Off-line memory reprocessing following on-line unsupervised learning strongly improves recognition performance in a hierarchical visual memory

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Abstract—Recently, experience-driven unsupervised learning was shown to create combinatorial parts-based representations in a model of hierarchical visual memory. Examining the memory’s ability to recognize persons from a database of natural face images, we show that an off-line, sleep-like operating regime of the memory domain results in a significant improvement of the system’s ability to generalize over novel face views. Surprisingly, the positive effect turns out to be independent of synapse-specific plasticity, relying entirely on a homeostatic mechanism equalizing the intrinsic excitability levels of the units within the memory network. We show that this excitability equalization is the main cause for the improvement of memory function. A possible relation to cortical off-line memory reprocessing during certain sleep stages is discussed.

I. INTRODUCTION

The neural processes of memory formation and maintenance are thought to rely on activity-dependent modification of synaptic transmission between the neurons [1], [2] and on homeostatic regulation of some intrinsic properties such as intrinsic excitability [3], [4]. However, only little is known about the nature and dynamics of the interactions when both mechanisms are involved.

To gain insight into these interactions and the coordination of local mechanisms across a distributed system, we here continue to explore a model [5] of hierarchical visual memory able to form combinatorial parts-based representations of visual objects through experience-driven unsupervised learning (Fig. 1). In that model, images of human faces are presented in an incremental fashion and are encoded as local Gabor filter banks extracted from dedicated facial landmarks [6] (Fig. 2). During on-line learning, the bottom-up and lateral synaptic structure within a lower memory layer is developed to represent local facial features and their relations. The identities of different persons are captured explicitly within a higher layer, which projects this contextual information back to the lower layer. In its mature connectivity state, the system is able to reliably recognize the stored persons from the original and novel face images by signaling their identity explicitly with higher layer units. The resulting face representations exploit the combinatorics of the local parts vocabularies established on the lower layer. These parts-based representations are sparse in terms of both the activity generated during the recall and the synaptic patterns constituting memory traces in the network [5].

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that seem to reflect previous experience can be also observed in the cortex in the absence of sensory stimulation during restful waking or sleep [7], [8], [9].

In previous work [5] we had observed that proper formation of synaptic structure during on-line learning was crucially dependent on homeostatic regulation of activity in the sense of equal participation of units in memory formation. This regulation lead, however, to unequal intrinsic excitability of units, an imbalance that is ironed out by the off-line reprocessing performed in the off-line regime. Without such reprocessing, after a prolonged on-line learning phase the network has difficulty to generalize to novel facial stimuli. This weakness is removed by off-line memory reprocessing, which significantly improves the recognition performance on novel images of known faces even after a short period of time spent in the off-line mode. The effect involves not only improvement in identity recognition rates but also in the accuracy of gender identification (male vs. female).

Surprisingly, this positive effect turns out to be independent of synapse-specific plasticity, as it persists unchanged if synaptic plasticity is completely disabled, showing that the homeostatic activity regulation can be identified as the sole cause for the functional improvement. This synapse-unspecific regulatory mechanism is shown to be responsible for the re-balance, or equalization, of the intrinsic excitability levels in the network during the off-line reprocessing. The observed beneficial effect of homeostatic activity regulation leads us to speculate that similar mechanisms might be involved in memory reprocessing and (re-)consolidation during slow wave sleep (SWS, NREM Stage 4) and restful waking [10], [11], [12].

II. Preliminaries

The model of a hierarchical visual memory introduced in [5] is based on two consecutive, reciprocally interconnected layers of distributed cortical modules, or simply modules (Fig. 1). We denote the lower layer as parts layer and the higher memory layer as identity layer, applying the same terminology to the layer-specific modules. Each module contains subunits (termed core units or simply units) receiving common excitatory afferents and being bounded by common lateral inhibition, which is modulated by excitatory and inhibitory rhythms in the gamma range [13]. Such rhythmic activity is a well-confirmed signature of cortical processing [14], [15]. The lateral inhibition within the module results in activity dynamics with a strongly competitive character, turning the module into a winner-take-all-like decision unit [16], [5]. Decisions are performed within the frame of the repetitive decision cycles that are defined by the ongoing excitatory and inhibitory gamma rhythms. These cycles constitute atomic fragments of competitive processing and learning in the network. Before learning, the initial undifferentiated, intermodular connectivity is all-to-all within and across the layers, all synapses - bottom-up, lateral and top-down - being excitatory and plastic. During on-line learning phase, the network is exposed to natural face images from the AR database [17], by incremental presentation of one facial image per decision cycle (Fig. 2). Experience-driven structure formation is guided by slow activity-dependent bidirectional plasticity and homeostatic regulation of unit activity, both processes being crucial for shaping the synaptic connectivity within and across the layers. In the mature connectivity state, the memory traces for different persons are residing in the scaffold of bottom-up, lateral and top-down connectivity established in the course of the exposure to facial images. The ability to recognize person identities improves gradually with learning time, as the stimulus-evoked activity patterns come to represent individual faces more and more faithfully as a coherent combination of their parts.

