The principle of coherence in multi-level brain information processing

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ABSTRACT

Synchronisation has become one of the major scientific tools to explain biological order at many levels of organisation. In systems neuroscience, synchronised subthreshold and suprathreshold oscillatory neuronal activity within and between distributed neuronal assemblies is acknowledged as a fundamental mode of neuronal information processing. Coherent neuronal oscillations correlate with all basic cognitive functions, mediate local and long-range neuronal communication and affect synaptic plasticity. However, it remains unclear how the very fast and complex changes of functional neuronal connectivity necessary for cognition, as mediated by dynamic patterns of neuronal synchrony, could be explained exclusively based on the well-established synaptic mechanisms. A growing body of research indicates that the intraneuronal matrix, composed of cytoskeletal elements and their binding proteins, structurally and functionally connects the synapses within a neuron, modulates neurotransmission and memory consolidation, and is hypothesised to be involved in signal integration via electric signalling due to its charged surface. Theoretical modelling, as well as emerging experimental evidence indicate that neuronal cytoskeleton supports highly cooperative energy transport and information processing based on molecular coherence. We suggest that long-range coherent dynamics within the intra- and extracellular filamentous matrices could establish dynamic ordered states, capable of rapid modulations of functional neuronal connectivity via their interactions with neuronal membranes and synapses. Coherence may thus represent a common denominator of neurophysiological and biophysical approaches to brain information processing, operating at multiple levels of neuronal organisation, from which cognition may emerge as its cardinal manifestation.

KEYWORDS: neuronal synchronisation, molecular coherence, functional connectivity, neuronal cytoskeleton, counterions, dissipative brain dynamics

1 INTRODUCTION

The tendency of natural systems to achieve order and harmony in their behaviour is a manifestation of open systems' self-organising capacity, existing everywhere in nature (Osipov et al., 2007). Synchronisation, a process whereby objects of a different nature adjust their internal rhythms to a collective operation regime due to their mutual interactions, is one of the most captivating phenomena encountered in complex systems, and has become a major scientific tool to explain this tendency. Technically, synchronisation refers to the establishment of stable phase relationships among the oscillating components within a system of coupled oscillators due to phase locking or frequency entrainment, whose oscillatory characteristics are more generally described as the coherence[1]. Synchronisation phenomena are encountered in areas as diverse as physics, chemistry, engineering, biology, medicine, economics, and social sciences, which implies its deep significance and explanatory power (Arenas et al., 2008; Osipov et al., 2007; Pikovsky et al., 2001).

Organisms are highly excitable dissipative systems whose responses to external and internal perturbations and energy flow throughout the system must be precisely and efficiently coordinated in time and space. Synchronisation phenomena have been observed at all basic levels of biological organisation – from the precisely coordinated gene expression and metabolic cycles (for example, glycolytic oscillations) to collective physiological rhythms[2] and social interaction dynamics[3]. The functional significance of coherent oscillatory dynamics lies in the *collective summation* of outputs of individual elements, which enables a powerful response to a weak external input, efficient communication between different systems (that is, transfer of energy and information) and encoding information in terms of the phase, frequency, or amplitude of the oscillating system. In other words, the power (or meaning) of coherence arises from a reduction in the uncorrelated degrees of freedom into a collective operation mode, which enables long

[1] Although not identical, both terms are often used interchangeably. Throughout this review, we will use both according to their traditional use in respective fields.

[2] These include, for example, heart contraction, brain oscillations, circadian rhythms, hormonal secretion, locomotion, etc.

[3] Common examples are synchronised signalling in crickets and fireflies, the dynamic behaviour of dense groups of animals, such as bird flocks or fish schools, bacterial quorum sensing, collective hunting strategies, etc. An interested reader may find further examples in the cited literatute.

range order and coordination of biological processes (Arenas et al., 2008; Bianchi, 2008; Binhi and Rubin, 2007; Goldenfeld and Woese, 2011; Ho, 2008; Klevecz et al., 2008; Strogatz, 2003; Winfree, 2001). Coherence and synchronisation are thus important concepts in biological organisation and systems biology (Plankar et al., 2011).

