SYNAPTIC ENERGY DRIVES THE INFORMATION PROCESSING MECHANISMS IN SPIKING NEURAL NETWORKS

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ABSTRACT. Flow of energy and free energy minimization underpins almost every aspect of naturally occurring physical mechanisms. Inspired by this fact this work establishes an energy-based framework that spans the multi-scale range of biological neural systems and integrates synaptic dynamic, synchronous spiking activity and neural states into one consistent working paradigm. Following a bottom-up approach, a hypothetical energy function is proposed for dynamic synaptic models based on the theoretical thermodynamic principles and the Hopfield networks. We show that a synapse exposes stable operating points in terms of its excitatory postsynaptic potential as a function of its synaptic strength. We postulate that synapses in a network operating at these stable points can drive this network to an internal state of synchronous firing. The presented analysis is related to the widely investigated temporal coherent activities (cell assemblies) over a certain range of time scales (binding-by-synchrony). This introduces a novel explanation of the observed (poly)synchronous activities within networks regarding the synaptic (coupling) functionality. On a network level the transitions from one firing scheme to the other express discrete sets of neural states. The neural states exist as long as the network sustains the internal synaptic energy.

1. **Introduction.** Energy flow and free energy minimization underpins (or at least contribute to) almost every known natural and physical mechanisms, e.g., from the atomic behavior, protein folding, metabolism and even the formation of hurricanes. The brain is a biological neural computing system and is not expected to be an exception. In order to track this fact within the biological neural system, following a bottom-top approach this study starts with the synaptic dynamics. Experimental observations have demonstrated that synaptic plasticity exists as set of well defined discrete set of states, and that states are a fundamental property of central synapses within the nervous system (CNS) [21]. They can provide a context for understanding outstanding issues in synaptic function, plasticity and development [21]. It has been shown that synapses change their strength by jumping between discrete mechanistic states, rather than by simply moving up and down in a continuum of dynamic strength, see e.g., [20, 21]. Furthermore, it has been postulated that the longterm potentiation (depression) dynamics of the synapse feature state transitions among six different biophysical states [1]. This was a model of synaptic

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plasticity at hippocampal synapses which reproduces several slice experiments. If the synapse is able to operate at a specific discretely defined state of activity as pointed out in the above cited papers, these findings raise questions about the energy related aspects of such behavior. Specifically, they call for investigating the kind of contribution attributed to the synapses in generating stable representations of input information among cortical neural ensembles .

On the level of detailed networks, some studies have investigated the concept of energy minimization and the involved synaptic dynamics in relation to synchronized activity of networks acting as dynamic systems, see e.g., [25]. It has been shown that in order to maintain the synchronized regime, there must be some kind of steady energy flow holding the coupling strength between the neurons. This flow of energy is also required for both the cooperative and collective behavior in any neural ensemble. It was stated that this energy should be supplied through the coupling mechanisms itself, i.e., through the maintained synaptic connections [29]. This postulates that synaptic dynamics are not only crucial in modulating the information processing in general, but also it underpins the manifestation of neural *states* in spiking neural networks (SNN). These remarks suggest that a synapse is able to operate at any stable operating point for a certain interval. Intuitively, this implies that a synapse as a physical system can exist in a certain *state* of activity and it is able then to switch from this state to a new one. Based on the mentioned argumentations, the energy-related intrinsic process that is involved in the synaptic action of different synaptic models has been investigated [7, 5, 2] where the basis of a synaptic energy function was proposed.

In the presented work and using the formerly presented basis of energy function from [5] we show that, a finite discrete set of energy levels exist in response to the temporal and statistical input features. This set is a function of the internal synaptic state parameters. For any specific input features, the number of maintainable levels within this set depends on the synaptic model, e.g. the modified stochastic synaptic model from [7, 2] offers more levels in comparison to the well known Markram-Tsodyks model in response to the same input [2].

Based on the observed set of energy levels, it is postulated that within a spiking neural network synaptic dynamics drives the network activity and firing behaviour in order to construct cell-assemblies (coherent firing or synchrony). Furthermore and using a novel definition of a neural state we discuss the plausibility of neural states that reflects the mechanisms of internal information processing within the network.

2. **Synaptic energy & emergence of neural states.** Based on the lattice Ising model, Hopfield introduced his network as a recurrent neural network having symmetric synaptic connection pattern [15]. Within a Hopfield network there is an underlying monotonically decreasing energy function controlling the network dynamics [15]. Started in any initial state, the state of the system evolves to a final state that is a (local) minimum of the energy function. Each energy minimum acts as a point attractor in the space field of the system. It is an ongoing task in neuroscience to quantify and define those operating points, even with less regard to the underlying energy concepts. Many behavioural aspects were analyzed trying to relate these behavioural observations to known attractor dynamics, see e.g. [9, 28]. It was illustrated that there is a class of features that can be described as dynamic attractors, referred as attractor networks. Levina et al. (2009) tackled the

self-organizing behaviour regarding critical-stability in a fashion similar to the analysis of Avalanche dynamics [19]. It has been shown that a network interacting via timing-dependent synapses attains criticality in a certain region of the parameter space. That space is bounded by phase transitions that can be reached by tuning the synaptic strengths. The ensuing remarks from the above are: a) The physical system that may describe a biological neural system tries to find stable (or critically stable) operating points. These operating points act, in an abstract way, as dynamic attractors. b) The search for such stable operating points is believed to be performed in a self-organized manner, i.e., either unsupervised or via reinforcement learning. Apart from those related to the Hopfield network, the idea of studying those operating points have, however, been less studied from the energy point of view.

Some studies have investigated the concept of energy minimization and its relation to synchronized activity of networks by viewing the network as a dynamic system, see e.g. [25]. Torrealdea et al. have studied extensively the energy and its related global balance in two bidirectionally coupled neurons [29]. It has been shown that in order to maintain the synchronized regime, there must be some kind of steady energy flow holding the coupling strength between the neurons. This flow of energy is also required for both the cooperative and collective behaviour in any neural ensemble. Furthermore, it was stated that this energy should be supplied (according to their analysis) through *the coupling mechanisms itself*, i.e., the synaptic connections [29]. As mentioned above, this strongly suggests that the synaptic dynamics can drive (or reinforce) synchrony in SNN rather than being a passive dynamic coupling element.

Friston et al. have theoretically shown that for a biological system to hold its self-organizing behavior, seeking for stable operating points, should always exhibit a bounded interaction with *its environment* [12]. Under the condition that this bound quantity can be defined in terms of the internal states of the system. It was therefore proposed that the *energy* of the system that is *delivered* to this environment can represent this bound functionality, and that the system continuously tries to minimize it. It was referred as the Free-Energy principle. This bound (or exchange energy) is not the thermodynamical free energy of the system.

Therefore, here we inspect the energy-related intrinsic process that may be involved in the synaptic action. By this, it extends the analysis made in [3, 6, 8] to determine the role of synaptic dynamics as whether it can be responsible for coherent activity (synchrony), neural states and to what extent. We adopt the energy-based principle for biological neural systems from Friston et al. [12] and consider the synapse as a dynamical system.

3. **Theoretical foundations.**

3.1. **The synaptic energy function.** The aforementioned free-energy principle can be adopted describing the dynamics of the synaptic behaviour, specifically regarding the synchronous activity. Considering each synapse as a physical dynamical system described by the system equations of the modified stochastic synaptic model (MSSM), the excitatory postsynaptic potential $EPSP(t)$ is the only output exchange quantity between the synapse and a postsynaptic neuron (See App. C.2 for detailed listing of model equations). The electrical energy held by (and transferred via) EPSP, consequently, represents, in an abstract way, what is termed here "the free synaptic energy" (FSE) and defined as:

Proposition 1. *As an open thermodynamic system, a synapse has a total free en-ergy that is a function of two parameters: The output state parameter corresponding to the presynaptic input, and the "recognition density that is encoded by its internal states"* [13]. *When the* $\mathrm{EPSP}(t)$ *is the synaptic response and output state param-eter,* $S(t)$ *is the synaptic dynamic strength (recognition density), and* $\tau > 0$ *is a presynaptic-dependent constant, the free synaptic energy (FSE) is defined as*

$$\mathrm{FSE} \equiv E_{\mathrm{syn}}(t) \approx S(t) \times \mathrm{EPSP}(t) \times e^{\frac{-\Delta_{\mathrm{isi}}}{\tau}}, \tag{1}$$

where Δ_{isi} *is the inter spike interval.*

Proof. For the derivation please refer to App. A.   □

In other words, the energy represented in EPSP is the bounded function that the biological system (here the synapse) tries to *minimize* and to *stabilize* by opti-mizing its internal states. These states (in the synapse) are the activity-dependent concentrations of the chemical constitutes holding (and responsible for) the synap-tic transmission. E_{Syn} *does not* represent the thermodynamic free energy of the synapse. The notation "free" is adopted since the synapse as a biological system tries to minimize this exchange energy in a fashion similar to that known from the second law of thermodynamics. This is performed through the minimization of the free energy of a system parallel to the maximization of its entropy. Based on the considerations above, the following concepts are postulated consequently:

1. A synapse is in a continuous trial to bound (regulate) the interaction between itself and its postsynaptic neuron. Assuming that the synapse is an open biological system (from a thermodynamic point of view), the bounding is accomplished, through its inherited dynamics, by keeping its energy as low as possible. It is implicitly assumed that the synapse is able to change those state parameters affecting these dynamics (via e.g., learning or an update rule) in a self-organizing manner.

