



The role of rhythmic neural synchronization in rest and task conditions

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Rhythmic neural synchronization is found throughout the brain during many different tasks and even at rest. Beyond their underlying mechanisms, the question of their role is still controversial. Modeling can bring insight on this difficult question. We review here our recent modeling results concerning this issue in different situations. During rest, we show how local rhythmic synchrony can induce a spatiotemporally organized spontaneous activity at the brain level. Then, we show how rhythmic synchrony decreases reaction time in attention and enhances the strength and speed of information transfer between different groups of neurons. Finally, we show that when rhythmic synchrony creates firing phases, the learning with spike timing-dependent plasticity of repeatedly presented input patterns is greatly enhanced.

Keywords: oscillations, resting state, attention, communication, learning

INTRODUCTION

Rhythmic neural synchronization is commonly found in the brain and involves a number of different frequency bands. Such activity is found during the execution of a number of tasks (Tallon-Baudry, 2009) and even when a subject is at rest (Nir et al., 2008). The origin of such rhythms has received quite a lot of attention either experimentally or in modeling studies and a number of mechanisms have been found. The issue of their role is far less clear, as a general consensus has not been attained. On one side, as rhythmic neural activity correlates with a number of cognitive processes and behavior, its role is believed to be important for information processing (Fries, 2009). On the other side, it is believed that this rhythmic synchrony is just concomitant to information processing but do not participate in it. Two facts make this question difficult to answer. Direct evidence of the role of rhythmic synchrony can be obtained by manipulating these rhythms but only few results have been obtained for the induced behavioral (Stopfer et al., 1997) and neural activity (Sohal et al., 2009) changes. Second, the way information is processed in the brain is not sufficiently characterized to attribute a well-defined role to rhythmic synchrony. As modeling allows a more complete and deeper investigation, this approach appears as a convenient tool to explore this question.

Based on our recent modeling work, we review here evidence for a constructive role of rhythmic neural activity in different situations. First, we show how local rhythmic synchrony can induce a spatiotemporally organized spontaneous activity at the brain level during rest (Deco et al., 2009). Then, we show how rhythmic synchrony contributes positively to attention (Buehlmann and Deco, 2008) and information transfer between different neural pools (Buehlmann and Deco, 2010). Finally, we show how the learning of repeatedly presented input patterns by spike timing-dependent plasticity (STDP) can be enhanced by rhythmic synchrony

(Masquelier et al., 2009). As we just review here the main results of these studies, we redirect the interested reader to the original references for more details.

ROLE OF RHYTHMIC NEURAL SYNCHRONIZATION IN SPONTANEOUS BRAIN ACTIVITY DURING REST

A growing body of neuroimaging research has documented that, in the absence of an explicit task—the so-called “resting state,” the brain exhibits structured spatiotemporal patterns of activity. In particular, analysis of the fMRI blood oxygen level-dependent (BOLD) fluctuations (<0.1 Hz) during such conditions has revealed the existence of consistent networks, called resting state networks (Biswal et al., 1995). Among them, the so-called default-mode network is believed to play an important role (Shulman et al., 1997; Gusnard and Raichle, 2001; Greicius et al., 2003; Fox et al., 2005; Raichle and Mintun, 2006). Although this network could be associated with daydreaming, free association, stream of consciousness, or inner rehearsal in humans, similar patterns have been found in anesthetized monkeys, demonstrating that this network reveals intrinsic properties of the brain (Vincent et al., 2007). Since, a series of other networks has been identified (Mantini et al., 2007). These findings using the hemodynamic BOLD signal are supported by direct measurements of the neural activity: namely, even for distant regions, the slow fluctuations (<0.1 Hz) of the neural firing rate and of the gamma band power of the local field potential (LFP) can be correlated (Nir et al., 2008).

