Synapses as Dynamic Memory Buffers

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Abstract

This article throws new light on the possible role of synapses in information transmission through theoretical analysis and computer simulations. We show that the internal dynamic state of a synapse may serve as a transient memory buffer, that stores information about the most recent segment of the spike train that was previously sent to this synapse. This information is transmitted to the postsynaptic neuron through the amplitudes of the postsynaptic response for the next few spikes. In fact, we show that most of this information about the preceding spike train is already contained in the postsynaptic response for just two additional spikes. It is demonstrated that the postsynaptic neuron receives simultaneously information about the specific type of synapse which has transmitted these pulses. In view of recent findings by [Gupta et al., 2000] that different types of synapses are characteristic for specific types of presynaptic neurons, the postsynaptic neuron receives in this way partial knowledge about the identity of the presynaptic neuron from which it has received information. Our simulations are based on recent data about the dynamics of GABAergic synapses. We show that the relatively large number of synaptic release sites that make up a GABAergic synaptic connection makes these connections suitable for such complex information transmission processes.

1 Introduction

Various experimental data (see [Thomson, 1997, Varela et al., 1997, Markram et al., 1998, Gupta et al., 2000]) show that the amplitudes of the postsynaptic potentials (EPSP's or IPSP's) that are produced by a synapse undergo systematic changes on a time scale of milliseconds and seconds, a time scale which is much shorter than the assumed time scale for learning (LTP or LTD). These data give rise to the question what role these rapid amplitude changes may play for information processing in a neural system. This question

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will be addressed in this article. Our analysis is based on the model for synaptic dynamics from [Markram et al., 1998], which has been shown to fit experimental data for a large variety of excitatory [Markram et al., 1998] and inhibitory [Gupta et al., 2000] synapses. This model is based on four synaptic parameters A, U, F, and D. A can be interpreted as the "weight" of the synapse, U as the fraction of synaptic resources that are used for a single spike, F as the time constant for recovery from facilitation, and D as the time constant for recovery from depression. For any assignment of positive values (with $U < 1$) to these four synaptic parameters the model predicts for any spike train S the sequence $A_1, A_2, \ldots$ of amplitudes of the postsynaptic potentials that are caused by the sequence of spikes in this spike train S. These amplitudes A_n are predicted according to the following recursive equations, which involve the current values u_n and R_n of two hidden dynamic variables u and R, that represent the *current dynamic state* of the synapse immediately before the arrival of the nth spike. A_{n+1} is the amplitude of the postsynaptic potential for the $(n+1)$-st spike, that arrives Δt_n milliseconds after the nth spike ($n \geq 1$).

$$A_n = A \cdot u_n \cdot R_n \tag{1}$$

$$u_1 = U \tag{2}$$

$$R_1 = 1 \tag{3}$$

$$u_{n+1} = U + u_n(1-U)\exp(-\Delta t_n/F) \tag{4}$$

$$R_{n+1} = 1 + (R_n - R_n u_n - 1)\exp(-\Delta t_n/D) \ . \tag{5}$$

The parameter A models the absolute synaptic efficacy. For the sake of notational simplicity we assign to A the value 1 in this paper. The variable R_n (ranging over $(0,1]$) models the fraction of synaptic efficacy available for the nth spike, and $u_n \cdot R_n$ models the fraction of synaptic efficacy that is actually used for the nth spike in a spike train S. Thus $R_n - u_n \cdot R_n$ models the fraction of synaptic efficacy that is left immediately after the nth postsynaptic potential. Hence $1 - (R_n - u_n \cdot R_n)$ models the fraction of synaptic efficacy that is *missing* immediately after the nth PSP. The term $(1-(R_n - u_n \cdot R_n))\exp(-\Delta t_n/D)$ describes the fraction of synaptic efficacy that is still *missing* at time Δt_n after the nth spike, assuming an exponential recovery of synaptic efficacy with time constant D. Hence the r.h.s. of equation (5), which can be rewritten as

$$1 - (1 - (R_n - u_n R_n))\exp(-\Delta t_n/D) \ ,$$

describes the fraction of synaptic efficacy that is *available* when the $(n+1)$-st spike arrives at time Δt_n after the nth spike.

