

Analogue resolution in a model of the Schaffer collaterals

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Abstract. We have analytically and numerically solved the mutual information expression for a quantitative model of the Schaffer collateral projections from the CA3 to the CA1 pyramidal cells within the hippocampus. Here we discuss in particular results from the model on the effect of analogue coding levels in the Schaffer collaterals, and the fact that this depends upon the sparseness of firing rate distributions in the hippocampus.

1 Introduction

Recent advances in techniques for the formal analysis of neural networks [1, 2, 3, 4] have introduced the possibility of detailed quantitative analyses of real brain circuitry. This approach is particularly appropriate for regions such as the hippocampus, which show distinct structure and for which the microanatomy is relatively simple and well known [5].

The Schaffer collateral model describes, in a simplified form, the connections from the N CA3 pyramidal cells to the M CA1 pyramidal cells. Most Schaffer collateral axons project into the stratum radiatum of CA1, although CA3 neurons proximal to CA1 tend to project into the stratum oriens [6]; in the model these are assumed to have the same effect on the recipient pyramidal cells. Inhibitory interneurons are considered to act only as regulators of pyramidal cell activity. The perforant path synapses to CA1 cells are here ignored, as are the few CA1 recurrent collaterals. The system is considered for the purpose of analysis to operate in two distinct modes: storage and retrieval. During storage the Schaffer collateral synaptic efficacies are modified using a Hebbian rule reflecting the conjunction of pre- and post-synaptic activity. This modification has a slower time-constant than that governing neuronal activity, and thus does not affect the current CA1 output. During retrieval the Schaffer collaterals relay a pattern of neural firing with synaptic efficacies which reflect all previous storage events.

For reasons of space the full description of the model and calculation cannot be given here; see [7] for more details. Each CA3 pyramidal cell is taken to code for independent information (a condition which will be relaxed elsewhere) with a firing rate distribution $P(\eta)$. Pyramidal cells are modelled using a threshold

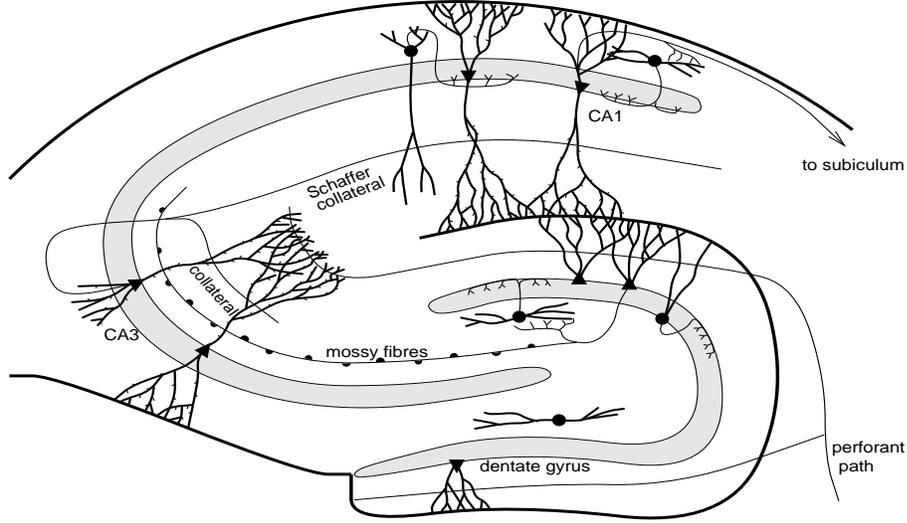


Fig. 1. A schematic diagram of the hippocampal formation. Information enters the hippocampus from layer 2 entorhinal cells by the perforant path, which projects into dentate gyrus, CA3 and CA1 areas. In addition to its perforant path inputs, CA3 receives a lesser number of mossy fibre synapses from the dentate granule cells. The axons of the CA3 pyramidal cells project commissurally, recurrently within CA3, and also forward to area CA1 by the Schaffer collateral pathway. Information leaves the hippocampus via backprojections to the entorhinal cortex from CA1 and the subiculum, and also via the fornix to the mammillary bodies and anterior nucleus of the thalamus.

linear transfer function with a gaussian fast noise distribution. The synaptic matrix is very sparse, as each CA1 cell receives inputs from C (of the order of 10^4) CA3 cells. A plasticity model for the Schaffer collaterals is used which corresponds to gradual decay of memory traces.

The aim of the analysis is to calculate how much, on average, of the information present in the original CA3 pattern $\{\eta_i\}$ is still present in the effective output of the system, the CA1 pattern $\{U_j\}$, i.e. to average the mutual information

$$i(\{\eta_i\}, \{U_j\}) = \int \prod_i d\eta_i \int \prod_j dU_j P(\{\eta_i\}, \{U_j\}) \ln \frac{P(\{\eta_i\}, \{U_j\})}{P(\{\eta_i\})P(\{U_j\})} \quad (1)$$

over the interaction variables of the system. This is achieved by making use of the replica trick and saddle-point approximation in the thermodynamic (infinite system size) limit.