To understand the origin of this type of activity, a large-scale model of the brain is necessary. This can be done by considering the network of anatomically connected brain regions, such as the one known for the macaque via the CoCoMac database (Kötter, 2004; Kötter and Wanke, 2005), as shown in **Figure 1A**. At this large-scale, propagation delays are taken into account, via the choice of an axonal conduction velocity and the use of inter-regional distances. At the local level, the underlying network of excitatory and inhibitory spiking neurons, considered

homogeneous for simplicity, can be modeled using the classical reduced model of a Wilson–Cowan unit (Wilson and Cowan, 1972), where noise is added. When each unit is driven under its oscillatory threshold – above which a gamma oscillation develops, it is shown that for a sufficiently large coupling all units oscillate, the network activity exhibiting an irregular dynamics. We divide the network in two structural communities (see **Figure 1B**), calculate the level of synchrony of each community using an analog of the Kuramoto (1984) order parameter and also calculate the BOLD signal using a hemodynamic model (Friston et al., 2003). We observe slow fluctuations of the communities synchrony levels and of their calculated BOLD signal (**Figure 2**). These fluctuations get anticorrelated for an intermediate range of noise levels (**Figure 2**), in line with the experimental observations (Fox et al., 2005). Note the optimal noise level where the anticorrelation is maximal, indicating the presence of stochastic resonance.

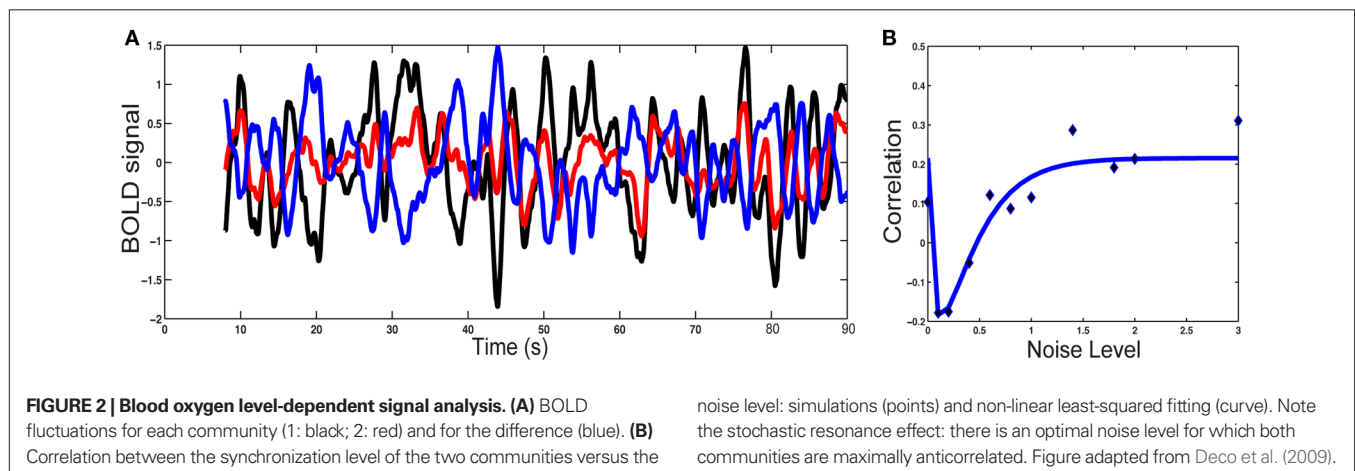
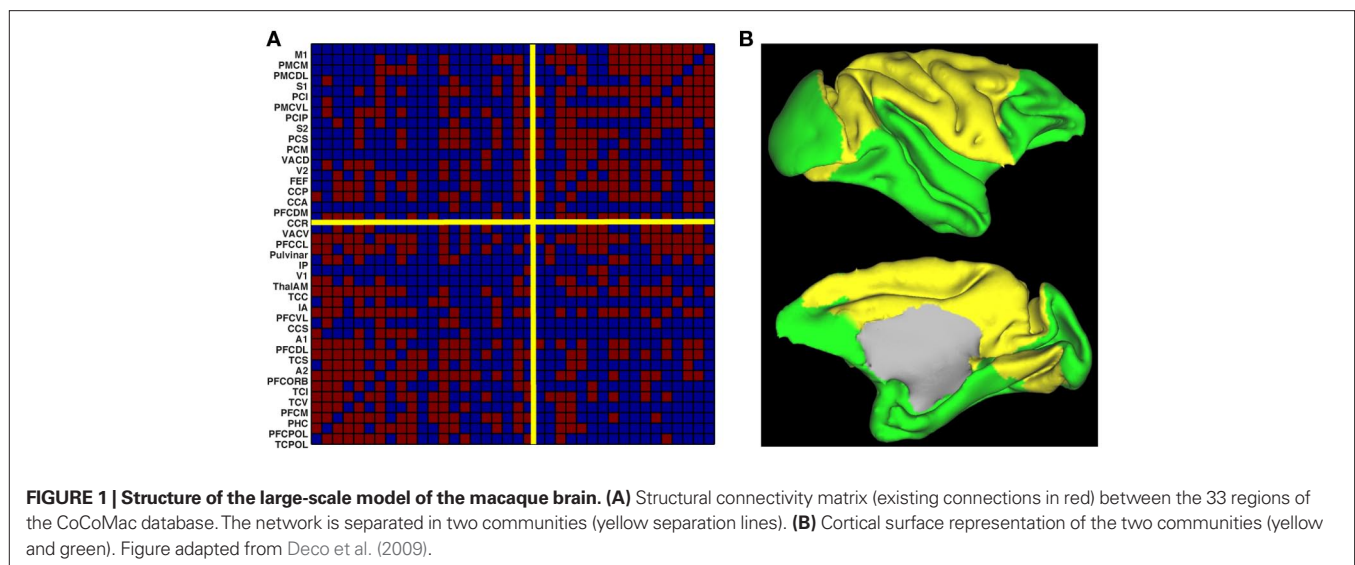
ROLE OF RHYTHMIC NEURAL SYNCHRONIZATION IN ATTENTION AND INFORMATION TRANSFER

