 622–641
- Bienenstock E (1995) A model of neocortex. *Network* 6, 179–224
- Diesmann M, Gewaltig O, Aertsen A, Abeles M (1994) On the formalization and conditions for syn-fire activity in cortical networks. In: *Göttingen Neurobiology Report 1994* (Elsner N, Breer H, eds) Thieme, Stuttgart, p 560
- Diesmann M, Gewaltig M-O, Aertsen A (1995) *SYNOD: An Environment for Neural Systems Simulations - Language Interface and Tutorial*. Technical Report GC-AA/95-3. The Weizmann Institute of Science, Rehovot, Israel
- Diesmann M, Gewaltig M-O, Aertsen A (1996) Characterization of synfire activity by propagating 'pulse packets'. In: *Computational Neuroscience Trends in Research 1995* (Bower J, ed) Academic Press, San Diego, 59–64
- Fetz E, Toyama K, Smith W (1991) Synaptic interactions between cortical neurons. In: *Cerebral Cortex, Vol 9* (Peters A, ed) Plenum Publ Corp, New York, 1–47
- Gewaltig O, Diesmann M, Aertsen A, Abeles M (1994) A realistic and computationally efficient model of cortical pyramidal neurons. In: *Göttingen Neurobiology Report 1994* (Elsner N, Breer H, eds) Thieme, Stuttgart, p 559
- Gewaltig M-O, Diesmann M, Aertsen A (1995) Propagation of synfire activity in cortical networks: a statistical approach. In: *Neural Networks: Artificial Intelligence and Industrial Applications* (Kappen B, Gielen C, eds) Springer, Heidelberg, 37–40
- Grün S (1996) *Unitary Joint-Events in Multiple-Neuron Spiking Activity - Detection, Significance, and Interpretation*. Verlag Harry Deutsch, Frankfurt
- Grün S, Aertsen A, Abeles M, Gerstein G, Palm G (1994) Behavior-related neuron group activity in the cortex. In: *Proc 17th Meeting Europ Neurosci Assoc*, Oxford Univ Press, p 11
- Murthy VN, Fetz EE (1994) Effects of input synchrony on the firing rate of a three-conductance cortical neuron model. *Neural Comp* 6, 1111–1126
- Riehle A, Seal J, Requin J, Grün S, Aertsen A (1995) Multi-electrode recording of neuronal activity in the motor cortex: Evidence for changes in the functional coupling between neurons. In: *Supercomputers in Brain Research: From Tomography to Neural Networks* (Herrmann H, Pöppel E, Wolf DW, eds) Singapore, World Scientific Pub, Singapore, 281–281
- Riehle A, Grün S, Aertsen A, Requin J (1996) Signatures of dynamic cell assemblies in monkey motor cortex. In: *Sartificial Neural Networks ICANN96* (Von der Malsburg C, Von Seelen W, Vorbrüggen JC, Sendhoff J, eds) Springer, Berlin, 673–678
- Shadlen MN, Newsome WT (1994) Noise, neural codes and cortical organization. *Curr Opin Neurobiol* 4, 569–579