Synchronised oscillations of large neuronal groups, whose frequency range spans several orders of magnitude, represent one of the most prominent characteristics of brain information processing (Buzsáki and Draguhn, 2004). It has been proposed for over twenty years that dynamic neuronal interactions rely on precise temporal coordination of single neuronal discharges and population activity in distributed neuronal assemblies. This phenomenon, generally termed neuronal synchrony, has been found to correlate strongly with cognitive functions: perception, attention, sensorimotor integration, learning, memory, consciousness, decision making etc., and pathological synchrony patterns appear in many different brain disorders. It is strongly argued that coherent neuronal oscillations are not merely an epiphenomenon, but have a direct functional relevance and a causal role in encoding representations, coordinating neuronal communication and regulating synaptic plasticity (Fell and Axmacher, 2011; Fries, 2009; Fries et al., 2007; Jensen et al., 2007; Senkowski et al., 2008; Singer, 2009; Uhlhaas et al., 2009; Uhlhaas and Singer, 2010).

There is however another type of coherence that may also be important for neuronal information processing, but which operates at the level of individual molecules and molecular complexes. The coherence of molecular dynamics has long been theoretically elaborated (Del Giudice et al., 1985; Fröhlich, 1968; Ricciardi and Umezawa, 1967), only recently gaining wider acceptance, when quantum coherence was experimentally demonstrated to directly coordinate energy flow, maximising efficiency of excitation transfer in several photosynthetic complexes (Collini et al., 2010; Engel et al., 2007; Lee et al., 2007). On the other line of research, the neuronal cytoskeleton or, more generally, the intraneuronal matrix (Woolf et al., 2009) – is increasingly acknowledged to have an important role in modifying the gating properties of ion channels and in coordinating neuronal plasticity (Janmey, 1998; Priel et al., 2010; Woolf, 2006; Woolf et al., 2009). Moreover, much theoretical and experimental effort has been focusing on the coherent properties and long-range signal transfer within cytoskeletal elements, most notably in the microtubules (Bandyopadhyay, 2010; Cifra et al., 2010; Jibu et al., 1994; Mershin et al., 2006; Priel et al., 2006a; Sahu et al., 2011; Tuszyński et al., 1997). It is hypothesised that such intrinsic

information processing capacity could provide the neurons with greater autonomy in response (Woolf et al., 2009), complementary to their classical membrane-dependent characteristics.

Here we take an integrative approach, combining neuroscientific and biophysical disciplines to develop the hypothesis that coherence is a generic property of dynamic brain information processing, operating at different levels of neuronal organisation. Moreover, as coherence is a form of (temporal[4]) self-organisation, it may represent an organising principle in biology from which cognitive phenomena emerge as its highest-order manifestation. The article's aim is not to establish conclusive mechanistic roles of coherence in cognition, nor to reiterate yet another version of the "quantum mind" theory; rather, we aim to provide a synthetic review of the recent progress in theoretical and experimental research, pointing out the many information processing contexts in which coherence could shape a dynamic ordering of the brain's integrative operation, bringing together utterly different scientific disciplines that independently recognised its importance. By partially relying on the synthetic approach of the dissipative brain dynamics theory (Freeman and Vitiello, 2006), we also speculate on how neuronal and molecular coherent oscillations could functionally interact by taking into account the electrodynamic properties of the intra- and extracellular filamentous matrices.

2 NEURONAL COHERENCE AS A FUNDAMENTAL MODE OF CORTICAL INFORMATION PROCESSING

Sherrington (1941) and Adrian (1942) hypothesised that brain processing likely involves some sort of a "population code" with collective properties not readily observable in the summed responses of single neurons. Currently, the most accepted view on how this might be achieved is through the integration of information based on neuronal synchrony (Womelsdorf et al., 2007). Although synchronisation of neurons or neuronal subgroups can also arise via strong common inputs that occur irregularly, oscillation-based synchrony is the most energy-efficient and established mechanism suited for temporal coordination and for response transmission (Buzsáki and Draguhn, 2004; Winfree, 2001) and could complement the slower and less flexible firing rate strategy for coding information (Singer, 2009). Mechanistically, oscillations in fact induce an

[4] As opposed to "topological" forms of self-organisation, epitomized by network modelling (e.g., Barabási and Oltvai, 2004; Huang, 2009; Kauffman, 1993).

alternation between membrane states of inhibition and increased excitability in neighbouring neurons, biasing neurons to increase spike timing precision and hence mediate their synchronisation (Buzsaki, 2006; Fries, 2005; Singer and Gray, 1995).