2. The synaptic transferred energy is a direct function of the internal synaptic electrochemical activities. The synaptic strength can be defined as the product of the state parameters of the synaptic model excluding the state parameters carrying the synaptic response ($\mathrm{EPSP}(t)$). Following the description of the MSSM from App. C.2, the dynamic synaptic strength can be defined as a function of the synaptic state parameters[1]:

$$S(t) \;=\; C(t) \;\cdot\; V(t) \;\cdot\; N_t(t) \tag{2}$$

Where $C(t)$ represents the concentration of the Calcium ions in the presynap-tic terminal, $V(t)$ models the size of ready-to-release pool of neurotransmitter vesicles in the presynaptic terminal and $N(t)$ is the concentration of neuro-transmitter in the synaptic cleft.

3. At each minimum (either global or local, if any exists) in the state space, the synapse undergoes a stable level of energy transfer that represents a certain state of stable activity.

4. The stable level of energy transfer at the local minima (which results in a specific firing activity) does not strictly imply a constant firing rate. It can be a firing pattern, if the system does not operate continuously and exactly at

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[1]Similarly this applies e.g., for the Markram-Tsodyks model, the state parameters are then u and r.

the minimum but within the finite region around it as well. This is actually the case when the synaptic background noise is considered in the simulations.

In order to analyze the MSSM as a dynamical system with regard to energy, the definitions of the synaptic strength and the synaptic energy (Eq. 2 and 1) are added to the listing of the MSSM equations (given in App. C), and then the synaptic dynamical system is solved to obtain the trajectories of solution describing the synaptic energy $E_{\mathrm{syn}}(t)$ and the dynamic synaptic strength $S(t)$ in response to a hypothetical input spike train with overall firing frequency $\Delta_{\mathrm{isi}}^{-1}$. It should be noted that there is no simulations involved in this analysis. The synaptic model is assumed to take an input with a constant frequency and the required quantities are the time evolutions of the $E_{\mathrm{syn}}(t)$ and $S(t)$. They are function of: a) The frequency of the input spike train $\Delta_{\mathrm{isi}}^{-1}$, and b) The synaptic resources and decay timing constants which are the values of the model parameters. The system is solved using Matlab (ode45-solver, MathWorks).

A family of curves are illustrated in Fig. 1 showing the time courses of the solutions in case of different starting initial conditions. Fig. 1(a) gives the time courses of the synaptic energy for three different initial conditions and model parameters (see Tab. 1), the input spike train features an input frequency $\Delta_{\mathrm{isi}}^{-1} = 200$ Hz. The synaptic energy raises at the beginning of applying the input, as time advances the energy level falls down to a set of stable steady state values $\boldsymbol{\sigma} = \{\sigma_1, \sigma_2, \sigma_3\}$. These states (i.e., these energy levels) are function of the initial conditions and timing values listed in Tab. 1. The solution of the dynamical system of the MSSM shows three different states of energy for the same input spike train following three different settings in terms of initial conditions and timing constants. From Fig. 1(b), it turns out that each state of synaptic energy correspond to a different course of the operating synaptic strength. This implies that in case this synaptic model is coupled to a postsynaptic neuron, the corresponding postsynaptic response (postsynaptic spiking activity) will be accordingly different with each energy state. Consequently, the postsynaptic firing pattern shall be unique to this energy state and it corresponds to the time course of the energy function and the related steady-state value of the synaptic strength. More analysis of the influence of the input frequency and noisy inputs are given in the supplementary materials, see Figs. S.1 and S.2.

The questions that remains is: How can the synaptic energy profile affect the collective network behaviour? In order to answer this question we present the next proposition that represents a theoretical bridge between the internal dynamics from a synaptic level to the top network level.

Proposition 2. *For a given network with n neurons, if s synapses operate at any of the local energy minima and sustain stable synaptic energy E_{Syn} to l neurons, then the rest of the network $((n-l)$ neurons) is forced to follow gradually the stable activity of the l neurons, provided that the temporal features of input signal are maintained. If the coherent activity of these neurons is observed over a time window $\mathcal{W}$, after a suitable time T, where $T \gg \mathcal{W}$, a general new state of synchronous discharge from all n neurons should be observed. This defines a network synchrony state.*

Proof. For the proof please refer to the Gedanken experiment given in App. B. □

3.2. **Neural states.** We make a formal distinction between a network state and a *neural* state. While the network state is the spiking activity across all neurons in the network at any time instant, a neural state must describe either the localized
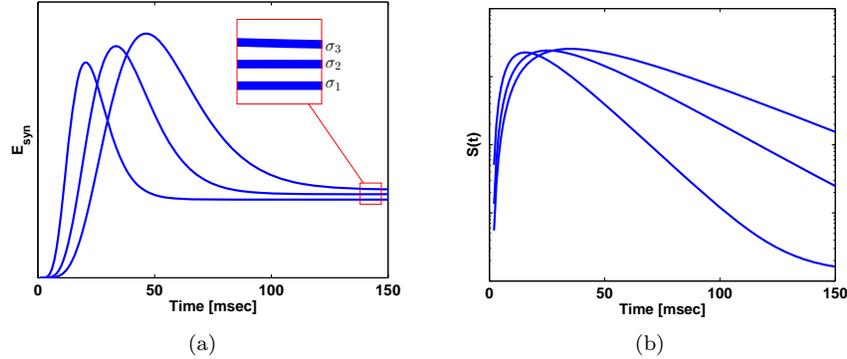
FIGURE 1. Solutions and time evolutions of synaptic energy and corresponding synaptic strength. (a) Time courses of E_{syn} with three different initial resources and timing constants, see Tab. 1. The final stable states of synaptic energies are the those labelled as σ_1, σ_2 and σ_3. (b) Semilog scale for the y-axis to show the final synaptic strength values corresponding to the different energy states from (a). The values for the model parameters to generate these solutions are summarized in Tab. 1. More variations from the illustrated solutions are shown in the supplementary materials Sec. S.1. Figure is adapted from [2].

TABLE 1. Model parameters for synaptic energy states. The values of both the controlling parameters and initial conditions involved in the solution of the dynamical system of MSSM. These values are chosen to be biologically plausible following [26, 14]. Table is adapted from [2].

Parameter	Comment	σ_1	σ_2	σ_2
τ_C		3 msec	5 msec	7 msec
τ_V		8.4 msec	14 msec	19.6 msec
τ_{N_t}		13.5 msec	22.5 msec	31 msec
α		0.0905	0.0905	0.0905
τ_{epsp}		9 msec	15 msec	21 msec
C_o		0.05	0.05	0.05
V_o		3.45	3.45	3.45
k_{epsp}		10	10	10
k_{N_t}		1	1	1
$k_{N_t,V}$		1	1	1
$C(0)$	Initial condition for ODE solver	0.0150	0.0090	0.0064
$V(0)$	"	0.1233	0.0740	0.0529
$N_t(0)$	"	0	0	0
$\mathrm{EPSP}(0)$	"	0	0	0
$S(0)$	"	0	0	0
$E_{\mathrm{syn}}(0)$	"	0	0	0

or general level of information processing within the network over a confined time interval. In the general sense, we propose in this work that the existence of a neural state exists implies that a group of neurons collectively act with their spiking activity over a limited (basically varying) duration to signalize the internal representation (low level perception) of input information and involved features.

In order to distinguish and observe certain spiking activity as being a representation for a neural state, i.e., carrying special features, this requires having a sort of a reference activity for the sake of comparison. Hence, states are relative and are defined as maintained distances between the network states in response to two inputs that are slightly different from each other.