The factor u_{n+1}, which describes how much of the fraction R_{n+1} of synaptic efficacy is actually used for the $(n+1)$-st spike, varies between U and 1. It is increased from u_n to $U(1-u_n) + u_n$ through the nth spike, and subsequently recovers back to U with time constant F. Hence for the $(n+1)$-st spike the factor u_{n+1} has the value

$$U + (U(1-u_n) + u_n - U)\exp(-\Delta t_n/F) \ ,$$

which is equivalent to the r.h.s. of equation (4).[1] We shall assume throughout this article that the synapse that we consider is at the beginning, when it receives the first spike in the spike train S, in a rested state (characterized by the values $u_1 = U$ and $R_1 = 1$) .

We would like to point out that for a *single* synaptic release site the synaptic response to an incoming spike is presumed to be stochastic with binary values: the synaptic release site releases with a certain probability a vesicle filled with neurotransmitter or it shows no response to an incoming spike. The *deterministic* synapse model defined by the equations (1)–(5) describes the cumulative response of a *population* of synaptic release sites.[2]

In the simulations that are discussed in this article we have focused on parameter values for GABAergic synapses that were reported in [Gupta et al., 2000]. The same effects can also be demonstrated for values of the synaptic parameters that are typical for excitatory synapses, but the usually smaller number of synaptic release sites of excitatory synapses is likely to make the amplitudes of postsynaptic responses more noisy (see Figure 4).

2 Storing Information in the Dynamic State of a Synapse

In this section we address the question how much information about a preceding spike train S can be contained in the values of the dynamic variables u and R of a synapse at a time point t_0 after this spike train S has reached this synapse. The subsequent Theorem 2.1 demonstrates that it is impossible to prove rigorously that the precise sequence of interspike intervals of spike trains consisting of more than two spikes can be recovered from the subsequent dynamic state of a synapse.

Theorem 2.1 *Fix any natural number $k \geq 3$. Then the function F_k, which assigns to each spike train S with k spikes the values of the dynamic variables u and R of a synapse at a fixed time t_0 after the spike train S has reached this synapse, is not $1-1$. In fact, for any spike train S there exist infinitely many other spike trains that all cause exactly the same values of the synaptic parameters u and R at time t_0. Hence it is impossible to recover from the values of u and R at time t_0 the precise sequence of interspike intervals of the spike train S that had previously reached this synapse, even if the number k of spikes in S is already known.*

A *proof* of Theorem 2.1 is given in the Appendix, along with a more formal statement of its claim. Spike trains of length k are naturally encoded by k real-valued parameters ($k-1$ interspike intervals, and the distance between t_0 and the last spike in the spike train, see Figure 2). Hence they can be viewed as points in a k-dimensional Euclidean space. On the other hand the internal state of a dynamic synapse is described by the values of

[1] Our equations (1)–(5) differ from the synaptic model characterized through equations (1)–(4) in [Markram et al., 1998] only in one detail: In equation (2) of [Markram et al., 1998] (which corresponds to our equation (5)) the term u_n was erroneously replaced by u_{n+1}. The mathematical model that was actually fitted to experimental data in [Markram et al., 1998] and [Gupta et al., 2000] was this corrected model, which is identical to the model discussed in this paper.

[2] Only the model for noise in synaptic transmission on which the simulations reported in Figures 3 and 4 are based reflects the assumption that each synapse is composed of several synaptic release sites with binary stochastic response, whose release probability is determined by the value of A computed according to the equations (1)–(5).

the 2 variables u and R, and hence can be viewed as a point in a 2-dimensional Euclidean space. Thus F_k maps some k-dimensional Euclidean space into a 2-dimensional Euclidean space. Even for $k > 2$ this does not automatically imply that F_k is not $1-1$. However if F_k would be a linear map, it would map some $k-2$ dimensional subspace of its domain (and hence infinitely many different points in case that $k > 2$) onto the same point. The map F_k that is here under consideration is highly nonlinear, but it can be shown to be continuously differentiable. According to a theorem from differential geometry this implies that F_k behaves locally (up to some smooth reparameterization) like a linear map. In particular it inherits the property of linear maps that infinitely many points from its k-dimensional domain are mapped onto the same value. Details of this proof can be found in the Appendix.

The negative result of Theorem 2.1 implies that for $k > 2$ there cannot be a rule that would allow us to infer from the current state of a dynamic synapse the spike train that had previously been sent to this synapse. However it leaves open the possibility that for some finite set of spike patterns all of these patterns are mapped by F_k uniquely (or almost uniquely) onto the resulting states of a dynamic synapse, so that all (or almost all) information about the identity of this spike pattern is contained in the resulting synaptic state. Computer simulations (see Figure 1) suggest that this is in fact the case for most randomly drawn sets of Poisson spike trains, provided that these sets are not too large.