2.1 Origins and modulatory influences

2.1.1 Generation of neuronal oscillations

Neuronal oscillation is a periodic wave-like variation of neuronal electromagnetic (EM) activity in the central nervous system, characterised by frequency (i.e., delta, theta, alpha, beta, gamma), amplitude, and phase (the angle of deflection of an oscillation). Neuronal oscillations are generated by intrinsic mechanisms of individual neurons (via the self-generated (pacemaker) ionic currents or resonant properties of the membrane potential[5] and/or by the internal recurrent network interactions (Buzsaki, 2006; Wang, 2010). While irregular, or stochastic activity is predominantly displayed in individual neurons (Wang, 2010) the interplay of both intrinsic and network mechanisms collectively generates rhythmic patterns of subthreshold and suprathreshold (spikes) potentials (Llinas et al., 1991; Steriade et al., 1990). The firing patterns or spike trains generated in such oscillatory networks are considered fundamental for information coding in the brain (Buzsáki and Draguhn, 2004; Schnitzler and Gross, 2005). Rhythmic firing patterns activate post-synaptic neurons, generating post-synaptic potentials (excitatory and inhibitory post-synaptic subthreshold potentials; EPSPs and IPSPs, respectively) which, when sufficiently summated and synchronized, give rise to oscillations of local gradients of electric potential in the extracellular space, known as local field potentials (LFPs) (Niedermeyer and Da Silva, 2005; Schnitzler and Gross, 2005).

At the level of a local neuronal assembly, oscillatory activity in groups of neurons generally arises from feedback (re-entrant) synaptic connections between the excitatory principal neurons, e.g., pyramidal neurons, input-driven by different sources, and inhibitory interneurons. The mutual feedback results in synchronisation via a collective periodic modulation of membrane excitability, and therefore of the firing probability or sub-threshold oscillations of target neurons. The inhibitory system affects a wide target neuronal pool of excitatory neurons, imposing upon them narrow time windows in which they can fire, which is especially relevant for the generation

[5] An intrinsic membrane potential pacemaker is typically based on a biphasic dynamics of depolarising and hyperpolarising ionic currents mediated by various transmembrane channels. Some neurons are not oscillators, but may have resonant membrane properties that increase their responsiveness to a specific frequency of stimulation (Alonso and Llinás, 1989; Hu et al., 2002; Hutcheon and Yarom, 2000).

of synchronous local gamma oscillations (Cardin et al., 2009; Fries, 2009; Whittington et al., 2011). On the other hand, ultra fast gamma (100-200Hz) oscillations are presumably generated via inhibitory interneuronal networks by themselves (Wang, 2010).

The local assemblies interact with the larger-scale feedback loops (Canolty and Knight, 2010; Donner and Siegel, 2011; Varela et al., 2001). Here, synchronous activity arises from excitatory-excitatory and excitatory-inhibitory feedback loops between distant brain regions, involving cortico-cortical, thalamo-cortical, cortico-subcortical, or cortico-hippocampal connections (Bollimunta et al., 2011; Buzsaki, 2006; Steriade, 2000). The frequency of oscillations is dependent on intrinsic neuronal characteristics, network size and connectivity, and information flow variables, such as coupling strength and time delay (Cardin et al., 2009; Nunez and Srinivasan, 2006; Zeitler et al., 2009). Theta rhythm, for example, originates from cortico-hippocampal loops or as a pacemaker drive within the hipocampus (Buzsaki, 2006; Goutagny et al., 2009; Miller, 1991; Wang, 2010). Alpha rhythms classically originate from thalamo-cortical loops, where they are modulated by intrinsic thalamic mechanisms, but they may also be autonomously established in the visual cortex circuits themselves (Lopes da Silva and Storm van Leeuwen, 1977; Steriade et al., 1990). The neuronal oscillators that generate the beta rhythm are presumably located in the cortex and operate via excitatory-inhibitory feedback similar to that of gamma oscillations, although beta typically operates over a longer range (Hipp et al., 2011; Lopes da Silva, 1991; Wang, 2010).