Specifically, for two sets of input spike trains $u(\cdot)$ and $v(\cdot)$, the corresponding network state at any time t is $\boldsymbol{y}_{\mathcal{N}}^u(t)$ and $\boldsymbol{y}_{\mathcal{N}}^v(t)$ respectively. $\boldsymbol{y}_{\mathcal{N}}^u(\cdot)$ and $\boldsymbol{y}_{\mathcal{N}}^v(\cdot)$ are referred to as the network states across all neurons. The quantity $\mathcal{D} = \|\boldsymbol{y}_{\mathcal{N}}^u(t) - \boldsymbol{y}_{\mathcal{N}}^v(t)\|$ is the average distance between the network states at any time t and $\|\cdot\|$ denotes the Euclidean norm. A depictive definition of a neural state within a dynamic network framework is presented in this paper, it reads:

Definition 3.1. Within a dynamic network $\mathcal{N} \in DN$, for all output vectors $\boldsymbol{y}_{\mathcal{N}}(t)$ and $t > 0$ corresponding to the input functions $\boldsymbol{u}(\cdot)$ and during the interval $t_1 < t < t_2$ a neural state σ is defined if $c - \delta < \|\boldsymbol{y}_{\mathcal{N}}^u(t) - \boldsymbol{y}_{\mathcal{N}}^{\mathrm{ref}}(t)\| < c + \delta$ where c is a constant and δ is small. $\boldsymbol{y}_{\mathcal{N}}^{\mathrm{ref}}(\cdot)$ is a fixed reference set of output functions where $|\boldsymbol{y}_{\mathcal{N}}^u| = |\boldsymbol{y}_{\mathcal{N}}^{\mathrm{ref}}|$.

Note that the quantity $\|\boldsymbol{y}_{\mathcal{N}}^u(t) - \boldsymbol{y}_{\mathcal{N}}^{\mathrm{ref}}(t)\|$ is, in abstract way, a distance calculated as the Euclidean norm between the network response and the reference one. This quantity is coined hereinafter as either the observed states or states level.

This definition illustrates how to observe the states if they exist rather than the rules of their existence. Following this definition and according to, Prop. 2, a spiking neural network with suitable synaptic dynamics (a dynamic network) experiences a neural state that can be characterized by a level of synchronous activity, this corresponds to a sustainable level of synaptic energy. In fact, the latter statement establishes the missing link among synaptic dynamics, collective spiking activity and neural states.

Following Def. 3.1, the next section shows simulation based examples that explore the aspects of internal states within a dynamic network in accordance with the synaptic energy states.

4. **Simulation & results.** The simulation setup follows basically the seminal work from [18] while the major changes are the synaptic parameterization and the correponding STDP dynamics. The details of the simulation and models are given in App. C. The input is a sustained single spike that is sustained over the simulation epoch and is fed to a single neuron drawn randomly from the network with each time step. A sample of this input is shown in Fig. 2, it represents a background thalamic input.

Using the mentioned network and simulation setup (see App. C), Fig. 3 illustrates the synchronous firing and the synaptic energy profile using a simulation case in contrast to the pure theoretical and analytical postulates given in Fig. 1. Fig. 3(a) shows the emergence of synchronous firing, Fig. 3(b) demonstrates the
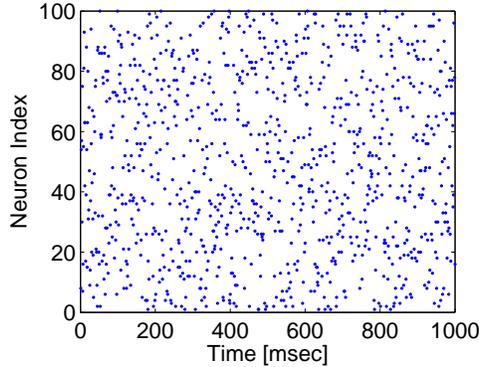
FIGURE 2. Sample input to the network over a simulation epoch of 1 Second. Only a single spike is fed to a single neuron at every msec.

corresponding time evolution of mean synaptic energy within the network[2] and the spike coincidence; both time series are scaled to unity. The illustrated time evolution of the synaptic energy from the simulation represents a simulation-based proof of the theoretically postulated synaptic energy behaviour. Specifically, the energy profile shown here comprises a repetition of the postulated behavior as the synaptic dynamics is in a continuous attempt of minimizing its energy.

In quest for analyzing the proposed concepts of neural states and their relation with synaptic energy, a basic reference synchrony-free response is needed. Fig. 4(a) shows the network firing activity where the synaptic parameters were chosen so that no specific neural assemblies can be constructed. This was accomplished by using e.g., low excitatory postsynaptic gain k_{epsp} and short timing constants for both neurotransmitter buffering τ_{Nt} and postsynaptic potential τ_{epsp}. This network response is taken as the reference response of the dynamic network $\boldsymbol{y}_{\mathcal{N}}^{\text{ref}}(\cdot)$. The mean time evolutions of synaptic strength across presynaptic connections per neuron are shown in Fig. 4(b), the corresponding synaptic energy evolutions are in Fig. 4(c). The corresponding mean time evolutions of synaptic strengths and synaptic energies over all neurons are shown in Figs. 4(d) and 4(e).

In contrast to the synchrony-free response, three cases of synchrony were generated in response to three different input pattern fed to the network using the same mechanism described above. The responses are summarized in Fig. 5. The values of the synaptic model parameters used to generate these responses are listed in Tab. 2 in App. C. Fig. 6(a) shows the time evolutions of the average synaptic energy across all neurons for the four involved simulations, i.e., the three synchronous responses and the reference synchrony-free one. Following the postulated definition of neural states from Def. 3.1, Fig. 6(b) demonstrates the observed distance between the spiking activity of each response (from cases I–III) and the reference synchrony-free one.

It is important to note that the first and second cases are intentionally selected to be alike in terms of spiking activity in order to illustrate the role of investigating the new aspects of synaptic energy and observing the existence of neural states. Put

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[2]Calculated first as mean over the presynaptic synapses of each neuron and then over all neurons.

differently, analyzing the synaptic energy evolution and the possibly involved neu-
ral states give more insights into the processing of information within the network
rather than observing the temporally coherent spiking. For the purpose of high-
lighting these differences, Fig. 7 shows the spiking activities, the synaptic energy
and observed states over arbitrarily selected intervals from the three synchronous
cases. It is important to observe that the three profiles of synaptic energy and
states are completely different from each other, even the first two cases are clearly
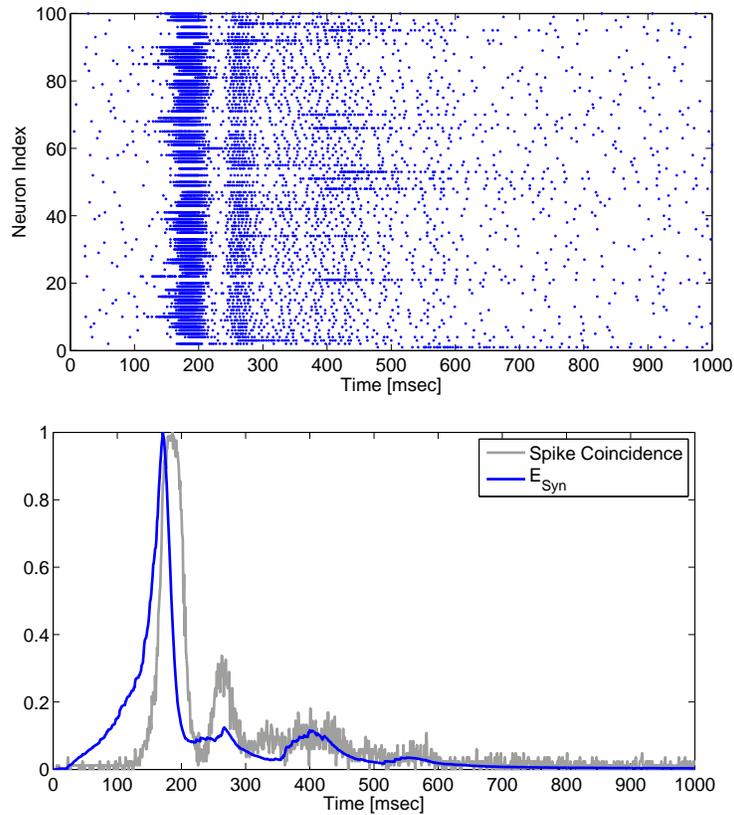distinguishable although their synchronous spiking activities might seem alike at
first glance.

FIGURE 3. Basic example of the simulation result with synchro-
nous activity (Upper panel) and the corresponding synaptic energy
illustrated over the spiking coincidence (Lower panel). The lower
panel illustrates the temporal relation between the appearance of
a synchronous firing and the time evolution of the synaptic energy.
It is important to note the likelihood between the time evolution
of the synaptic energy between this simulation and the theoretical
analysis shown in Fig. 1: The energy profile comprises a repeti-
tion of the postulated behavior as the synaptic dynamics is in a
continuous attempt of minimizing its energy.