To draw an analogy, one could compare the storage of information about a preceding spike train S in the dynamic state of a synapse to hashing in computer science, where items from a very large universe V are to be assigned addresses in a memory structure whose number of slots is much smaller than the number of items in the universe V [Cormen et al., 1990]. In our case the slots in the memory structure correspond to the (distinguishable) dynamic states of the synapse, and V is the universe of all possible preceding spike trains. Whereas the hashing problem is obviously not solvable in the worst case without collisions (i.e., several items from V receive the same address in the memory structure), one has found in computer science various efficient hashing schemes that work practically with a rather small probability of collisions if the number N of items from V that actually need to be stored simultaneously is sufficiently smaller than the number of slots in the memory structure. In that sense one may also consider the synaptic dynamics defined by equations (1) – (5) as a hashing scheme, that assigns dynamic states of a synapse to spike trains S in such a way that different spike trains S from a fairly large set of N randomly chosen spike trains will usually give rise to different dynamic states.[3] Figure 1 also shows that this hashing scheme is not optimal for the particular distribution of spike trains that was used for these simulations, since the occupancy of slots is not uniformly distributed. However neither the real distribution of spike trains in nature, nor the regions of the $u-R$ plane where the values of these variables u and R can be read out by a neural circuit with the highest resolution are known.

[3]This effect is quite stable in the range of naturally occurring firing rates. For the simulations reported in the article we have used mean firing rates between 20 and 40 spikes/s and did not encounter any significant dependence of the results on the specific choice of firing rate.

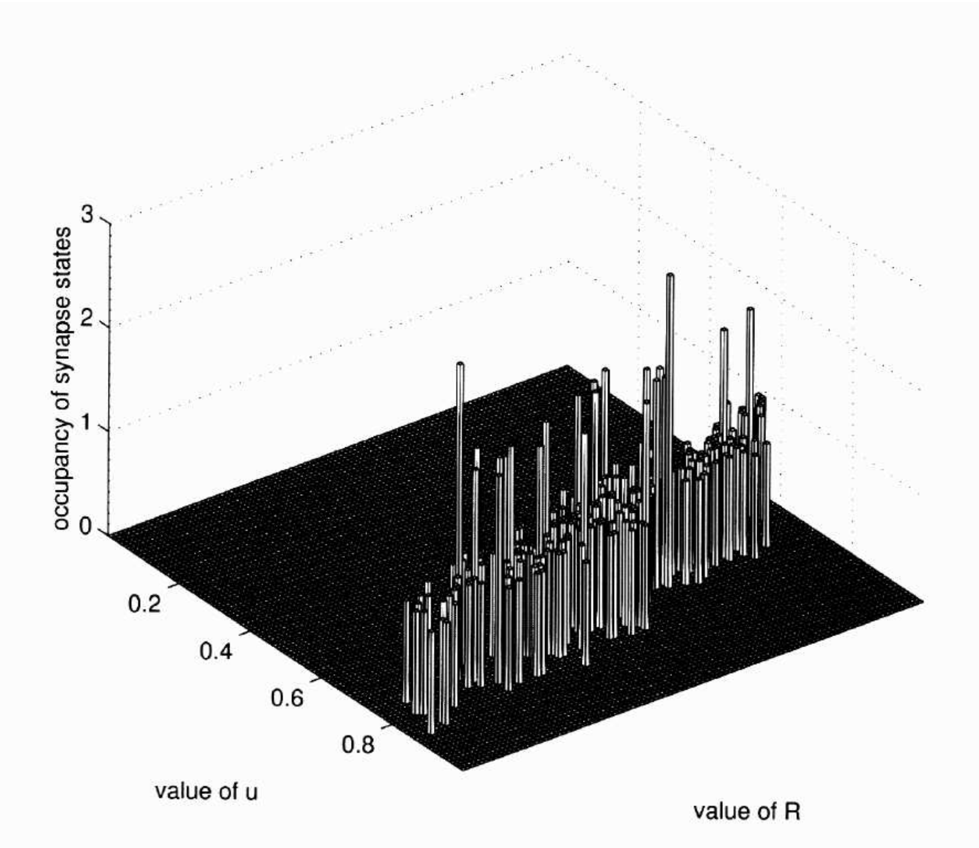

Figure 1: *Occupancy of dynamic states of a synapse (values of u and R, each divided into 100 equal sized bins) after different spike trains were sent to this synapse.* $N = 250$ *Poisson spike trains, with an average firing rate of 30 spikes/s over a time interval of 1000 ms, were sent to a synapse with synaptic parameters* $U = 0.16, F = 376, D = 45$ *(F1-type synapse in the terminology of [Gupta et al., 2000]).*