In area V4 of behaving monkeys, attention has been shown to modulate the firing rate of neurons whose receptive fields contain the attended stimulus. When the receptive field contains one stimulus,

attention increases the firing rate. When two stimuli are presented, the firing rate increases if the stronger stimulus is attended but decreases when the weaker one is attended. This behavior is called biased competition (Moran and Desimone, 1985; Desimone and Duncan, 1995). Furthermore, associated with an increase of gamma frequency range power of the LFP with attention, neurons activated by an attended stimulus exhibit increased gamma frequency synchronization compared with neurons activated by a distractor stimulus¹ (Fries et al., 2001). Although rate and gamma synchrony modulations occur simultaneously, it is not clear if and how they are mechanistically related.

A number of theoretical studies have investigated the neural mechanisms subserving attention. In the presence of a gamma oscillation, a number of these studies have found that attentional modulations could be reproduced (Niebur et al., 1993; Tiesinga et al., 2004; Borgers et al., 2005, 2008; Buia and Tiesinga, 2006, 2008; Borgers and Kopell, 2008; Buehlmann and Deco, 2008; Zeitler et al.,

¹Note that, in V1, a decrease in gamma frequency synchronization has recently been found (Chalk et al., 2010). However, different mechanisms than in V4 are believed to be at play.



2008; Ardid et al., 2010). In other studies (Deco and Rolls, 2005; Hugues and Jose, 2010), it was found that attentional modulations could be induced by a top-down bias to a non-oscillating asynchronous network. In conclusion, while network gamma oscillations could help, these results demonstrate that they are not mandatory to induce attentional modulations. We review here a study investigating this question further.

Biased competition has been implemented in a network of excitatory and inhibitory spiking neurons (see **Figure 3A**), where attention is modeled as an additional input to the neurons encoding the attended stimulus (Deco and Rolls, 2005). When the attentional effects on gamma synchronization are included (Buehlmann and Deco, 2008), the model results are compatible with the experiments: when a stimulus is presented there is correlated neural activity in the gamma frequency band, and its power is stronger in the neurons encoding the attended stimulus than in the neurons encoding the unattended stimulus. By increasing the AMPA synaptic conductance and decreasing simultaneously the NMDA one to preserve charge entry, we can create a gamma oscillation in the network and increase its power. When the gamma power level is increased, the attentional rate modulation decreases monotonically but the gamma modulation first increases up to a maximum and then decreases (**Figure 3B**). These results suggest that rate and gamma modulations can occur independently of each other and are therefore not concomitant effects. However, if the rate modulation is accompanied by a gamma modulation, reaction times are found to be shorter, implying a behavioral relevance for gamma synchronization.