(a) Reference Response

(b) Presynaptic cross-neuronal mean $S(t)$

(c) Presynaptic cross-neuronal mean E_{Syn}

(d) Overall mean $S(t)$
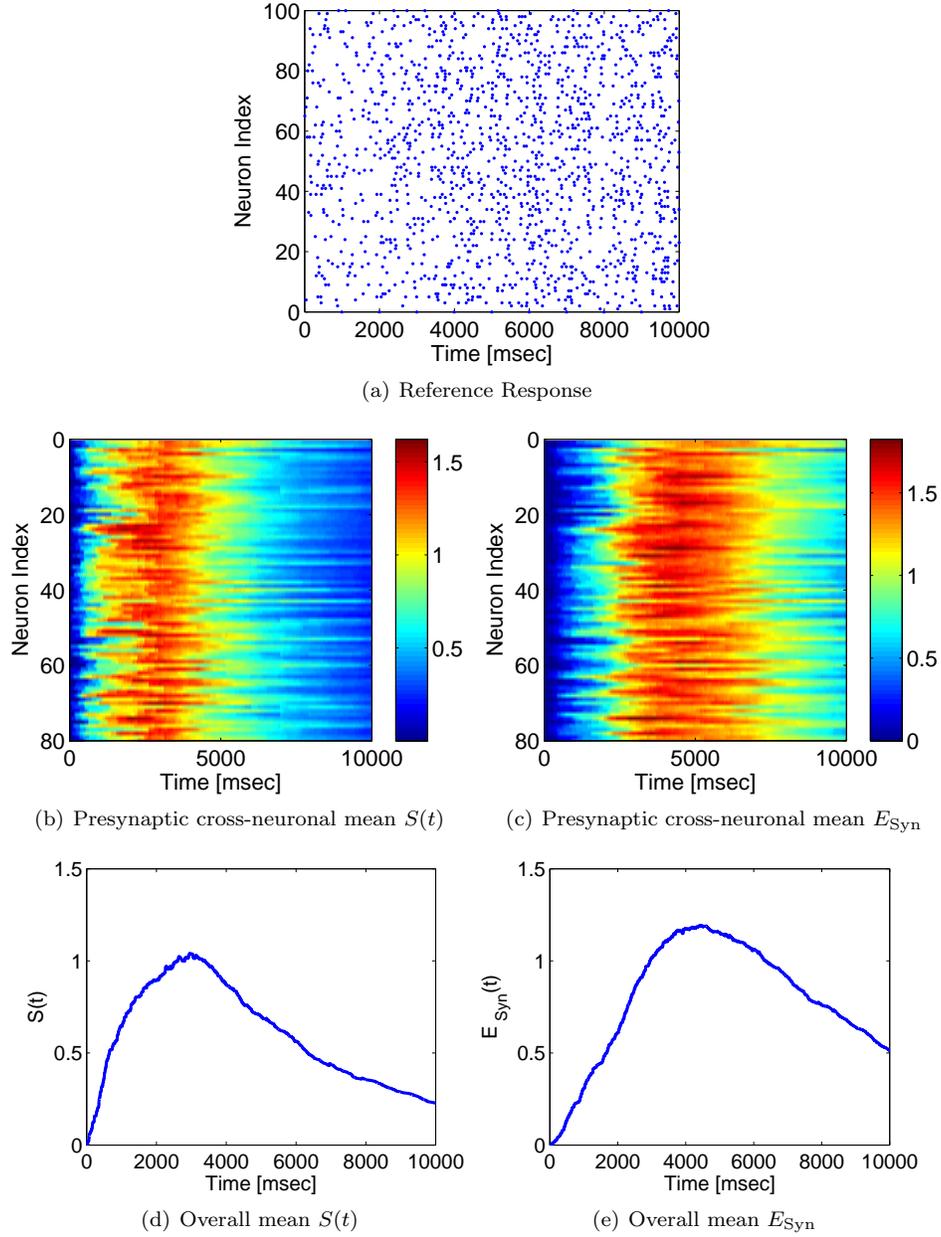

(e) Overall mean E_{Syn}

FIGURE 4. Synchrony-free network response and the corresponding internal network dynamics. a) Spiking activity of the network response, details of synaptic parameters are listed in Tab. 2 in App. C. b) and c) The time evolutions of the presynaptic strength S and energy E_{Syn} of the excitatory neurons (averaged over 10 presynaptic connection per neuron). d) and e) The overall average time evolutions of S and E_{Syn} over all neurons in the network.

(a) Response Case I

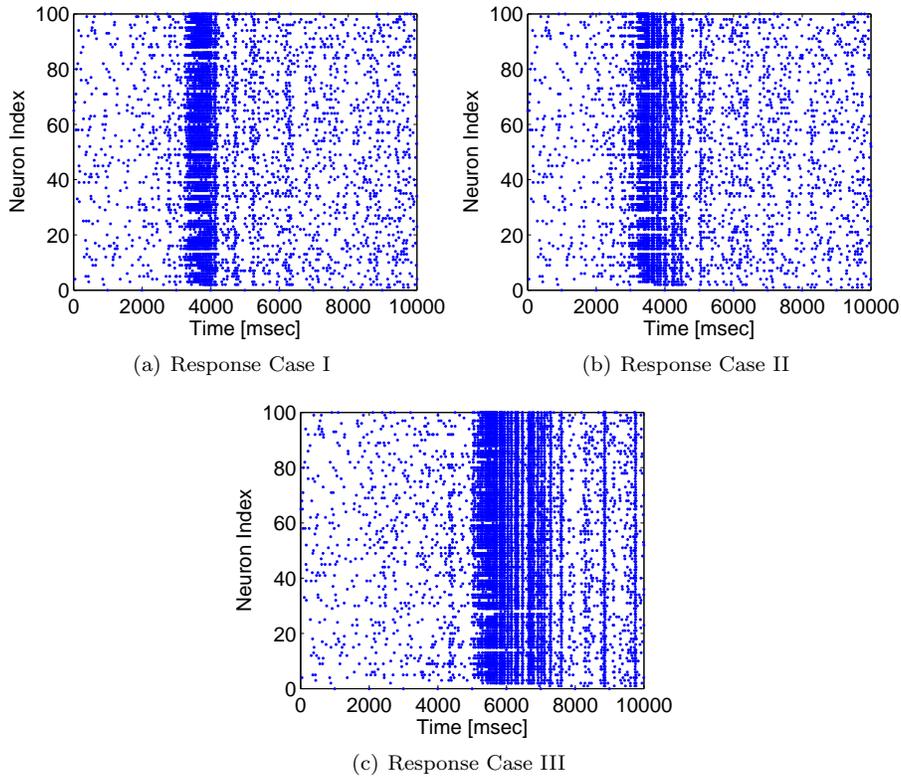(b) Response Case II

(c) Response Case III

FIGURE 5. Network responses that involves different patterns of synchronous firings. The values of model parameters are listed in Tab. 2 in App. C. This response is different from the reference (synchrony-free) response depicted in Fig. 4(a).
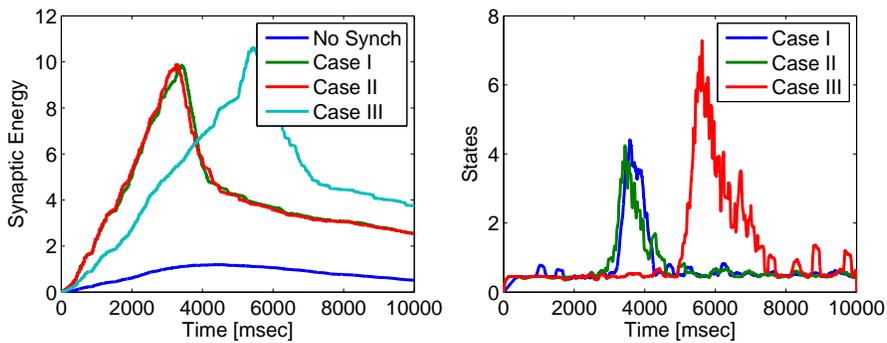