3 Retrieving Information from the Dynamic State of a Synapse

In the preceding section we have shown through computer simulations that when a spike train S is sent to a synapse, a large fraction of the information contained in S remains present in the current values of the dynamic variables u and R of the synapse, even after the spike train S is gone. In this section we investigate how a neural system could possibly retrieve this information. More precisely, we investigate the possibility of inferring the values u_0, R_0 of the dynamic variables u, R of a synapse at time t_0 from the amplitudes $A_1, A_2, \ldots$ of synaptic responses to additional spikes at times $t_0 + \Delta s_1, t_0 + \Delta s_1 + \Delta s_2, \ldots$ (see Figure 2).

This will be applied in situations where the synapse is not in a rested state at time t_0, because some unknown spike train S had previously been sent to this synapse. We assume that the value of the synaptic parameters U, F, D of this synapse as well as the time intervals $\Delta s_1, \Delta s_2, \ldots$ of the test spikes are "known" to the neural circuit that wants to infer the values u_0, R_0 of u and R at time t_0.[4]

[4]This assumption is not biologically implausible. The empirically data of [Gupta et al., 2000] show

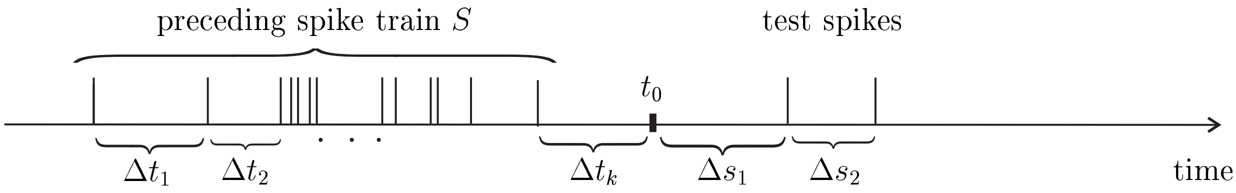

Figure 2: *Protocol for using a dynamic synapse for storing and retrieving information. Information about a preceding spike train S (i.e., information about k and $\langle \Delta t, \ldots, \Delta t_k \rangle$) is stored in the dynamic state of a synapse at any later time point t_0, and can subsequently be retrieved by measuring the amplitudes of postsynaptic responses for "test spikes" at time points $t_0 + \Delta s_1$ and $t_0 + \Delta s_1 + \Delta s_2$.*

We first observe that if U, F, D and Δs_1 are known, then inferring the values u_0, R_0 of u and R at time t_0 is equivalent to inferring the values u', R' of u and R for the first test spike at time $t_0 + \Delta s_1$. More precisely: one can compute $\langle u_0, R_0 \rangle$ from $\langle u', R' \rangle$, and vice versa (if Δs_1 is known). Assuming that at least one spike arrived before time t_0, but none during the time interval $[t_0, t_0 + \Delta s_1)$, one has according to equations (4) and (5):

$$\begin{aligned} u' &= U + (u_0 - U)\exp(-\Delta s_1/F) \\ R' &= 1 + (R_0 - 1)\exp(-\Delta s_1/D) \ . \end{aligned} \tag{6}$$

From the equations (6) one immediately gets the following equations for computing the values u_0 and R_0 from u' and R':

$$\begin{aligned} u_0 &= U + \frac{u' - U}{\exp(-\Delta s_1/F)} \\ R_0 &= 1 + \frac{R' - 1}{\exp(-\Delta s_1/D)} \ . \end{aligned} \tag{7}$$

From the value of the amplitude $A' = u' \cdot R'$ of the postsynaptic potential for the first test spike one can infer just a small amount of information about the values of u' and R', and hence about the values of u_0 and R_0 (and thereby about the preceding spike train S). There are in general infinitely many different pairs $\langle u_0, R_0 \rangle$ of possible values of u and R at time t_0 that all yield the same amplitude $A' = u' \cdot R'$ for the first test spike at time $t_0 + \Delta s_1$ (for fixed values of $\Delta s_1, U, F, D$).