Technically, two oscillatory signals are considered coherent (synchronised/phase-locked/phase-coupled) when there is a consistent relationship between the phases (phase coherence) and/or power (spectral coherence) of the two signals over time (Fell and Axmacher, 2011; Lachaux et al., 1999; Rappelsberger and Petsche, 1988; Senkowski et al., 2008), albeit not necessarily with a zero phase difference (zero lag) between them[6]. Coherence may refer to correlations between the spikes in different regions, between spikes in one region and LFP in the same or another region ("spike-field coherence") (Fries et al., 2001; Jutras et al., 2009; Womelsdorf et al., 2007) or between LFPs in different regions (Fell and Axmacher, 2011; Fries, 2005; Varela et al., 2001). Cross-frequency coupling of the phase or amplitude is also a common mode of neuronal

[6] The phenomenon of zero-lag despite conduction delays between distant neurons represents a specific challenge for neuroscience. Although several mechanisms have been proposed, there is as yet no general consensus regarding its explanation (see Uhlhaas et al., 2009 for a discussion).

synchronisation and gives rise to nested functional interactions of slow and fast rhythms (Axmacher et al., 2010; Canolty and Knight, 2010; Lisman, 2010; Roopun et al., 2008).

Various external and intrinsic contexts can trigger and modulate oscillatory patterns, e.g., periodic external stimuli (typically, light flashes or sounds), task- or event-related[7] non-periodic sensory or cognitive stimulation, or motor preparation and output. The oscillatory signal is phase-locked if there exists a stable phase relationship with an external event (stimulus onset) or other signal. Phase resetting refers to a shift in the phase of an ongoing oscillation, which can lead to phase-locking to the stimulus or it can modulate the phase coherence level with respect to other oscillatory signals (Jensen and Lisman, 1998; Kahana, 2006; Klimesch et al., 2007; McCartney et al., 2004; Rizzuto et al., 2003; Senkowski et al., 2008; Tass, 2007; Varela et al., 2001). Brief durations of phase resetting are typically followed by relatively longer periods of phase stability in a range from tens to hundreds of milliseconds, giving rise to multistable spatio-temporal patterns of neuronal activity with rapidly alternating periods between coherent and incoherent states (Breakspear et al., 2004; Fell et al., 2001; Freeman and Rogers, 2003; Friston, 2000; Rodriguez et al., 1999; Roelfsema et al., 1997; Thatcher et al., 2009).

On the other hand, synchronisation can arise spontaneously by interacting of signals from internal sources corresponding to some self-generated cognitive action (Başar, 1999; Başar et al., 1999) or even in the absence of any obvious task (the "resting-state activity"[8]). When signal processing of the external world input is inhibited, such as in sleep, this is subserved by large-scale synchronisation of low-frequency oscillations (Steriade, 2000). Thus the basic patterns of oscillatory synchrony are very much state-dependent (Fries et al., 2001; Palanca and DeAngelis, 2005; Thiele and Stoner, 2003; Van Der Togt et al., 2006). Ongoing oscillations in turn affect neuronal processing of subsequent external stimulus perception and other behavioural or mental events (Busch et al., 2009; Haider et al., 2007). For example, ongoing activity in the alpha rhythm

[7] "Induced" and "evoked" activity (Başar, 1999; Başar et al., 2001; Niedermeyer and Da Silva, 2005); for example, induced gamma oscillations may increase during object representation (Tallon-Baudry and Bertrand, 1999). Event-related synchronisation and desynchronisation are frequency-specific oscillatory activity responses with highly specific functional roles (Başar et al., 1999; Pfurtscheller and Lopes da Silva, 1999), non-phase-locked to events, as opposed to event-related potentials.

[8] Baseline ongoing 1-80 Hz electrophysiological oscillations and slow (<0.1 Hz) fluctuations of functional imaging signals mediated by the brain intrinsic "default networks", which can not be considered as mere noise, but reflect certain self-referential and other inner (mental and emotional) states (Cabral et al., 2011; Fox and Raichle, 2007; Freyer et al., 2009; Mantini et al., 2007).

in visual areas at rest could be a reflection of an "idling rhythm", enabling the brain to react more quickly to unexpected novel stimuli (Hari and Salmelin, 1997).