FIGURE 6.   a) Summary of time evolutions of overall average synaptic energy in all four network response-cases, including the synchrony-free response and the cases I–III. b) States level calculated according to the definition of observing states given in Def. 3.1. Lines correspond to cases I–III (from Fig. 5) relative to the reference one given in Fig. 4(a).
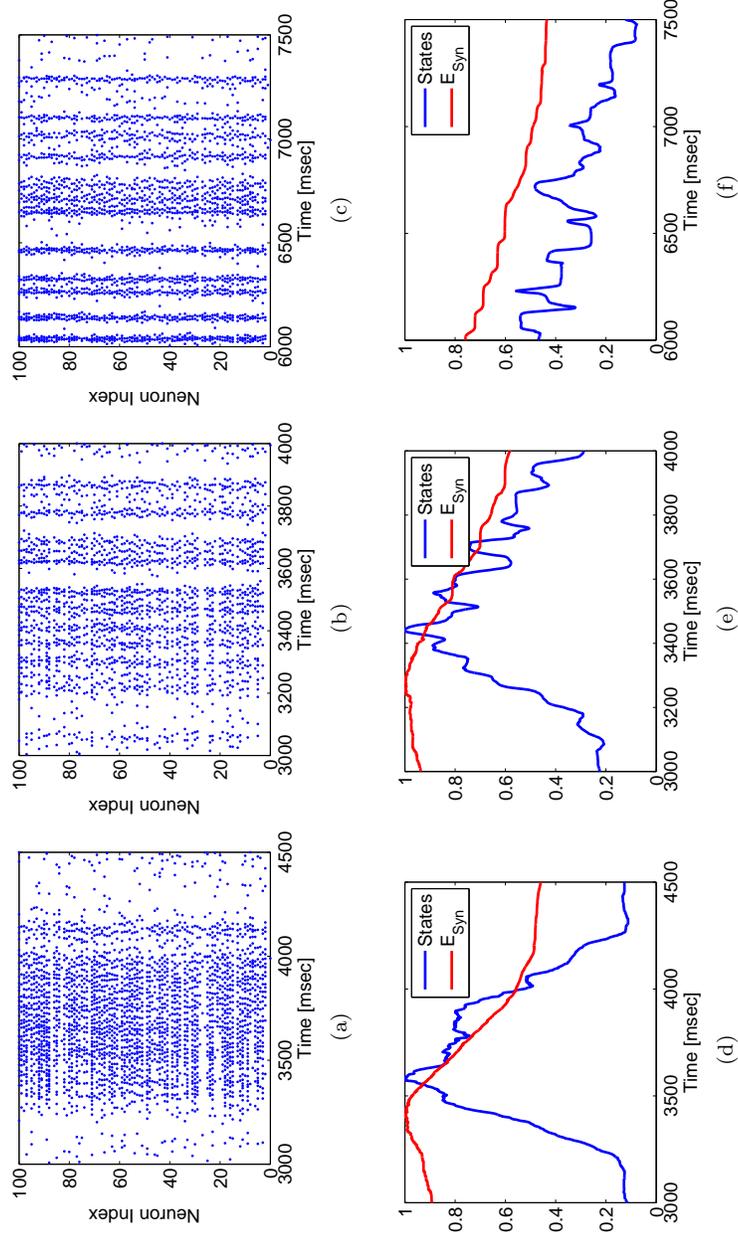
FIGURE 7. Arbitrarily selected sections from cases I–III that illustrate the network spiking response (Upper panels) and the corresponding average synaptic energy across all neurons in the network and the observed track of states calculated as given in Def. 3.1 (Lower panels). A neural state is then defined when the observed states line tends to be horizontal or to oscillate around a mean value. The more detailed (color-mapped) presynaptic strength and synaptic energy for excitatory neurons for these selected sections are given in Fig. S.3 in the supplementary materials.

In order to get a more detailed insight into the coupling between the synaptic energy dynamics and the detection of neural states, Fig. 8 shows the detected states in accordance with the time evolution of the synaptic energy for case III. Each state is denoted with the Greek letter σ. According to Def. 3.1, the sequence of detected states represents the discrete set of neural states that represents the internal processing of the input information. This set of states can be a characteristic attribute for the combination of network structure, synaptic parameters and input information. It should be noted that although the input here is not more than a random spike train that represents abstractly a random thalamic activity fed to the cortex, it is assumed that such input definitely carry a (yet unknown) certain amount of information. Surprisingly, one of the detected states $\sigma_{(6)}$ is revisited along the time evolution of the states level.
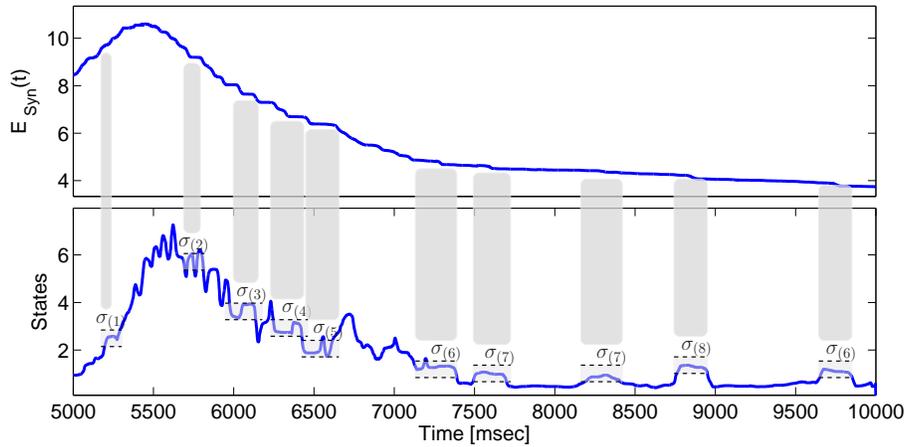

FIGURE 8. Detailed illustration of the detected states level for case III (Lower panel) and the corresponding time evolution of synaptic energy (Upper panel). Detected states are highlighted with the shaded horizontal bars between dashed lines and named with the letter σ and and index. The index corresponds to the temporal sequence of appearance. When the detected state level has appeared previously, the same state symbol is given, e.g., $\sigma_{(6)}$. The vertical shaded bars indicate the temporal span of the detected state in order to highlight the portion of the synaptic energy that corresponds to the interval of this state.

5. **Discussion & conclusions.** Using a hypothetical synaptic energy function and based on solid analytical procedures, this work integrates the paradigms of synchronous firing (cell assemblies) and computing through temporal states into a consistent working framework. By this integration this work establishes a consistent connection that spans the multi-scale ranges of biological neural systems. For this purpose, the analysis started with investigating the key role of synaptic dynamics in driving the dynamics of a spiking neural network.

Hence, the simulation result shown in Figs. 3(b) supports the proofs of the basic theoretical and analytical solutions of the synaptic energy profile proposed in

Sec. 3.1 and as depicted in Figs. 1 and S.1.These results indicate a temporal relation, e.g., coupling, between the synaptic energy profile and the synchronous firing within the dynamic network.

Further, both the basic theoretical and analytical solutions of the synaptic energy concept and the corresponding synaptic strength, proposed in Sec. 3.1, are strikingly supported and proofed by Figs. 4(d) and 4(e). Although no synchronous firing is observed in this case, the associated energy profile is still in complete accordance with the postulated concept of overall *synaptic* energy minimization within a dynamic network. This does contradict with the existence of a relation between synaptic energy minimization and the construction of cell assemblies via synchronous firing. In order to experience a synchronous firing within the dynamic network, the excitatory synaptic coupling should be strong enough to build the required internal linkage leading to synchronous firing. This occurs while the synaptic dynamics seeking a minimum level of postsynaptic energy. That is, energy minimization is an emergent inherited feature that is always active while synchrony is a modus of activity that might appear or not depending on the synaptic dynamics within the network. Put differently, the synaptic energy concept presented here proposes that energy minimization should be considered as necessary but not sufficient for a synchronous spiking. On contrary, reaching either a local or an absolute minimum synaptic energy level is necessary and sufficient for synchronous firing.

The results of the analysis with the MSSM presented here so far strongly agree with the experimental findings from [21, 25, 29, 1]. These experimental studies have pointed out implicitly that synapses seem to feature a set of discrete operating points. However, there was no indication about why and how these states may emerge or on which basis these states are developed. The here presented energy-based analysis based on the MSSM dynamics answers these questions.

Fig. 6(a) and 6(b) reveal that the time evolutions over synaptic energy and states across the three cases I–III are almost alike in terms of overall shape and trends; the involved amplitudes and local minima/maxima are the major differences. This indicates that the overall energy profile and the corresponding state transitions characterize both the network structure and the input information. This agrees with preliminary results reported on the change in the network perception with a change in the network structure in response to the same input information [6].

Figs. 7 and 8 emphasize the relevance of the presented analytical framework, the paradigms of coherent firing, binding or cell assemblies are a sort of a final result for a deep and intrinsic mechanism on the synaptic level. By investigating this level through the analysis of its energy flow, one can think that synapses and their dynamics play a more crucial role than even known or expected. Synapses and their biologically inherited tendency to minimize their energy drive the information processing within neural systems.