A markedly larger amount of information about the values u_0 and R_0 (and thereby about S) can be inferred from the amplitudes A' and A'' for the first *two* test spikes (at times $t_0 + \Delta s_1$, and $t_0 + \Delta s_1 + \Delta s_2$). Our theoretical analysis shows that the number of possible values of u_0 and R_0 is reduced though the additional information provided by the amplitude A'' for the *second* test spike from *infinitely many* to *at most two*. The equations (4) and (5) imply that the value u' of the dynamic variable u at the first test spike satisfies

$$a u'^{\,2} + b u' + c = 0 \quad \text{, where} \tag{8}$$

$$a := (1 - U)\exp(-\Delta s_2/F) - (1 + A')(1 - U)\exp(-\Delta s_2/F - \Delta s_2/D)$$

that at least for GABAergic synapses there exists substantial regularity in the association of specific types of neurons with specific types of dynamic synapses. Furthermore for a spike train with known interspike intervals the amplitudes of postsynaptic responses convey information about the parameter values of a synapse. We will show in Figure 5 that in fact even for unknown spike trains the amplitudes of postsynaptic responses convey some information about the parameter value of the synapse.

$$b := U - A'' - U(A'+1)\exp(-\Delta s_2/D) + A'(1-U)\exp(-\Delta s_2/F - \Delta s_2/D)$$

$$c := UA'\exp(-\Delta s_2/D)\ .$$

If $A', A'', \Delta s_2, U, D, F$ are known, one can compute via the quadratic equation (8) the possible values u' of the dynamic variable u at time $t_0 + \Delta s_1$. Since $c > 0$ this equation is nontrivial, and hence has at most two solutions.

If $a \leq 0$, then equation (8) has at most a single solution for *positive* reals, which are the only values for u' that are relevant in this context. This is obvious for $a = 0$, since $c > 0$ requires in this case that $b \neq 0$, and $u' = -\frac{c}{b}$ is then the unique solution of equation (8). If $a < 0$ then the solutions u'_1 and u'_2 of equation (8) satisfy $u'_1 \cdot u'_2 = c/a$, hence exactly one of the solutions u'_1, u'_2 has a positive real value. The condition $a \leq 0$ is equivalent to $\exp(\Delta s_2/D) \leq (1 + A')$, and hence to $\Delta s_2 \leq D \cdot \ln(1 + A')$.

The amplitude A''' for a third test spike provides another quadratic equation in u'. This additional quadratic equation will in general narrow down the number of possible values for u' to just one.

Note that in either case one can infer from u' also the value R' of the other dynamic variable R at time $t_0 + \Delta s_1$ (since we assume that the amplitude $A' = u' \cdot R'$ for the first test spike is known), and hence according to our earlier remark also the values u_0, R_0 of both dynamic variables u and R of the synapse at time t_0.

The preceding theoretical analysis yields direct information only about the unrealistic case where the amplitudes A' and A'' of the postsynaptic responses can be measured with infinite precision, and on the other hand the values $\langle u_0, R_0 \rangle$ of u and R at time t_0 are supposed to be determined with infinite precision. Our computer simulations – some results of which are reported in Figure 3 – show that the results are quite similar for the realistic case of finite precision , where the values of A' and A'' can only be measured with some finite resolution, but on the other hand only a finite number N of preceding spike trains S need to be distinguished. Figure 3 shows that the postsynaptic responses for two additional spikes contain substantially more information about S than the postsynaptic response for a single one, and that the mutual information quickly saturates with more test spikes.

4 Contributions of Different Time Windows and the Influence of Synaptic Noise

If one takes a closer look and asks which part of the preceding spike train is best remembered by the dynamic state of a synapse, one finds that the information stored in the synaptic state is dominated by information about the most recent segment of the preceding spike train. This is demonstrated in Figure 4, which shows the mutual information between the amplitudes of postsynaptic responses for 2 test spikes and 3 different segments of a preceding Poisson spike train.