Fig. 2. Unsupervised on-line learning procedure used to form the network structure of the memory domain. (A) Different face views used as input (one person out of total 40). Top left is the original view with neutral expression taken for training. Other views were used for testing (the bottom row shows duplicate views taken two weeks after the original series). (B) Example of individual faces used for on-line learning (4 of total 40 shown). (C) Facial landmarks used for the sensory input to the memory in the form of Gabor filter banks extracted at each landmark point. (D) During the on-line learning, the face images are presented incrementally showing one image per decision cycle. Decision cycles are defined by excitatory and inhibitory gamma rhythms $\omega$ and $\nu$.

Fast activity dynamics with winner-take-all-like behavior. Each module contains a number of $n$ core units and is modeled by a set of $n$ stochastic differential equations. Each equation describes activity dynamics of a core unit with activity variable $p$, which stands for the firing rate of a (sufficiently large, $N > 100$) population of neurons:

$$\tau \frac{dp}{dt} = \omega(1 + I^{LAT} + I^{TD})p^2(1 - p) - p^3$$

$$- 2 \cdot \omega \nu \max(p_i) - p + I^{BU}p^2 + \theta p + \sigma \eta p + \omega \epsilon,$$

where $\tau = 0.02 \text{ ms}$ is the time constant, $\max(p_i)$ is the activity of the strongest unit in the module, $I^{BU}, I^{LAT}, I^{TD}$ are bottom-up, lateral and top-down inputs, time-varying
parameters $\omega$ and $\nu$ define the excitatory and inhibitory rhythm, respectively, $\theta$ is the intrinsic excitability of the unit, $\sigma = 0.001$ is parameterizing the multiplicative Gaussian white noise $\eta$, and $\epsilon$ is an unspecific excitatory drive which depends on the number $n$ of units in the module.

A crucial characteristic of the module dynamics that makes the module act like a winner-take-all decision unit is the bifurcation system undergoes when the growing inhibition $\nu$ crosses a critical point of structural instability $\nu_c = 0.5$ [5], [16]. The excitatory and inhibitory rhythms $\omega$ and $\nu$ (Fig. 2 (D)) are given by:

$$\omega(t) = \omega_{\min} + \frac{\text{mod}(t, T)}{T} (\omega_{\max} - \omega_{\min}),$$  
$$\nu(t) = \nu_{\min} + \frac{1}{k} \sum \left[ e^{-g (\text{mod}(t, T) - 0.5 (T + T_{\text{init}}))} + (\nu_{\max} - \nu_{\min})^{-1} \right],$$

with the period $T = 25\, ms$, which is in the gamma range of neuronal oscillations abundantly evident in cortical processing [14], [15]. The term $\text{mod}(t, T)$ denotes the modulo operation, $\nu_{\min} = 0.005$, $\nu_{\max} = 1.0$, $\omega_{\min} = 0.25$, $\omega_{\max} = 0.75$ are the lower and upper bounds for the amplitudes of rhythms, and $T_{\text{init}} = 5\, ms$, $k = 2$, $g = 0.5$ are parameterizing the sigmoid curve defining the inhibitory rhythm. The critical bifurcation point $\nu_c = 0.5$ subdivides each decision cycle spanned by the rhythms in two phases. In the first phase, $\nu < \nu_c$, the inhibition is low and any subset of the core units can remain active. The second is the “decision” phase ($\nu > \nu_c$), where due to strong inhibition only one single winner unit remains active in stable states. The excitatory rhythm $\omega$ elevates the activity of the core units by self-excitation as long as they are able to resist the rising inhibition $\nu$. A series of successive decision cycles implements thus a rapidly repeating winner-take-all decision mechanism [13].