Although the presented definition of neural states relies on the concepts of temporal coherence, it cogitates the debated issue of states as steady state attractors. Because the states are defined as relative quantities by the comparison to a reference activity. This allows for more flexible analysis of the involved states and consequently the states transitions; state transitions are the more crucial issue in information processing. From a state-machine point of view, it remains to be seen how the existence of neural states and the transitions among them are regulated within the network.

Furthermore, the proposed concept of neural states as being only defined as relative behavior resolves a major conflict between the two main approaches that have addressed the issue of neural states and the basis of temporal coherence. The conflicting approaches are: a) The studies proposing that temporal coherence indicates indeed a neural state of internal information processing (low level internal perception) within cortical circuits [30, 24], and b) Studies argue that temporal coherence is only a sort of internal rhythm that organizes the flow of information among neural circuitries rather than signalizing a neural state, see e.g., [10, 11]. By accepting that neural states can only be described as relative behavior in comparison to a reference one, both perspectives about temporal coherence can be regarded correct. Let us start with the assumption that a reference firing activity indicates a low level of input information processing or the activity in absence of input information, e.g., during sleeping. If the reference firing behavior of a neural ensemble is taken to be spontaneous (random) and incoherent, a temporally coherent activity within this ensemble indicates indeed a different collective behavior which is plausibly a neural state. The situation can be turned around, i.e., when the reference behavior is then taken to be a standard cortical activity that contains a sort of internal coherence e.g., synfire chains [16]. In this case it is difficult to identify temporal coherence and cell assemblies as being of special meaning or that they signalize a different level of information processing than the normal (reference) one. Thus, the plausibility of defining neural states as a relative neural behavior is supported from the opposing studies that discuss the relevance of temporal coherence and its interplay in defining neural states of information processing.

The presented theoretical concept resolves a set of basic problems and brings together a number of isolated theoretical and experimental paradigms. For example, this work reveals potential relation among binding-by-synchrony [22, 27] and the information processing within biological neural networks as finite state-machines, for more about this topic please review the preliminary work [8, 6] and the extensive analysis in [2].

This study discusses the involvement of the temporal dimension as a basis of defining the neural states within the neural network; this extends our preliminary work from [6]. We show how time is associated with the processed pieces of information through the transitions among the different states. The involvement of time in defining states and its association with the information processing is generally a crucial issue because it distinguishes the processing within the CNS from the general class of finite-state machines or the more general Turing machines. Based on the concept of synaptic-related states, the presented work introduces a novel conceptual as well theoretical framework that permits both the capture and implementation of the information processing methods found in the CNS.

The brain is a spatio-temporal multi-scale system, and the presented work postulates the missing linkage through the main abstraction levels: the low-level synaptic dynamics, the mid-level collective spiking activity and the potential higher cognitive level of neural states. The linkage is the interplay between the biologically inherited feature of energy minimization within synapses and the emergence of synchronous firing along with the involved neural states. This coupling between the deep network dynamics and the collective network behavior on a cognitive level open new avenues in understanding the multi-scale, and rather complicated, information processing mechanisms within the brain. This work establishes a framework that spans the multi-scale range of biological neural systems and integrates synaptic

dynamic, synchronous spiking activity and neural states into one consistent working paradigm.

Appendices

A. **Proof of synaptic energy function.** It starts with the energy function of a Hopfield network. In such a network, the total energy of the network with n neurons $E_{\text{tot,net}}$ is defined as [23]

$$E_{\text{tot,net}} = \underbrace{-\frac{1}{2}\sum_i^n \sum_j^n w_{ij}x_ix_j}_{\text{Synaptic term}} - \underbrace{\sum_i^n I_ix_i}_{\text{Input}} + \underbrace{\sum_i^n \frac{1}{\tau}\int_{x_o}^x g^{-1}(x)dx}_{\text{Neuronal term}} \qquad (3)$$

In Eq. 3, $x_{i(j)}$ are the graded (rate coded) activity value of neuron $i(j)$. w_{ij} is the static synaptic weight between neurons i and j. Only the first term (the synaptic term) is important in the case considered here. Since a single synapse is investigated, the summations can be ignored. Hence, the synaptic energy directly from the Hopfield definition reads

$$E_{\text{syn}} = w_{ij} \times x_i \times x_j, \qquad (4)$$

This implies that the synaptic energy is the product of the synaptic weight between the pre- and postsynaptic activity levels and these activity levels. In case of the MSSM, the neuron activity is bounded with the threshold mechanism and this mechanism is directly a function of the postsynaptic potential. Since EPSP is a continuous time-varying function, it maybe viewed as an indication that determines the postsynaptic activity. That is

$$x_i \leftarrow \text{EPSP} \qquad (5)$$

Estimating presynaptic activity is, however, not a straight forward task. The input to the MSSM as well as any other dynamic synaptic model is a spike train. In case of a regular spike train, the presynaptic activity scales with input frequency. The presynaptic activity can be estimated to be rate coded value

$$x_j \leftarrow e^{\frac{-\Delta_{\text{isi}}}{\tau}}, \qquad (6)$$

where τ is a scaling constant. With this definition, the presynaptic activity satisfies $x_j \in]0,1[$ as the input frequency spans from infinity to zero. The synaptic weights can be replaced with the dynamic synaptic strength, i.e.,

$$w_{ij} \leftarrow S(t). \qquad (7)$$

Substituting Eqs. 5–7 in Eq. 4, the FSE reads

$$E_{\text{syn}}(t) \approx S(t) \times \text{EPSP}(t) \times e^{\frac{-\Delta_{\text{isi}}}{\tau}}$$

The approximation sign emphasizes that the derived quantity represents only an *estimation* of the actual synaptic energy. As for the units, according to the basic definition E_{syn} has units of energy per unit resistance, i.e., Volts^2. This is accomplished by considering that $S(t)$ is dimensionless and that the quantity x_j has the same units as EPSP since it indicates the presynaptic activity in response to electrical input stimulation.

B. **Proof of Prop. 2.** The following Gedanken experiment illustrates the theoretical proof of the relation between minimizing synaptic energy and driving the synchronous firing within a dynamic network:

Proof. According to this proposition, an energy state (or actually a set of synaptic energy states) is(are) encoded within the neural network into a state of synchrony. The proof follows a Gedanken experiment. Fig. 9 gives an illustrative example of the process described in Prop. 2. For the network schematic in this figure, it is a recurrent network with three spiking neurons and the interconnections are synapses modeled with the MSSM. After certain time duration, the synapses shall be able to operate at an operating point that corresponds to this low stable energy level in response to the input spike train, the hypothetical operating point is indicated with the big red point in Fig. 9. This operating point corresponds to stable level of synaptic energy that reflects a stable transfer of postsynaptic potential. Since the temporal and statistical input features are stationary, the synapses remain operating at this level. When the synapses start operating at the stable synaptic strength level, a certain firing pattern from neurons N_2 and N_3 is expected. As long as other synapses are not experiencing a change in their values, N_1 renders a firing pattern that integrates both the latter firing pattern from other neurons via backward synapses and the input one. Again, S_1 and S_2 will try to adopt the new changes in the input pattern from N_1. At this point there is two possible cases: a) The new N_1 firing pattern still carries the same information content as the original one from the input alone. Or, b) The N_1 firing pattern carries new information content that encodes the network response through the synergetic contributions from S_1, S_2, N_2 and N_3. In the first case, the synapses shall keep their energy level, i.e., they will not search for another stable level of energy. Consequently, the over all network firing pattern shall continue over time till either new information content is presented or when the synaptic background noise adds this new information content. In the second case, the synapses will seek for another new level of energy that corresponds to the new information content. This search shall be sustained till the network stabilizes again or it stays in search till some new information is fed in. □