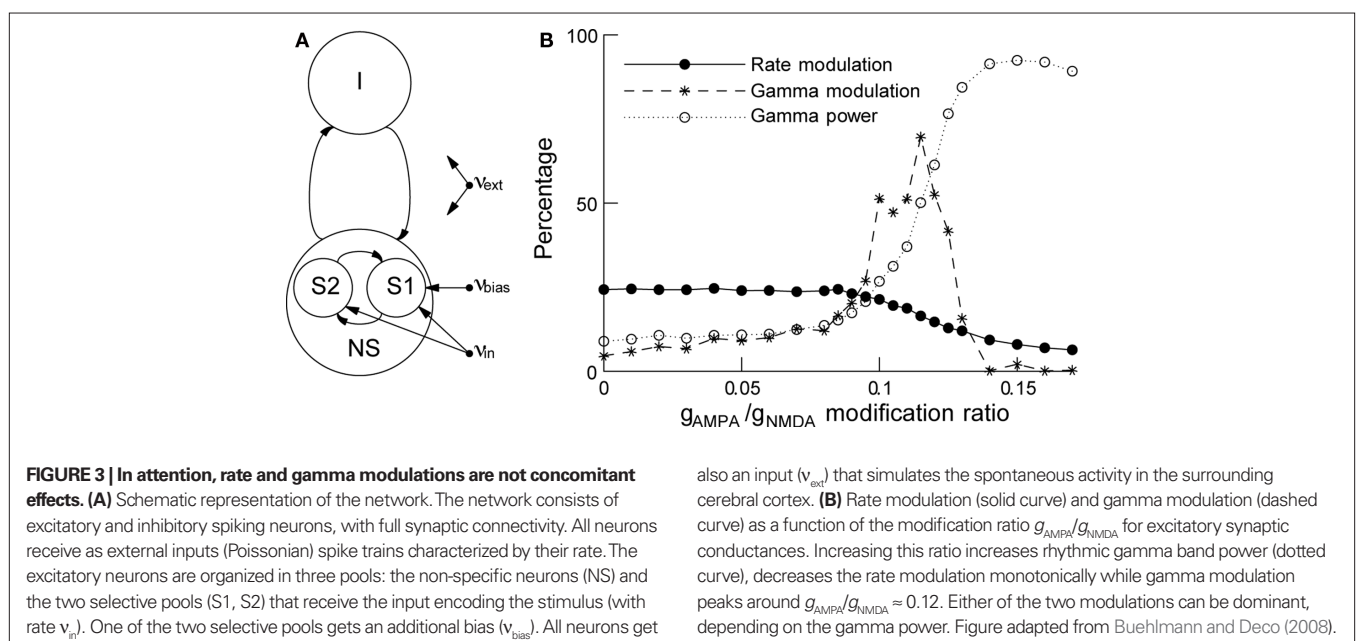
One potential role of rhythmic neural activity may be to enhance communication between neural pools. In fact, an experimental study has shown that the correlation of neural activity in two neural clusters depends on the phase relation of the neural activity in the two clusters (Womelsdorf et al., 2007). This result suggests that effective connectivities in a network can be maximized or minimized by synchronization, a hypothesis also known as communication through coherence (CTC; Fries, 2005). In a similar