GABAergic synapses tend to have many more synaptic release sites (up to 30) than glutamergic connections, which usually have just 4-8. For each spike a synaptic release site releases a vesicle (in general at most one) with a certain release probability, which depends on the dynamic variables u and R. We assume here that this release probability follows the dynamics of the variable A that is defined by the equations (1)–(5). The amplitude

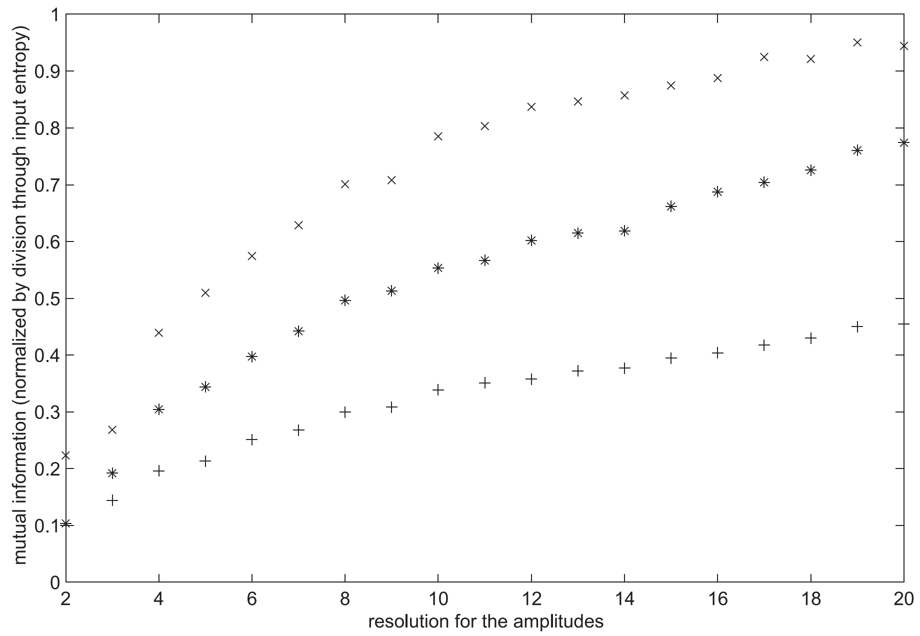

Figure 3: *Mutual information that the amplitudes of postsynaptic responses for* $1, 2, 3$ *subsequent "test spikes" (results marked by* $+, *, \times$*) contain about the identity of the preceding spike trains (in this case: uniform distribution over* $N = 300$ *randomly chosen Poisson spike trains over 1000 ms, average firing rate 30 spikes/s), normalized by dividing through the entropy* $\log N$ *of the input distribution. Results shown are for the same* $F1$*-type synapse as in Figure 1. Noise in the amplitudes of postsynaptic responses is modeled by assuming that the synaptic connection consists of 20 binary (release/no-release) stochastic contacts, each with current release probability* $u_n \cdot R_n$ *according to equations (2)-(5). The resolution (= number of bins) for amplitudes is plotted on the* x*-axis.*

of the postsynaptic response depends on the fraction of synaptic release sites for which a vesicle release takes place. Therefore the postsynaptic response has a larger variance if the synaptic connection consists of just a few synaptic release sites. The y-axis of Figure 4 indicates the dependence of the mutual information on the number of synaptic release sites.

5 Retrieving Information about the Identity of the Synapse

Figure 5 shows that the sequence of amplitudes of postsynaptic responses contains information not just about the temporal structure of the spike train that had previously been sent to this synapse, but also about the type of synapse that caused the postsynaptic responses. In view of the findings of [Gupta et al., 2000] that specific types of synapses – that can be characterized in terms of the relationship between the parameters U, F, and D that control their dynamic behavior – are associated in a systematic manner with specific types of pre- (and post-) synaptic neurons, this computer simulation shows that sequence of amplitudes of postsynaptic responses transfers information not just about the sequence of interspike intervals of a preceding spike train, but also about the specific type of presynaptic neuron