C. **Simulation setup.** The simulation setup is based on the seminal simulation code provided by E. Izhikevich in studying the formation of polychronous groups [18]. The network consists of $N = 100$ neurons with the first $Ne = 80$ of excitatory regular spiking (RS) type, and the remaining $Ni = 20$ of inhibitory fast spiking (FS) type [18]; the details about the neuronal model are given in the next subsection. The ratio of excitatory to inhibitory cells is 4 to 1, as in the mammalian neocortex. Each excitatory neuron is connected to $M = 10$ random neurons, so that the probability of connection is $M/N = 0.1$, again as in the neocortex. Each inhibitory neuron is connected to $M = 10$ excitatory neurons only. The indices of postsynaptic targets are in the $N \times M$-matrix post. Different from the simulation setup from [18], this work uses an explicit dynamic synaptic model instead of the α-function-based spike-timing dependent potentiation (STDP). The synaptic model is the modified stochastic synaptic model (MSSM) from [2, 7], the model is given below in details after listing the details of the neuronal model. The input represents background thalamic activity that is implemented as a sustained single spike fed to a randomly drawn neuron from the network.
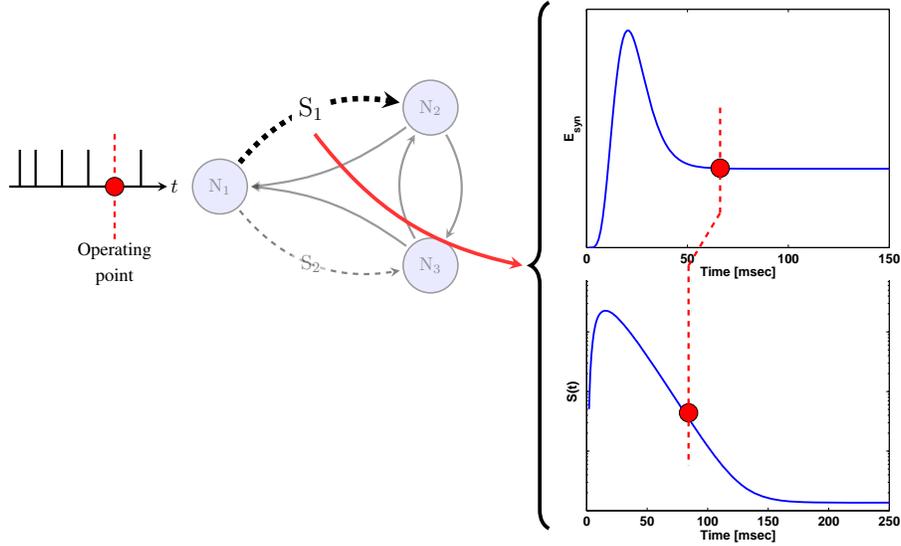
FIGURE 9. Influence of synaptic dynamics and the involved synaptic energy on the network dynamics (In relation to Prop. 2). The schematic illustrates a hypothetical simulation to indicate the relevance of defining the synaptic energy and its relation to network dynamics. The example given in this illustration is generalized in Prop. 2. When a synapse operated at a stable energy level which corresponds to an operating point that features a stable synaptic energy, the synaptic dynamics drive the network to a regime of synchronized firing. The firing pattern can be a regular or an irregular pattern. For details see the text in the proof of Prop. 2. Figure is adapted from [2].

Following the original simulation code from [18], a fixed integer conduction delay D is implemented for each synaptic connection; D is set between 1 ms and 10 msec (M/D must be integer in the model). The delay implemented here does not model modifiable delays or transmission failures. The list of all synaptic connections from neuron i having delay j is in the cell array $delays{i, j}$. The MATLAB implementation assigns 1 msec delay to all inhibitory connections, and 1 to D msec delay to all excitatory connections.

C.1. **The neuron model.** Each neuron in the network is described by the simple spiking model [17].

$$\dot{v} = 0.04v^2 + 5v + 140 - u + I, \tag{8}$$

$$\dot{u} = a(bv - u) \tag{9}$$

with the spike-reset mechanism

$$\text{if } v \geq 20 \text{ mV, then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \tag{10}$$

Variable v models the membrane potential of the neuron, and u is a membrane recovery variable, which accounts for the activation of K^+ ionic currents and inactivation of Na^+ ionic currents, and it provides negative feedback to v. After the spike reaches its max. at $+20$ mV, which is not to be confused with the firing threshold, the membrane voltage and the recovery variable are reset according to the reseting mechanism, Eq. 10. Depending on the values of the parameters, the model can exhibit different firing patterns.

For all simulations listed in this study, b and c are set at 0.2 and -65 respectively. For excitatory neurons, a and d are set at 0.02 and 8 respectively corresponding to cortical pyramidal neurons exhibiting regular spiking (RS) firing patterns. For inhibitory neurons, a and d are set at 0.1 and 2 respectively corresponding to cortical interneurons exhibiting fast spiking (FS) firing patterns.

Variable I in the model combines two kinds of input to the neuron: (1) random thalamic input (if exists) and (2) the output of the dynamic synaptic model, it is the overall postsynaptic potential EPSP from the presynaptic connections feeding each neuron.

C.2. **Synaptic model: The modified stochastic synaptic model.** The modified stochastic synaptic model (MSSM) introduced in [7] estimates the transmission probability of an arriving action potential, i.e., a spike, from a presynaptic neuron via a synapse to a postsynaptic neuron. Thus, $P(t_i)$ is the probability that the ith spike in a presynaptic spike train $\sum_i \delta(t - t_i)$ (input spikes) triggers the release of a vesicle at time t_i at the synapse. The involved probability-of-release $P(t) = 1 - \exp(-C(t) \cdot V(t))$ is governed by two counteracting mechanisms: facilitation and depression. Facilitation reflects the calcium concentration in the presynaptic neuron, $C(t)$, while depression represents the effect of the concentration of ready-to-release vesicles in the presynaptic terminal, $V(t)$. The model reads [3, 4]:

$$\dot{C} = \frac{(C_o - C)}{\tau_C} + \alpha \cdot \sum_i \delta(t - t_i), \tag{11}$$

$$\dot{V} = \frac{(V_o - V)}{\tau_V} - P(t) \cdot \sum_i \delta(t - t_i), \tag{12}$$

$$\dot{N_t} = max(0, -\dot{V}) + (\frac{N_{to} - N_t}{\tau_{N_t}}), \tag{13}$$

$$\tau_{\text{epsp}} \dot{\text{EPSP}} = -\text{EPSP} + k_{\text{epsp}} \cdot N_t, \tag{14}$$

In Eq. 11, the intracellular calcium concentration starts at C_o. It is raised incrementally by each stimulus impulse, approximated herein by a Dirac Delta function $\delta(t - t_i)$. The impact of each stimulus impulse to the intracellular calcium concentration is equal to the product of calcium gain (calcium current), α, caused by action potential and set to 0.095. Once the stimulus sequence ends, $C(t)$ decays with time constant τ_C toward C_o. $C(t)$ represents, in an abstract way, the intrinsic synaptic processes of synaptic facilitation [7]. In Eq. 12, $V(t)$ is the expected number of vesicles of neurotransmitter molecules in the ready-for-release pool at time instant t. V_o is the maximum number of vesicles that can be stored in the pool.

In a similar fashion to $C(t)$, $V(t)$ follows first-order nonlinear differential equations with a time constant τ_V.

N_t determines the concentration of the released neurotransmitter in the synaptic cleft, Eq. 13. This concentration can be estimated by tracing the amount of vesicles of neurotransmitter that remains in the presynaptic neuron, $V(t)$, over time. It is worth mentioning that there is a formal distinction between release site and synapse. Alternatively, each quantum of neurotransmitter is stored in one synaptic vesicle. The concentration of neurotransmitter in the synaptic cleft is meant to be the corresponding concentration of quanta of neurotransmitter. Hence, in Eq. 13 we use here a first-order nonlinear differential equation similar in nature to Eq. 11. The incremental raise in this case is then the decrease in the concentration of vesicles (first term). The drift term (second term) allows the value of N_t to decay, in case of no input, to a minimum accepted concentration N_{to} with a decay time constant τ_{N_t} et to 0 and 0.05 sec respectively. This decay reflects the biological cleaning action (or complete removal) of the neurotransmitter from the cleft. As the binding process of neurotransmitter in the postsynaptic membrane induces EPSP, it is calculated as in Eq. 14; where τ_{epsp} is a decay time constant and k_{epsp} is a scaling factor.

TABLE 2. Model parameters for generating the different network responses.

Parameter	No Synch.	Case I	Case II	Case III
τ_C	3.5 msec	3.5 msec	3.5 msec	3.5 msec
τ_V	9.3 msec	9.3 msec	9.3 msec	9.3msec
τ_{N_t}	8 msec	15 msec	12 msec	8 msec
α	0.09	0.09	0.09	0.09
τ_{epsp}	10 msec	5 msec	6 msec	10 msec
C_o	0.45	0.45	0.45	0.45
V_o	3.49	3.49	3.49	3.49
k_{epsp}	0.25	1.5	1.5	0.75
k_{N_t}	1	1	1.2	0.1
$k_{N_t,V}$	1	0.4	0.4	5

Supplementary materials.