Whereas phasic oscillatory patterns are transient and usually correlate with volitional task- or event-related cognitive performance, tonic neuronal oscillations are slower, less volition-dependent and more related to global brain states such as fatigue, distress, neurological disorders, circadian rhythms, arousal, etc. (Canolty et al., 2006; Haider and McCormick, 2009; Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller et al., 1996; Sirota et al., 2008). For example during slow-wave sleep, tonic responses result from spontaneous background activity mediated by dense local connectivity patterns from which slow oscillations (< 1 Hz) emerge (Chen and Fetz, 2005; Poulet and Petersen, 2008; Steriade et al., 1993b).

The spatio-temporally integrated oscillations, which comprise both phase-locked and non-phase-locked (i.e., intrinsic or induced) oscillatory components, exhibit changes in their amplitude and power spectra that depend on both neuronal number and synchronisation level. Globally summated signals give rise to macroscopic brain rhythms, categorised into distinct frequency bands: delta (1–3 Hz), theta (4–7 Hz), alpha (8–13 Hz), beta (14–30 Hz), gamma (30–80 Hz), fast (80–200 Hz), and ultra fast (200–600 Hz) (Schnitzler and Gross, 2005), each with specific functional and behavioural correlates, activating contexts, mechanisms, spatial scales, and inter-relations (Niedermeyer and Da Silva, 2005; Nunez and Srinivasan, 2006; Whittington et al., 2000). Generally, higher frequency oscillations operate more locally and are thought to represent the neuronal code for cognitive content, whereas large networks are integrated during slow oscillations, which predominantly mediate processual aspects of cognition, collectively resulting in highly interdependent and parallel information processing at multiple spatio-temporal scales (Buzsáki and Draguhn, 2004; Jensen and Lisman, 2005).

2.1.2 Modulation of neuronal oscillations

Neuronal oscillations are primarily mediated by chemical synapses, where GABA is the most important neurotransmitter in inhibitory systems, whereas excitatory synapses use mainly glutamate and acetylcholine. Different neuromodulatory systems via ascending projections from deep brain nuclei can additionally regulate the neurotransmitter levels (e.g. norepinephrine, acetylcholine, serotonin or dopamine) thereby modulating oscillations on a slower time scale. The neuromodulators typically influence the global state of arousal, e.g., wakefulness, sleep, and finely tune distinct cognitive functions by modulating different brain waves (Berridge and

Waterhouse, 2003; Goard and Dan, 2009; Montague et al., 2004; Rodriguez et al., 2004; Steriade, 2000). For example, acetylcholine concentration increases in attentive states and has been shown to play a crucial role in affecting oscillatory synchronisation patterns in the gamma band (Rodriguez et al., 2004).

Electrical synapses, gap junction mediated neuronal connections, which predominantly couple type-specific interneuronal networks in the cortex, also actively contribute to electrotonic neuronal synchronisation (Connors and Long, 2004; Hormuzdi et al., 2004; Wang et al., 2010). The mechanisms of their regulation are still poorly understood, but their main advantages are their rapidity and bidirectionality of signal transfer, which makes them very suitable for synchronising the sub- and suprathreshold activity of neurons (Bartos et al., 2007; Bennett and Zukin, 2004; Hestrin and Galarreta, 2005). Apart from their role in electrically coupling the neurons, they also participate in transmission of chemical signals (Connors, 2009; Wang et al., 2010).

Neuronal synchronisation, however, is not modulated exclusively by the neurons themselves. Approximately half of human brain tissue volume is composed of astrocytes, a type of glial cell that globally connect different brain regions, whose active role in brain information processing has only recently been fully recognised. Astrocytes comprise a brain-wide astro-glial network coupled via the gap junctions (Giaume et al., 2010). As excitable cells with neurotransmitter receptors, capable of releasing their own chemical messengers, gliotransmitters, they cooperate with both pre- and post-synaptic neurons in a recently proposed novel functional unit, the tripartite glutamatergic synapse (Araque et al., 1999).