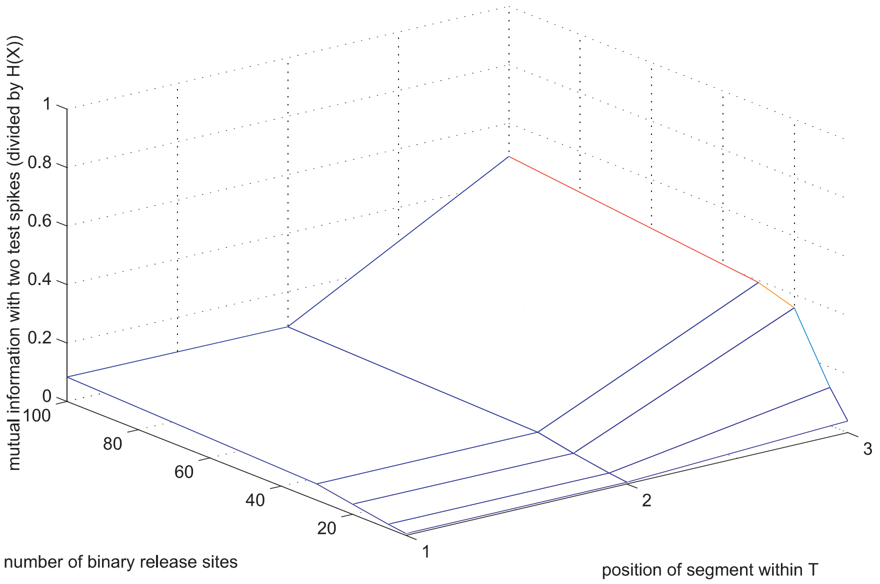

Figure 4: *Mutual information about past spike train contained in the amplitudes of postsynaptic responses for 2 subsequent test spikes* ($\Delta s_1 = 5, \Delta s_2 = 50$) *is shown on the z-axis (normalized like in Figure 3). More precisely, the past Poisson spike trains with an average firing rate of 40 spikes/s over 900 ms are divided into 3 segments of length 300 ms each, and mutual information with each of the 3 segments is measured separately (the numbers 1,2,3 on the x-axis denote the segment number). 10 Poisson spike trains over this segment are each combined with 1000 Poisson spike trains over the other 2 segments, which play here the role of additional "noise". Apart from that the same model for noise in the amplitude of postsynaptic responses as in Figure 3 is assumed, but for varying numbers of binary synaptic release sites (5,10,20,30,100; plotted on the y-axis). Results shown are for the same* $F1$*-type synapse as in Figure 1. One can see that the information about the preceding spike train that the amplitudes of postsynaptic responses for subsequent spike contains is dominated by information about the most recent segment of the preceding spike train. Furthermore this simulation shows that the amplitudes of postsynaptic responses contain a significant amount of information about the preceding spike train only for synapses with 20 or more synaptic release sites.*

from which this spike train came.

6 Conclusions

We have shown that the values of the hidden dynamic variables of a synapse provide a memory trace of the preceding spike train S. This memory trace is dominated by spikes arriving during the last few hundred ms, and hence provides a continuously moving window into the past. Via the amplitudes of postsynaptic responses for a very small number of subsequent spikes the synapse is able to communicate to the postsynaptic neuron not just this information about the recent past, but also about its "identity", i.e. about the approximate values of its synaptic parameters. In the computer simulation for this article we have focused on synaptic parameters that are are characteristic for GABAergic synapses. The results for glutamergic synapses are similar. However typical numbers of synaptic release sites for GABAergic synapses are higher, and therefore provide sufficient precision