For the manuscript

Synaptic Energy Drives the Information Processing Mechanisms in Spiking Neural Networks

Karim El Laithy and and Martin Bogdan

S.1. **On synaptic energy.** The relevant theoretical details about the concept of synaptic energy and the related energy minimization attributes are given in the main manuscript, please review Sec. 3 for the details. Apart from the main synaptic energy profile given in the manuscript text, more information are given here about the other possible alterations that might be induced to this energy profile. Specifically, Figs. S.1 and S.2 show the effect of changing the input frequency and

noisy inputs on the solution of the synaptic energy model respectively. Figures are adapted from [2].
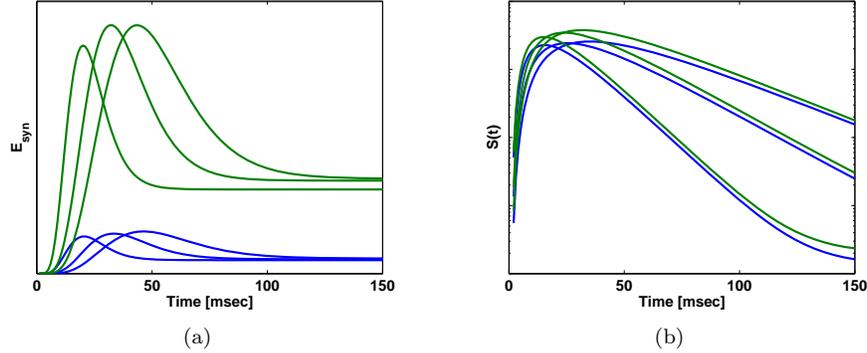

(a)   (b)

FIGURE S.1. Solutions and time evolutions of synaptic energy and corresponding synaptic strength in case of two different input frequencies $\Delta_{\mathrm{isi}}^{-1}$ in Eq. 1: the blue lines correspond to 200 Hz (the same from Fig. 1) while the green lines are for the 50 Hz. Model parameters and initial conditions are the same from Tab. 1 used to generate the solutions in Fig. 1. a) The time evolutions of the synaptic energy in case of both input frequencies. The relative positioning of energy states is function of the used initial resources and timing constants. b) Semilog scale for the y-axis to show the final synaptic strength values corresponding to the different energy states from (a).

Adding background noise to the model dynamics is not practical during solving the dynamical system within the Matlab solver. Instead, the input frequency is perturbed with $\pm 10\%$ during the second half of the simulation time. This change in the input frequency represents the influence of a background synaptic noise on the input frequency. The results of this trial are illustrated in Fig. 2(a). When the change in input frequency is fed after a while, the final states are considered variations from the main one. The opposite of this process is tested as well, the $\pm 10\%$ change in frequency value is used during the first half of the simulation time then followed by the standard input frequency. The response to the latter case is given in Fig. 2(b). On contrary to the previous case, using different input frequencies at the beginning lead to three distinguishable energy profiles with final three different states. At a glance, this analysis suggests that the synaptic model keeps a kind of memory to the stimuli interrupting its normal flow of energy over time. Although this might not be new, it supports the main goal of studying the synaptic dynamics from an energy-related point of view. That is, considering this energy profile of the MSSM and its relattion to synaptic responses gives novel and more insights into the potential roles of this model in regulating and may be controlling the network behaviour.

S.2. **On neural states.** In order to view the intrinsic flow of synaptic dynamics and involved synaptic energy for the selected time windows of Fig. 7, the following
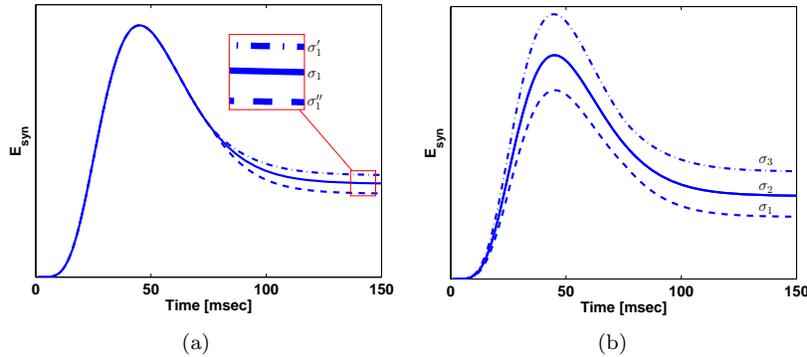
FIGURE S.2. Solution of the dynamical system with the same settings for model parameters from Fig. 1 while the input frequency is altered. a) Solution in case of feeding standard input with 200 Hz for the first half of the simulation epoch followed by $\pm 10\%$ change in input frequency for the second half of the simulation epoch. The final three states are considered a main states with two variations (as deviations from the main central one) b) Opposite to the case in a), this is the solution in case of feeding input of 200 Hz with $\pm 10\%$ change in input frequency for the first half of the simulation epoch followed by standard input with unchanged frequency for the second half of the simulation epoch. Three unique states are observed in this case.

Fig. S.3 illustrates using color-maps the presynaptic strength and synaptic energy for all excitatory neurons averaged over the presynaptic connections per neuron.

It is important to note that although the similarity of coherent spiking activities among the three different cases, the corresponding intensity of synaptic strength and the level of synaptic energies are far from being alike. This reinforce the importance and relevance of the proposed analytical measures in studying the synchronous firing of spiking neural networks in terms of the comprised synaptic dynamics.

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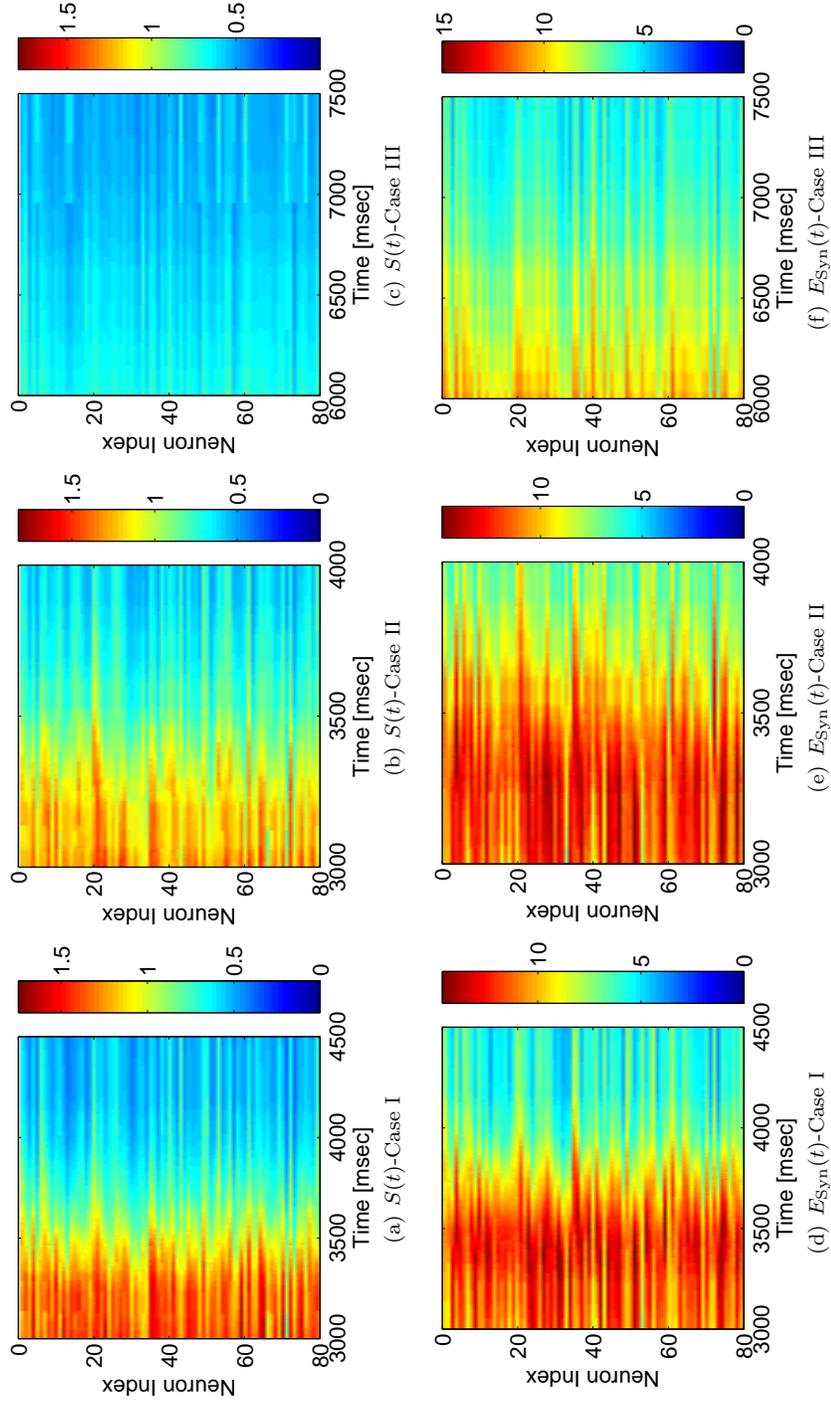
FIGURE S.3. Detailed (color-mapped) presynaptic strength and synaptic energy for excitatory neurons for these selected sections in Fig. 7

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