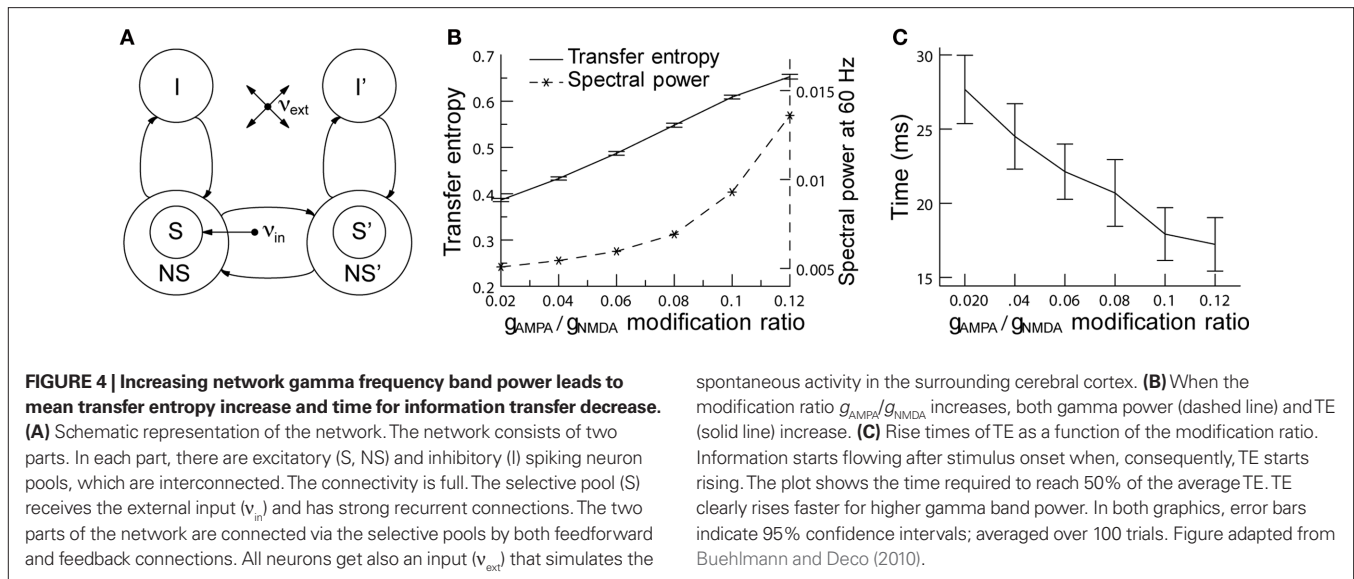
modeling framework (see **Figure 4A**), general effects of gamma synchronization on information transfer between two neural pools were studied by measuring the transfer entropy (TE) between these two clusters (Buehlmann and Deco, 2010). TE is an information theoretical measure that quantifies the statistical coherence between systems and is able to distinguish between shared and transported information (Schreiber, 2000). In accordance with the experiments we found that (i) there is an optimal phase relation at which TE is highest between the two groups of neurons, (ii) TE increases as a function of the gamma power (**Figure 4B**), and (iii) the time required to reach 50% of the TE after stimulus onset decreases as a function of gamma power (**Figure 4C**). Taken together, these findings support the CTC hypothesis and, as rhythmic neural synchronization makes information transport more efficient, they suggest that it has a behavioral relevance.

ROLE OF RHYTHMIC NEURAL SYNCHRONIZATION IN LEARNING WITH SPIKE TIMING-DEPENDENT PLASTICITY

Recent experiments have established that in cortex information can be encoded in the spike times of neurons relative to the phase of a background oscillation in the LFP – a phenomenon referred to as “phase-of-firing coding” (PoFC; Montemurro et al., 2008; Kayser et al., 2009; Vinck et al., 2010). These firing phase preferences could result from combining an oscillatory drive with a stimulus-dependent current that would produce the variations in preferred phases (Hopfield, 1995), a mechanism that has experimental support *in vitro* (Tiesinga et al., 2002; Schaefer et al., 2006; McLelland and Paulsen, 2009). However, it remains unknown if such a firing activity can be decoded, that is if downstream neurons can respond selectively to patterns of phases in their inputs and if this behavior can be learnt.