2 Results

Specification of the probability density $P(\eta)$ allows different distributions of firing rates in CA3 to be considered in the analysis. Clearly the distribution of firing rates that should be considered in the analysis is that of the firing of CA3 pyramidal cells, computed over the time-constant of storage (which we can assume to be the time-constant of LTP), during those periods in which biophysical conditions are appropriate for learning to occur. It is reasonable to assume that the distribution of firing rates during storage is graded, sparse, and exponentially tailed [8, 9]. This accords with the observations of neurophysiologists. The easiest way to introduce this to the current investigation is by means of a discrete approximation to the exponential distribution, with extra weight given to low firing rates. This allows quantitative investigation of the effects of analogue resolution on the information transmission capabilities of the Schaffer collateral model.

The required CA3 firing rate distributions were formed by the mixture of the unitary distribution and the discretized exponential, using as mixture parameters the offset between their origins, and relative weightings. The distributions were constrained to have first and second moments $\langle \eta \rangle$, $\langle \eta^2 \rangle$, and thus sparseness $\langle \eta \rangle^2 / \langle \eta^2 \rangle$, equal to a . In the cases considered here a was allowed values of 0.05, 0.10 and 0.20 only. The width of the distribution examined was set to 3.0, and the number of discretized firing levels contained in this width parameterized as l . The binary distribution was completely specified by this; for distributions with a large number of levels, there was some degree of freedom, but its numerical effect on the resulting distributions was essentially negligible. Those distributions with a small number of levels ≥ 2 were non-unique, and were chosen fairly arbitrarily for the following results, as those that had entropies interpolating between the binary and large l situations. Some examples of the distributions used are shown in Fig. 2a.

The total entropy per cell of the CA3 firing pattern, given a probability distribution characterised by L levels, is

$$i(\eta) = - \sum_{l=1}^L P_{\eta_l}(\eta_l) \ln P_{\eta_l}(\eta_l). \quad (2)$$

The results are shown in Fig. 2b–d. The entropy present in the CA3 firing rate distributions is marked by asterisks. The mutual information conveyed by the retrieved pattern of CA1 firing rates, which must be strictly less than the CA3 entropy, is represented by circles. It is apparent that maximum information efficiency occurs in the binary limit. More remarkably, even in absolute terms the information conveyed is maximal for low resolution codes, at least for quite sparse codes. The results are qualitatively consistent over sparsenesses a ranging from 0.05 to 0.2; obviously with higher a (more distributed codes), entropies are greater. For more distributed codes (i.e. with signalling more evenly distributed over neuronal firing rates), it appears that there may be some small absolute increase in information with the use of analogue signalling levels.