Intracellular calcium waves represent a a prominent feature of astrocytes' excitability. They are initiated in astrocytic processes of individual astrocytes, but may under proper synaptic input, as imposed and sustained by the synchronous neuronal oscillations, elicit intercellular waves, spreading coherently throughout the astro-glial network (Pereira and Furlan, 2009). Importantly, feedback from active astrocytes can in turn modulate not only synaptic plasticity, but also the dynamic properties of high-frequency neuronal oscillations, and they thus contribute to EEG signals (see a review by Pereira and Furlan, 2010 and references within). There is a strong indication that coherent calcium waves are frequency and amplitude modulated, which implies their capability of encoding information (De Pittà et al., 2009; De Pittà et al., 2008). In a model

by Pereira and Furlan (2010)[9], it is hypothesised that their modulatory potential is utilised for integration of neuronal signals based on wave interference patterns, which implies a long-range (field-like) interaction. The authors further suggest that some macroscopic coherent process might be required for such complex integration which, in addition to chemical signals from tripartite synapses, likely incorporates ephaptic (see below) signals from endogenous EM fields as well (Banaclocha, 2007; Pereira and Furlan, 2010).

The recent research on external brain stimulations by trans-cranial magnetic stimulation (Thut and Pascual-Leone, 2010a; b; Thut et al., 2011), transcranial electric stimulation (Kirov et al., 2009; Marshall et al., 2006) and stimulation by weak EM fields (Bawin et al., 1996; Deans et al., 2007; Ozen et al., 2010) has shown that neuronal oscillations can also be modified by these externally induced rhythmic stimulations, which latter also affect cognitive and behavioural responses. EM field-mediated interactions between juxtaposed neurons have been demonstrated in the cortex even at very weak naturalistic EM stimulation, affecting the APs, PSPs and spike-field correlations only indirecty, because electric fields caused very small (below stochastic fluctuation) changes in the membrane potential of individual neurons (Anastassiou et al., 2010; Anastassiou et al., 2011; Aur et al., 2010; Fröhlich and McCormick, 2010; Ozen et al., 2010). For example, intra- and extracellular recordings in the rat brain *in vivo* showed that both spiking and subthreshold activity were under the combined influence of forced fields and network activity, where an imposed voltage gradient as low as 1 mV/mm at the recording sites was sufficient to phase-bias neuronal spiking (Ozen et al., 2010) – direct evidence of a feedback loop between neuronal activity and endogenous electric fields. Such EM field-mediated neuronal interaction is also known as "ephaptic" coupling.

The early studies of Adey and others (Adey, 1975; Adey, 1981; 1993) corroborated that externally applied weak (non-thermal) EM fields may exert significant biological effects and influence behavioural responses in the nervous system (Adey, 2003; Bawin et al., 1996; Gavalas-Medici and Day-Magdaleno, 1976; Gavalas et al., 1970). The hypothesised mechanisms of these effects focussed upon modulations of the membrane proteins and ionic flows, calcium signalling, free radicals, charged molecules in the extracellular space, etc. (Adey, 1981; 2003; Blackman et al.,

[9] Interestingly, this model predicts that intracellular calcium waves disperse along the microtubules. The conductive properties of cytoskeletal filaments and functional potential are further discussed in Sections 3.2.2 and 3.5.2, respectively.

1985; Blackman et al., 1982)[10], by asserting that sensitivity to weak low-frequency EM fields could be a generic property of cells and tissues serving for intrinsic communication and amplification of weak initial triggers (Adey, 1981; 1993). The suggested concept was that the threshold sensitivity of excitable tissues to EM fields is mediated by highly cooperative properties of a population of elements, arising from the non-linear electrodynamic properties of biological tissues and resonant responses, rather than by a single detector (Adey, 1992; 1998; 2003).

Both lines of research together suggest that weak EM fields can modulate macroscopic oscillations at the network level, and may thus influence oscillations that generated them in the first place, giving rise to emergent properties of synchronous oscillations that could not be simply deconstructed to the contributions of single components (Fröhlich and McCormick, 2010). This brings a new perspective to the possibility that not only external, but also endogenous EM fields could contribute to information processing in the brain by non-synaptic mechanisms (Anastassiou et al., 2011; Fröhlich and McCormick, 2010; Ozen et al., 2010). Some researchers even suggest that fluctuating ionic gradients and the resultant patterns of EM fields, in combination with neuronal synchronisation as a "binding agent", could represent the substrate of cognitive representation and consciousness (Cook, 2008; McFadden, 2002).