In the mature connectivity state formed by learning, local decisions are influenced not only by the sensory bottom-up input, but also by the contextual support provided through lateral and top-down connections. Importantly, $\omega$ modulates also the impact of lateral and top-down signals on the local decision. The higher the value of $\omega$, the higher the influence of the context-dependent signaling on unit activity. Thus, the contribution of contextual information to local decisions is varied from weak to strong by increasing $\omega$ in the course of a decision cycle (Fig. 2 (D)). At the end of each decision cycle, the amplified subset of winner units can be clearly interpreted as an individual face composed of the local features within the respective landmarks and labeled with the person’s identity (Fig. 3 (B), for further details, refer to [5]).

Homeostatic activity regulation. Here we focus on one of the adaptive mechanisms acting in the network, namely homeostatic regulation of a unit’s activity, leaving out the bidirectional plasticity as it is not relevant for the studied effect and will therefore be disabled in the off-line phase. Activity homeostasis is achieved via adaptation of the dynamic variable $\theta$ (Eq. 1), which corresponds to the intrinsic excitability of the unit. It is updated according to:

$$\frac{d\theta}{dt} = \tau_\theta^{-1} (p_{\text{aim}} - \langle p \rangle),$$

where $\langle p \rangle = \frac{1}{T} \int_0^T p(t) dt$ is the average activity of the core unit measured over the period $T$ of a decision cycle, $p_{\text{aim}}$ specifies the target activity level and $\tau_\theta^{-1} = 10^{-4} ms^{-1}$ is the inverse time constant. The target activity level $p_{\text{aim}}$ is a simple function of the number of core units $n$ in a module, $p_{\text{aim}} = \frac{1}{n}$. The initial value of the intrinsic excitability is $\theta(0) = 0$.

The mechanism of intrinsic excitability regulation has a sound neurophysiological basis described in numerous experimental works [3], [4]. It is widely used in neural modeling to stabilize the neural circuits and to optimize their function [18], [19]. Here, the homeostatic regulation of unit activity encourages a uniform duty cycle across units in the network to assure their equal participation in memory trace formation during the on-line learning phase [5]. Bearing in mind the strong competitive character of the neuronal dynamics, the regulation of the intrinsic excitability $\theta$ changes the a priori probability of a core unit to be the winner in a decision cycle. So, if a certain unit happens to take part too frequently in encoding of the memory content, violating the requirement of uniform win probability across the units, its excitability will be downregulated so that the core unit becomes more difficult to activate, giving an opportunity for other core units to participate in the representation. Reversely, a unit being silent for too long is upregulated, so that it can get excited more easily and contribute to memory formation.

On-line training procedure, off-line mode and performance evaluation. The system was trained in an incremental, unsupervised fashion on natural face images from the AR database [17], which contains different alternative views for 40 persons (Fig. 1 (B)). Each image of the training set (with neutral facial expression) was picked randomly and presented at the begin of a decision cycle as a collection of local Gabor filter banks extracted from specified landmarks (6 landmarks in total, Fig. 1 (C)). Each module on the lower memory layer subserves one landmark and contains $n = 20$ part-specific units. The identity module on the higher layer contain $m = 40$ core units, being able to explicitly memorize and signal identities of 40 persons from the database. As the learning procedure is open-ended, the system ran until a stable mature connectivity state was reached and no significant changes could be registered neither in the connectivity structure nor in the learning error on the training data set (after approximately $3 \cdot 10^5$ decision cycles). Both adaptive mechanisms, bidirectional synaptic plasticity and homeostatic activity regulation, were actively involved in structure formation during the learning phase.

The memory network which emerges during the on-line learning is able to self-generate activity in the absence of the external stimuli, so that we can put it in an off-line regime by removing the images from the input. The network continues then to run autonomously, reprocessing the memory content.
Fig. 3. Activity patterns over 20 successive cycles during the off-line ("sleep", (A)) and on-line ("wake", (B)) network regimes. In the off-line regime (A), the memory network generates spontaneous activity patterns in absence of external stimuli, replaying content stored in memory. During the off-line phase (Fig. 3 (A)), synaptic plasticity can be disabled without disturbing the positive effect of the off-line reprocessing on the memory function. While synaptic connectivity is fixed, the homeostatic activity regulation is active in the network during the off-line phase. To observe the changes in the excitability levels for a prolonged period, the off-line mode is run for a fixed time of $20 \cdot 10^3$ cycles.