A recent modeling study has shown that PoFC has a major impact on downstream learning and decoding when associated with the now well-established STDP (Masquelier et al., 2009). STDP is a physiological mechanism of activity-driven synaptic



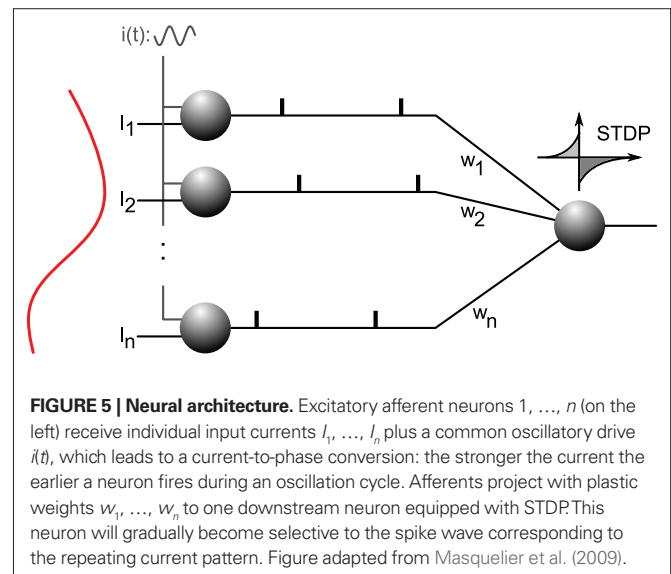


regulation, where an excitatory synapse receiving a spike before a postsynaptic one is emitted is potentiated (Long-Term Potentiation) whereas its strength is weakened the other way around (Long-Term Depression). STDP has been observed both *in vivo* and *in vitro*, in many species (from insects to mammals) and in many brain areas (see Caporale and Dan, 2008 for a review).

Specifically, a single neuron equipped with STDP (Figure 5) can robustly detect a randomly repeating pattern of input currents hidden in a subset of its afferents when it is encoded in their firing phases (Figure 6). The oscillatory drive improves the spike times' reliability, by decreasing their sensitivity to initial conditions and avoiding jitter accumulation, so that they depend mainly on the current input values. The ability of STDP to detect repeating spike patterns had been noted before in continuous activity (Masquelier et al., 2008), but it turns out that oscillations greatly facilitate learning, which is possible even when only a small fraction of the afferents (~10%) exhibits PoFC. A benchmark with more conventional rate-based codes demonstrated the superiority of oscillations and PoFC for both STDP-based learning and speed of decoding, which only takes one oscillatory cycle.

Simultaneously resetting all the afferents' potentials every now and then is a similar alternative to adding a common oscillatory drive, which also leads to reproducible spike times that STDP can pick. This may be a valid description of what happens during discrete sensory processing such as saccades or sniffs (Uchida et al., 2006), or with "stimulus onset paradigms," in which a given sensory system is in a spontaneous state before being presented with a stimulus. But the fact that periods of oscillatory activity are found throughout the brain, and the suggestion that they could be particularly useful for the continuous cognitive processes, in which no reference time such as stimulus onsets is available, means that the oscillatory drive model may be of great practical importance.

Even if they are still speculative, these results suggest how two simple mechanisms present in the brain may combine constructively to induce a kind of temporal coding: oscillations allow infor-



mation to be encoded in the spike phases, and STDP provides an appealing mechanism to learn how to decode them. Consistent with our scheme a growing body of experimental evidence in animals and humans demonstrates that successful Long-Term Memory encoding correlates with increased oscillatory activity across a broad range of frequencies (from the theta to the gamma frequency bands), in both sensory and associative areas (see Jensen et al., 2007; Klimesch et al., 2008; Tallon-Baudry, 2009 for recent reviews).

DISCUSSION

In this review, we have presented recent modeling results which suggest that rhythmic neural synchronization can have a variety of roles. During rest, when the brain is close to a spontaneous state, we have found that if local rhythms are sustained, they tend to form synchronized clusters of brain regions, creating in this

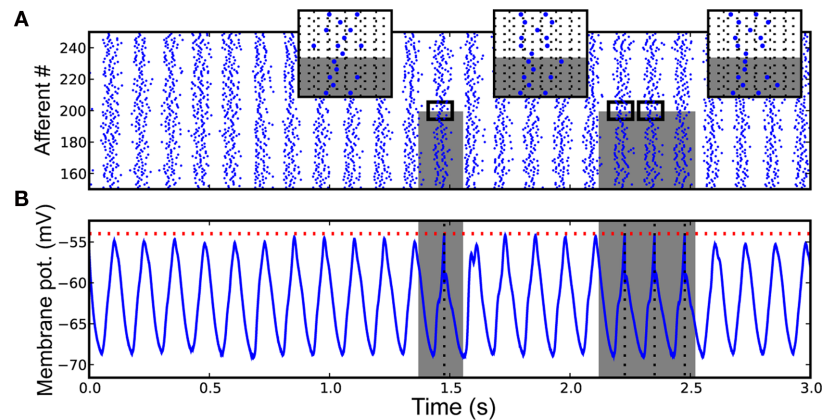


FIGURE 6 | Downstream neuron input and response after learning (A)