We may expect that significant ephaptic effects *in vivo* indeed require synchronous neuronal activity and a precise spatial arrangement of many neighbouring neurons (Connors, 2009). Nonetheless, the mechanisms of network entrainment by weak EM fields remain unclear. As pointed out, the emergent properties of neuronal networks as a whole are clearly more sensitive than the measurable effects of EM fields in single neurons, which were safely below normal membrane noise (Deans et al., 2007). It is possible that the network dynamics can change due to a direct effect on membrane potential fluctuations by a stochastic process, or alternatively, via highly cooperative dynamics originating at the subcellular level that could collectively amplify the effects of an EM field, as anticipated by Adey and here further elaborated. This may be yet another reason to examine more closely the functional connection of neuronal synchronisation and various endogenous electrodynamic processes.

[10] The full spectrum of EM interactions with biological structures has been extensively reviewed elsewhere (Cifra et al., 2011; Funk et al., 2009).

2.1.3 Methods for analysing synchronised oscillations

Electro-magnetic activity in the brain can be measured as the summed LFPs across a large brain area with the millisecond-range temporal resolution of electroencephalography (EEG), electrocorticography (ECoG) and magnetoencephalography (MEG), all capable of monitoring the high speed of of cognitive processing. To obtain a better spatial resolution, single- or multi-unit microelectrode recordings can be applied extracellularly (measuring LFPs confined to small areas and thus with a better spatial precision) or intracellularly, where individual spikes can be measured; combinations of different techniques, each having its own advantages, are frequently applied (Buzsaki, 2006; Niedermeyer and Da Silva, 2005).

Combinations of stimulation, lesion techniques and classical electrophysiological recording methods seem promising for more precise and conclusive monitoring and evaluation of cortical network dynamics. Interestingly, with the recent optogenetic approach it now became possible to selectively depolarise or hyperpolarise selected neurons with the application of light and observe their functional roles with high spatio-temporal resolution, which also provides better causality measures (Boyden et al., 2005; Cardin et al., 2009; Zhang et al., 2010). Using specific deep brain stimulation it is now possible to interfere with an ongoing activity in such a way that a focussed oscillatory phase reset could be produced that leads to inter-regional desynchronisation, which enables us to infer the functional role of synchrony, and to observe the outcome of specific synaptic connectivity degradation over time due to disturbance of synchrony (Hauptmann et al., 2009; Hauptmann and Tass, 2009; Tass et al., 2009).

Analytical methods employing complex mathematical and statistical procedures for analysing oscillations have however provided major progress in understanding their complexity by revealing the much more dynamic nature of (de)coupling between particular neurons or assemblies. The higher spatio-temporal precision relating neuronal oscillatory correlates to specific brain functions, and the additional minimisation of possible physical artifacts or statistical biases provided further evidence that synchronisation indeed regulates various cognitive processes and is not merely an epiphenomenon or a reflection. Some of these newer methods are: instantaneous coherence (Schack and Krause, 1995) and event-related coherence (ERCoh) (Andrew and Pfurtscheller, 1996), which allow a high temporal and frequency resolution; dynamic topographic analysis and other methods that employ Hilbert transform to visualise rapid bursts of desynchronisation and phase reset (e.g., Breakspear et al., 2004; Freeman and Rogers, 2003; Thatcher et al., 2009); methods that enable assessment of direction of

information transmission, like partial directed coherence (Astolfi et al., 2006) and directed transfer function (Babiloni et al., 2005); the unitary event analysis, which employs complex statistics (Pipa et al., 2007; Pipa et al., 2008) and can detect individual events of coincidence firing; spike-field coherence (Fries et al., 2002), which estimates consistent phase relations between the discharges of individual neurons and LFP oscillations; and pairwise phase consistency (Vinck et al., 2010b), which computes how similar the relative phase observed in one trial is to the relative phase observed in another trial, suitable for measuring rhythmic synchronization for both EEG–EEG, MEG–MEG, spike–LFP, and spike–spike pairs.

2.2 Functional roles in basic cognitive functions

In recent years it has become increasingly clear that neuronal oscillatory coherence correlates with all basic cognitive functions. Coherence mediates not only coupling of distinct brain regions involved in the same function, but also cooperation between different ongoing cognitive processes in different regions, from which unified mental constructs and goal-oriented meaningful behaviour emerge (Başar, 2006; Başar et al., 2001).