After putting the system in the off-line regime, we test its recognition performance for both the person identity and gender on the original views from the training data set and on the alternative face views not shown before. We can then compare the performance after the off-line memory reprocessing with the performance the system showed before going into the off-line regime. During the test, both synaptic plasticity and homeostatic activity regulation are disabled, so that it is reassured that no further changes in the network structure can occur.

As the on-line learning is done in a completely unsupervised fashion without providing any data labels, we define a form of prediction error using the previous history of identity units responses observed during the learning phase while face images were presented. From these observations, the conditional probabilities for a certain face identity on the input given a particular winner identity unit $P(person|winner)$ are computed. During the test, presenting a face image on the input elicits response in form of distributed activity pattern across the network (see also Fig. 3 (B)). In particular, one identity unit becomes the winner among the identity module units in course of the decision cycle. This is taken as prediction for the face identity on the input by simply determining the most likely person from the previously computed probability table: $person = \arg\max_{person} P(person|winner)$. Now the identity error rate can be easily computed as fraction of the number of wrong guesses ($person \neq person_{true}$) over the number of total cycles during the test phase. The same can be done for determining the gender error rate by taking the conditional probabilities $P(gender|winner)$, with $gender = \{male, female\}$, instead.

III. MAIN RESULTS

Following the procedures described above, we disable the synaptic plasticity while leaving the homeostatic activity regulation active and put the memory network into the off-line mode after the prolonged on-line learning from natural face images. In the off-line mode, a replay of the memory content in form of self-generated patterns of distributed activity can be observed in absence of external stimuli. The activity formation in this sleep-like state resembles that of the “wake”, on-line regime. A small subset of units is amplified on the expense of the rest, so that only few units are able to stay active and become the winner within their module in course of the decision cycle. As the total number of the modules instantiated here is seven, we then observe in each cycle seven winner units that manifest the hierarchical parts-based representation of a possible face identity.
Some of the self-generated activity patterns correspond exactly to the stimulus-evoked response generated in the on-line regime if a particular individual face were presented on the input. Such patterns can thus be considered as replay of the face identities stored in the memory. Other patterns are in turn not just the replay of the faces seen before, but can be arbitrary combinations of parts-specific units, corresponding to the “phantasized” faces never experienced during the on-line learning. The amount of self-generated patterns corresponding to stored or phantasized faces can be influenced by tuning the ongoing rhythms. In particular, increasing the amplitude of the excitatory rhythm $\omega$ (and, in the same time, the amplitude of inhibitory rhythm $\nu$ to keep the activity formation sparse) will lead to a more coherent, storage-based replay. This reflects the role of $\omega$ as a modulator of the strength of global contextual signal exchange between distributed modules mediated via lateral and top-down connectivity (see Eq. 1). The stronger this contextual binding, the more probable is the recall of a coherent activity pattern, which is composed of the parts that belong to an individual face experienced before and stored in the memory.

After a fixed period of time ($20 \times 10^3$ cycles), the network is switched from the off-line back to the on-line regime. Alternatively, the off-line reprocessing can also be terminated flexibly as soon as no significant changes in excitability levels across the network can be detected anymore. Back in the on-line mode, the system shows a tremendous boost of recognition performance across all face views, the original and the alternative ones not shown before (Fig. 4). The strong drop in the error rates is observed for the identity error (up to 30% on the alternative views) as well as for the gender classification error (up to 10% on the alternative views). The improvement effect is even stronger if, in addition, oscillation tuning is performed by increasing the amplitude of excitatory and inhibitory rhythms, which enhances the influence of contextual lateral and top-down signaling. Furthermore, the stronger the alternative views deviate from the original view used during the on-line learning, the more evident is the observed improvement against the condition before the off-line reprocessing.

To find the cause for this dramatic improvement of memory network function, we concentrate on the changes in the excitability levels across the network caused by the homeostatic activity regulation, as this was the only adaptive mechanism active during the off-line mode. The time course of change in intrinsic excitability across the network during the off-line regime reveals a striking global trend towards equalization of initially widespread unit excitability levels (Fig. 5). This trend is reflected in the decrease of standard deviation of intrinsic excitability on the both network layers, going close to zero already within a short time spent in the off-line regime (around $3 \times 10^3$ cycles, see Fig. 5). That means, that initially different intrinsic excitability levels move closer together, approaching a certain common value. Being obviously the main effect of the off-line reprocessing, this equalization, or regularization, of intrinsic excitability in the network suggests itself as the main cause of the improvement in recognition rates after the off-line mode.