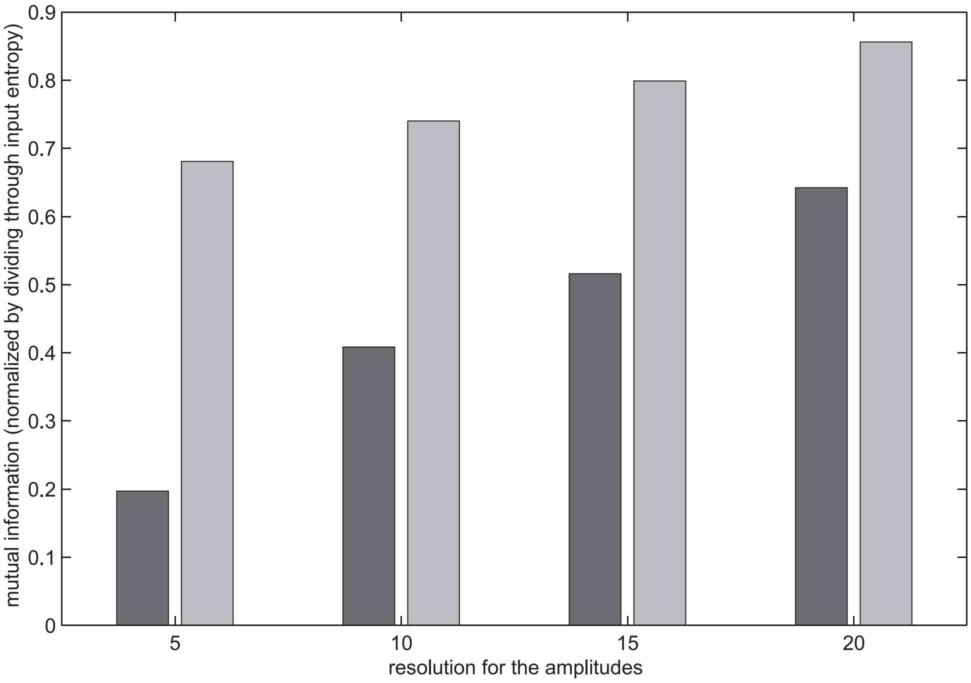

Figure 5: *Mutual information in the amplitudes of postsynaptic responses for 2 subsequent spikes about the identity of the preceding spike train (dark bars) and the identity of the synapse-type (light bars). 200 Poisson spike trains (mean 20 spikes/s, over 1000 ms) were sent to* $F1$*-,* $F2$*-, and* $F3$*-type synapses (in the terminology of [Gupta et al., 2000]); assumed parameters* $U = 0.25, F = 21, D = 706$ *for* $F2$*-type and* $U = 0.32, F = 62, D = 144$ *for* $F3$*-type synapses. Different levels of resolution in terms of the number of equal sized bins for amplitudes are plotted on the x-axis.*

for such information transmission, whereas the information transmitted by glutamergic synapses would be more ambiguous.

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Appendix

Proof of Theorem 2.1. For this mathematical analysis we represent spike trains S from the set $\mathcal{S}_k$ of spike trains with k spikes by a vector of k positive real numbers $\langle \Delta t_1, \ldots, \Delta t_k \rangle$, where Δt_i for $i < k$ is the length of the interspike interval between the ith and $(i+1)$-st spike in S, and Δt_k is the amount of time that has passed between the last spike in S and the current time t_0 (see Figure 2). The distance between two spike trains S and S' from $\mathcal{S}_k$ is defined as the Euclidean distance between the corresponding vectors.

Let $\mathbb{R}^+$ be the set of positive real numbers. Then the function F_k, which assigns to each spike train S with k spikes the values of the dynamic variables u and $\mathbb{R}$ of a synapse at a fixed time t_0 after the spike train S has reaches this synapse, maps $(\mathbb{R}^+)^k$ into $(\mathbb{R}^+)^2$. The claim of Theorem 2.1 is that this function is not $1-1$. Obviously for $k > 2$ the domain of this function F_k has a higher dimension than its range. Since there do exist functions which map higher dimensional spaces in a $1-1$ manner into lower dimensional spaces[5], the proof of Theorem 2.1 needs to take a more special property of the function F_k into account. It turns out to be sufficient to use that F_k is continuously differentiable. F_k is continuously differentiable because by successively plugging in the recursive definitions (4) and (5) for $n = k, \ldots, 1$ one gets formulas for the value $\langle u_0, R_0 \rangle$ of $\langle u, R \rangle$ at time t_0 that can be written as sums of products of the terms $U, \exp(-\Delta t_i/F)$, and $\exp(-\Delta t_i/D)$ for $i = 1, \ldots, k$. This implies that F_k is continuously differentiable with regard to the arguments $\Delta t_1, \ldots, \Delta t_k$. In order to complete the proof of Theorem 2.1 it just remains to show that no continuously differentiable function can map some open subset of a higher dimensional space $1-1$ into a lower dimensional space. For that purpose one applies the rank theorem from differential geometry, see for example Theorem 7.1 in [Boothby, 1986]. For any $S \in \mathcal{S}_k$ and any $\varepsilon > 0$ there exists an open subset U of the ε-neighborhood of S on which the Jacobian of F_k has some constant rank r. One has $r \leq 2$, since the range of F_k is contained in $\mathbb{R}^2$. According to the rank theorem one can view F_k on U – up to some smooth reparametrization of the domain and range – as a linear function from an open subset of $\mathbb{R}^k$ into an open subset of $\mathbb{R}^r$. Since $k > 2$ and $r \leq 2$, any such linear function maps infinitely many different points onto the same value. In our context this implies that F_k maps infinitely different

[5]Consider for example a function which maps pairs $a = a_0, a_1 a_2 \ldots$ and $b = b_0, b_1 \ldots$ of real numbers in decimal notation onto the real number $a_0 b_0, a_1 b_1 a_2 b_2 \ldots$.

spike trains S' from the ε-neighborhood of S on exactly the same values of the synaptic parameters u and R at time t_0.