Input spike trains from afferents 150, ..., 250, for the [0, 3]-s period. Spikes come in waves because of the oscillatory drive. Gray rectangles designate the periods where the pattern is presented, and the afferents that are involved in it (0, ..., 199 here). Three inserts [horizontal grid size = 1 rad (in phase) = 20 ms] zoom on adequate periods to illustrate that the spike phases of the afferents involved in the pattern are the same (except for the noise) for different pattern

presentations, which is not true for other afferents (200, ..., 1999 here). The repetition of the pattern spike wave allows the pattern to be learned by STDP. **(B)** Postsynaptic membrane potential as a function of time: it oscillates at the same frequency as the afferents (and possibly with a phase lag due to conduction delays), but reaches the threshold if and only if the pattern is presented. See Masquelier et al. (2009) for details. Figure adapted from Masquelier et al. (2009).

way spatiotemporally organized activity at the brain scale level. Rhythmic synchrony was also found to decrease reaction time in attention and enhance information transfer between different groups of neurons, in line with the CTC hypothesis (Fries, 2005). Finally, when rhythmic synchrony creates firing phases (PoFC), the learning with STDP of repeatedly presented input patterns is greatly enhanced.

Among the mechanisms we have considered in this review on rhythmic neural synchronization, PoFC, CTC, and STDP involve spike timing and may be at work simultaneously. An interesting issue is to understand how they relate to each other in the brain, and if they facilitate each other or not. An oscillation in a network, either of intrinsic or extrinsic origin, can induce PoFC in the discharge of its neurons, the mean input to a neuron controlling generally its mean firing phase with respect to this oscillation. When a first neural network projects to a second one, and that both exhibit an oscillation in the same frequency band, the phase to which the incoming spikes arrive to the second network relative to its oscillation (taking into account an eventual conduction delay) is believed to play a role in the effective communication between the two networks (CTC; Fries, 2005; Womelsdorf et al., 2007). The information conveyed from the first network spikes will be “filtered” by the second, some neurons having a more important effect on the second network activity than others due to their firing phase. Note that beyond these phenomena at the individual neuron level, the phase between the oscillations in the two networks will also depend on the global behavior of the neural populations in these networks.

In the case where synapses between these two networks are equipped with STDP, learning will of course depend on the relative timing between the spikes in the first and in the second network, and therefore on the firing phases in the case of oscillatory networks. This learning will sculpt the connectivity between these

networks, potentiating some synapses, and depressing others, which can change the interaction between the two networks and the relative phase of their oscillations and in turn how synapses evolve. What controls this complex dynamical process is a fundamental issue to understand how brain connectivity evolves with experience, but still very little is known. However, it is reasonable to think that selection of incoming information can be done in this way. Consider two neural groups A and B, projecting on a second network, all of them oscillating in the same frequency band. Depending on the mean phase of A and B spikes, the patterns of A spikes may be learned with STDP (following the results presented in section ‘Role of Rhythmic Neural Synchronization in Learning with Spike Timing-dependent Plasticity’), but synapses from B neurons may be systematically depressed. This selection mechanism may be flexible, the phase relationships changing for example with the context: in the previous example, the learning of the patterns of B spikes would then become possible, while the patterns of A spikes would be forgotten. Note that, as STDP is a slow process, this mechanism will occur on a much longer timescale than communication occurs.

At a broader level, these results show that rhythmic synchrony can have an important impact on the efficiency of neural communication at different scales, by providing a temporal organization of neural activity. However, these findings should also be investigated experimentally to check if the modeling hypotheses are appropriate and the rhythms sufficiently strong so that these effects are effectively present.

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