Indeed, if the excitability levels are set to the same value directly by hand, surpassing the reprocessing in the off-line regime, the very same improvement effect is found if comparing the recognition performance of the regularized condition against the initial non-regularized one. Hereby, the value the excitabilities are set to can be the minimum, the average or the maximum of the excitabilities, without a significant difference in the produced positive effect. The common value can be computed either over the whole layer or within each module. This observation is also in line with the insensitivity the positive effect shows against the direction the excitability levels shift to during the off-line phase. Namely, using different tuning of oscillatory rhythms...
Fig. 5. Excitability regularization in the off-line regime. (A) shows the lower parts layer, (B) the higher identity layer. Left column: the time course of changes in excitability due to homeostatic activity regulation across the network during the off-line phase. Right column: excitability levels are regularized across the network layers within a short time period (about $3 \times 10^3$ cycles). The standard deviation of intrinsic excitability computed layerwise goes almost to zero, indicating that the initially different intrinsic excitability levels move close together within the layers.

During the off-line regime can produce either up, down or balanced regulation of the equalized excitability levels. In all these cases, the positive effect on the recognition performance is expressed to the same extent after the off-line reprocessing, being independent of a particular direction of excitability regulation. Taken together, these findings deliver abundant evidence that the main cause of the positive effect is definitely the regularization of the excitability levels across the network, performed by the homeostatic activity regulation during the sleep-like state in absence of external stimuli.

IV. CONCLUSIONS

In this study, a model of hierarchical visual memory formed by unsupervised learning was found to have strongly improved recognition performance after intrinsic excitability regulation during a sleep-like, off-line regime. This improvement over the initial condition before off-line memory reprocessing applied to both identity as well as gender recognition. The improvement in recognition performance was as strong or stronger on novel alternative face views than for the images presented during on-line learning, showing that off-line reprocessing is elevating the generalization capability of the memory network. We find it remarkable that this functional improvement does not depend on synapse-specific plasticity, relying only on the tuning of synapse-unspecific, global excitability of units. It seems that there is no preferred direction the excitability levels should be regulated to. What really counts is that the regulatory process runs towards the equalization of intrinsic excitability across the memory units, being largely independent of the direction of their regulation.

Fig. 6. Comparison of recognition performance before and after manual regularization of excitability levels done module-wise by setting the levels to the minimum within the respective modules. Identity error rate for identity layer is shown. The positive effect resembles that of the reprocessing done in the off-line regime (compare to Fig. 4), providing the evidence for the causal role of the excitability regularization in the observed functional improvement.

Fig. 7. Comparison of recognition performance among different after sleep conditions (downregulated, upregulated and balanced excitability levels, each condition with or without additional tuning of oscillation rhythms), showing identity error rate for identity layer. These is no significant difference in positive effect provided by the different after sleep conditions, indicating that no particular direction of excitability regulation is more favorable for the effect strength than another. The positive effect can be thus fully accounted by the equalization of the excitability levels, being largely independent of the direction of their regulation.
which seems to be a favorable state of network organization after a prolonged on-line phase of unsupervised learning.

The causal link between regularization of intrinsic excitability in the memory network and subsequent improvement of memory function is very remarkable if interpreted from the perspective of hypothetically different memory processing strategies employed by the brain in waking and sleep states. The cortical processing and learning in the on-line regime of the wake state is biased by external stimuli which happen to occur with certain frequency in a given fragment of waking experience. In the limited episode of waking, one cannot expect to see a uniform sample of all the relevant objects, even if they could be drawn from an uniform distribution. The on-line learning have thus to operate on the restricted data available during the wakefulness. The non-uniform exposure to certain stimuli over a prolonged waking time (like it may happen while visiting an ocean beach on a hot summer day) could then lead to an overexpressed divergence of excitability levels in the cortical network, caused by the homeostatic activity regulation in response to imbalanced usage of neuronal units. This in turn could create a performance deficit for the recognition function, because the strong excitability bias induced by the specific stimuli experienced in the given waking period may influence and distort processing of other and related content. In its nature, the impairment would be similar to the overfitting phenomenon which may occur if the learner adapts too strongly to the limited data in the training set, or in other words, overlearns it. This bias, or prior, could be removed from the memory network in a sleep state. There, unbiased replay of memory content in form of spontaneously self-generated neuronal activity becomes possible, as indeed evidenced from numerous experimental findings [8], [9], [20]. Without intervening external stimuli, this off-line memory reprocessing could flatten the artificial prior created during the wake period by simply regularizing network excitability levels, resetting the internal representation closer to the true environmental statistics and restoring the ability of the memory to cope with the external stimuli in an unbiased way.