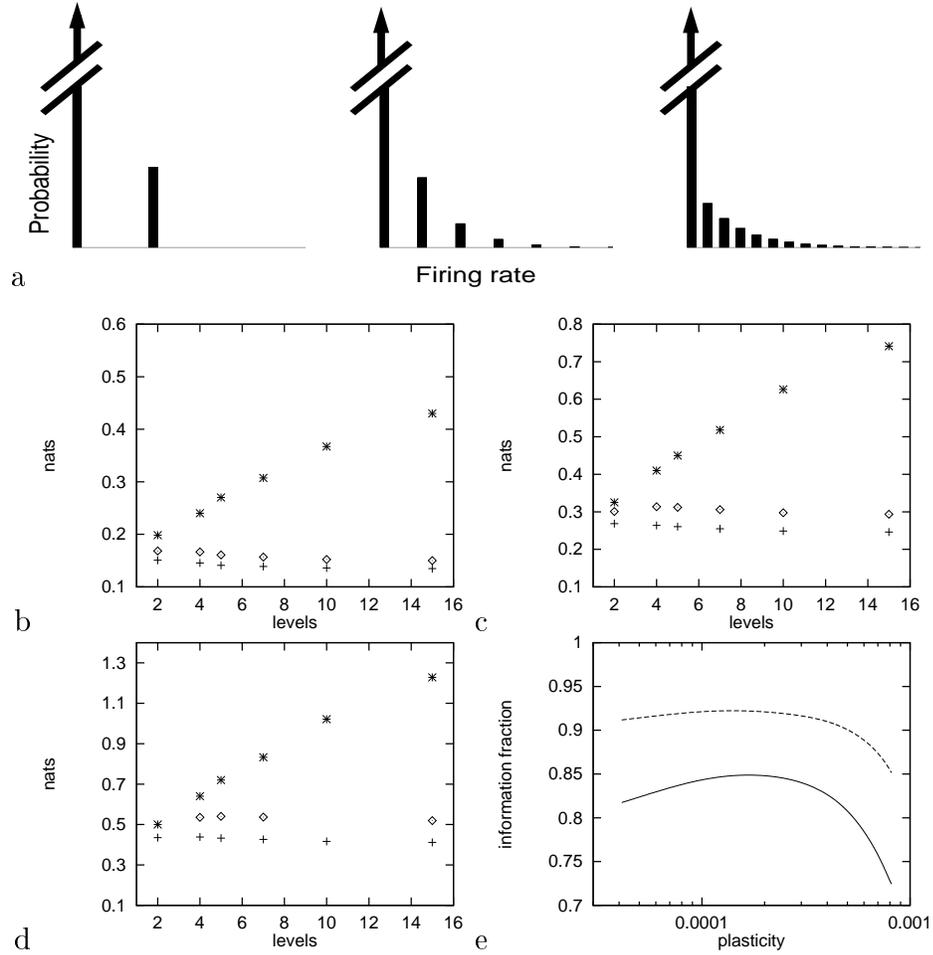


Fig. 2. **a** Some of the CA3 firing rate distributions used in the analysis. These are, in general, formed by the mixture of a unitary distribution and a discretized exponential. **b – d** The mutual information between patterns of firing in CA1 and patterns of firing in CA3, expressed in natural units (nats). Asterisks represent the entropy of the CA3 pattern distribution, diamonds the CA1 retrieved mutual information, and crosses the CA1 information during the storage phase. The horizontal axis parameterizes the number of discrete levels in the input distribution: for codes with fine analogue resolution, this is greater. **b** is for $a = 0.05$ (sparse), **c** for $a = 0.10$, and **d** for $a = 0.20$ (slightly more distributed). **e** The dependence of information transmission on the degree of plasticity in the Schaffer collaterals, for $a = 0.05$ (solid) and $a = 0.10$ (dashed). A binary pattern distribution was used in this case.

For comparison, the crosses in the figures show the information stored in CA1. This was computed using a simpler version of the calculation, in which the mutual information $i(\{\eta_i\}, \{\zeta_j\})$ was calculated. Obviously, in this simpler calculation, the CA3 and CA1 retrieval noises are not present; on the other hand, neither is the Schaffer collateral memory term. Since the retrieved CA1 information is in every case higher than that stored, we can conclude that for the parameters considered, the additional Schaffer memory effect outweighs the deleterious effects of the retrieval noise distributions.

It follows from the forgetting model used that information transmission is maximal when the plasticity (mean square contribution of the modification induced by one pattern) is matched in the CA3 recurrent collaterals and the Schaffer collaterals [10]. It can be seen in Fig. 2e that this effect is robust to the use of more distributed patterns.

3 Discussion and summary

This chapter has presented quantitative results, for a model of the Schaffer collaterals, of the effect of analogue resolution on the total amount of information that can be transmitted using relatively sparse codes. What can these results tell us about the actual code used to signal information in the mammalian hippocampus? In themselves, of course, they can make no definite statement. It could be that there is a very clear maximum for information transmission in using binary codes for the Schaffer collaterals, and yet external constraints, such as CA1 efferent processing, might make it more optimal overall to use analogue signalling. So results from a single component study must be viewed with due caution. However, these results can provide a clear picture of the operating regime of the Schaffer collaterals, and that is after all a major aim of any analytical study.

The results from this paper reiterate some previously known points, and bring out others. For instance, it is very clear from Fig. 2 that, while nearly all of the information in the CA3 distribution can be transmitted using a binary code, this information fraction drops off rapidly with analogue level. The total amount of information transmitted is similar regardless of the amount of analogue level to be signalled – but this is a well known and relatively general fact, and accords with common sense intuition. However, the total amount of information that can be transmitted is only *roughly* constant. It appears, from this analysis, that while the total transmitted information drops off slightly with analogue level for very sparse codes, the maximum moves in the direction of more analogue levels for more evenly distributed codes. This provides some impetus for making more precise measurements of sparseness of coding in the hippocampus.

Clearly it is essential to further constrain the model by fitting the parameters as sufficient neurophysiological data becomes available. As more parameters assume biologically measured values, the sensible ranges of values that as-yet unmeasured parameters can take will become clearer. It will then be possible to address further issues such as the quantitative importance of the constraint

upon dendritic length (i.e. the number of synapses per neuron) upon information processing.

In summary, we have used techniques for the analysis of neural networks to quantitatively investigate the effect of analogue resolution of signalling on information transmission by the Schaffer collaterals. We envisage that these techniques, developed further and applied in a wider context to networks in the medial temporal lobe, will yield considerable insight into the organisation of the mammalian hippocampal formation.

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