Interestingly, there are some recent findings about beneficial effects of slow-wave sleep (SWS, NREM stage 4) and also restful waking on performance in cognitive tasks that were trained before, like memorizing word pair lists or sequences of finger tapping movements [10], [11], [12]. This indicates that off-line memory reprocessing in the cortex may indeed enhance learning, improving declarative and non-declarative memory formation. Paradoxically, the conditions for conventional synapse-specific plasticity are rather unfavorable in the brain states where off-line memory reprocessing is thought to occur. In SWS, the low level of cholinergic neuromodulation and strongly diminished activity of plasticity-related early genes effectively disable individual, correlation-based synaptic potentiation [21], [20]. Short periods of restful waking and ultra-short naps [12], [22] do not offer enough time for the rather slow classical synaptic plasticity to induce the beneficial functional changes in the memory structure. So it is unclear, what plasticity processes underlie the structural changes made during the off-line memory reprocessing, causing different memory function improvements observed experimentally after off-line states in a behavioral setting.

In the face of our findings, we hypothesize that a homeostatic activity regulation mechanism can be made responsible for the reorganization and optimization of the memory network’s structure, causing synapse-unspecific changes of global neuronal excitability [23], [24] that lead to the functional improvements observed in behavioral experiments. It can do so without relying on synapse-specific plasticity, and it can do it fast, so that already a short time spent in the off-line regime can be enough to get the improvement effect.

The main prediction of this hypothesis is that a regularization of excitability levels in the cortical memory network would be necessary after a prolonged time spent with on-line learning. If this excitability regularization wouldn’t occur for some reason, the recognition performance, particularly with regard to the less familiar inputs requiring generalization, should be severely impaired because of the artificial bias imposed by the restricted stimuli set available during the on-line learning period. Then a neuronal process would be expected to initiate memory reprocessing that takes place in an off-line mode, either during a sleep state or during restful waking. This neuronal process would use the mechanism of homeostatic activity regulation to adjust the intrinsic excitabilities and equalize their levels across the units of the memory network, downregulating the units overactive during the replay and upregulating the units underactive during the replay. This off-line reprocessing should lead to a strong improvement in recognition and generalization capability back in the on-line wake state, removing the artificial bias induced in the previous period of on-line learning.

A related hypothesis, with focus on synaptic homeostasis, was provided by Tononi and Cirelli. The authors discuss homeostatic synaptic scaling performed during sleep as a mechanism to re-obtain the ability to potentiate synapses after a prolonged waking period [25]. This perspective stresses rather the importance of local synaptic strength homeostasis [26], as opposed to the activity homeostasis and global reorganization of the network state proposed here. It may well be the case that both synapse-unspecific homeostatic regulation mechanisms act in the off-line state in the memory network, one equalizing the unit excitability to remove the artificial bias induced by the wake period, the other rescaling the synapses to recover their plasticity when back in the on-line mode again.

The off-line regime we examined here is only one of possible alternatives how the off-line reprocessing can be performed in the studied memory network model. Different off-line modes can be induced by tuning the ongoing rhythms, for instance by simply changing the excitatory and inhibitory amplitude. In future work we plan to investigate a second sleep-like state where off-line memory reprocessing occurs with activated synaptic plasticity and increased contextual
influence via lateral and top-down pathways, mimicking the REM sleep phase. In this state, we may expect that the replay of the memory content, combined with activity-dependent bidirectional plasticity [27], [28], could lead to a different quality of structural reorganization of the memory, including memory trace stabilization and amplification and reduction of interference between competing traces that overlap substantially.

This agenda could guide us ultimately towards modeling of a complete wake-SWS-REM cycle and investigating the functional consequences of such tri-phase memory processing for the organization and performance of memory, comparing the effects with experimental observations. In addition, more elaborate modeling could include separate hippocampal and neocortical subsystems [29]. Such a model of tri-phase memory processing would support the view of memory formation and maintenance as a constantly evolving dynamic multi-stage process having different functional properties during wake and sleep states. The ultimate aim of such a process is of course the optimization of memory function, delivering an evolutionary explanation for the different regimes of sleep being manifest in the nervous system of most living organisms [30].

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