2.2.1 Perception/representation and the binding problem

In a pivotal study, Gray and co-workers (1989) provided strong evidence that highly synchronised spike discharges in the 40-60 Hz gamma frequency range of neurons in the primary visual cortex of anaesthetized cats could serve as a tag for relatedness of different features in a visual field, represented by the selective responses of different neurons or groups of neurons separated in space, thus binding them together into a coherent percept (the dilemma of how the functional coupling is achieved is known as the binding problem). This temporal binding hypothesis, or binding by synchrony[11] (Crick and Koch, 1990a; Eckhorn, 1994; Engel and Singer, 2001; Singer and Gray, 1995; von der Malsburg, 1995; von der Malsburg and Buhmann, 1992) took centre stage in systems neuroscience and has since expanded to include many other cognitive functions. In addition to visual cortex, stimulus induced coherence in the gamma frequency range has been described in other primary neocortical areas, for example in auditory (Brosch et al., 2002) and somatosensory (Bauer et al., 2006) cortices. Odours elicit global oscillatory activity of 20–30 Hz

[11] Critics of this theory argue that oscillatory synchrony cannot explain the organism's ability to identify objects and that spike synchrony could instead provide the relevant information about the stimulus (Jermakowicz and Casagrande, 2007), or that synchrony itself could not be a general mechanism of feature binding because it is too weak (Palanca and DeAngelis, 2005) or due to large trial- to trial spike timing variability (Shadlen and Movshon, 1999).

in the insect olfactory antennal lobe, which routes olfactory information to higher areas in the insect brain, as disruption of the synchrony impairs olfactory discrimination (Sivan and Kopell, 2004; Stopfer et al., 1997).

Alongside unimodal processing via neuronal coherence, evidence based on diverse experimental paradigms is emerging that synchronised oscillations within different unimodal regions may synchronize among themselves as well as with higher-order regions to foster multisensory integration and processing. Gamma power and coherence is generally greater when the multisensory inputs are perceptually or semantically congruent (Bauer, 2008; Senkowski et al., 2008). A recent study on humans, which enabled imaging synchronised networks across the entire human brain, has indeed revealed multiple large-scale brain regions that are selectively (depending on individual perception characteristics) synchronised at beta and gamma frequency bands in response to ambiguous audiovisual input (Hipp et al., 2011).

2.2.2 Motor activity and sensori-motor integration

At the simplest level, synchronised firing of neurons drives periodic motor signals for rhythmic movements in a special type of pacemaker network, called the central pattern generator, which is located in the spinal cord and coordinates automatic modes for locomotion, breathing, swallowing, etc. (Marder and Bucher, 2001) and operates in the absence of sensoric feedback, but can be modulated by it and by neuromodulation (Hooper, 2000; 2004; Kiehn, 2006). During voluntary movements, execution of complex action depends on the coordinated action of multiple motor and non-motor cortical areas (Rizzolatti and Luppino, 2001; Roland and Zilles, 1996). Synchronised oscillations function as integrators between such neuronal networks, as measured during spontaneous movements and during bimanual motor learning (Andres and Gerloff, 1999; 1999; Gerloff et al., 1998; Pfurtscheller and Andrew, 1999). Interestingly, oscillations spread like a travelling wave across the motor cortex, reflecting information transfer (Rubino et al., 2006). There also seems to be a direct correlation between physical parameters of specific movements, such as force generation and the patterns of oscillations (Logar et al., 2008b; 2008c).

In sensory-motor integration, beta-rhythm oscillations become (de)synchronised over a larger scale when motor control, attention or “status quo” maintenance is required (Andrew and Pfurtscheller, 1996; 1999; Engel and Fries, 2010; Kristeva-Feige et al., 2002; Neuper et al., 2006; Pfurtscheller et al., 2003). Theta rhythm and gamma synchrony also seem to be involved in sensori-motor integration and movement preparation (Aoki et al., 1999; Caplan et al., 2003). Such

coupling seems logical, as for any goal-directed, purposeful movement or action, the brain has to develop a strategy, a motor program. For this purpose, premotor and supplementary motor areas (SMA) cooperate with posterior sensory areas and with the primary motor area (Krakauer and Ghez, 2000). In visuomotor control, EEG-coherence increases between visual and motor areas in tasks which require visuomotor integration, in accordance with the concept of synchronisation as a neuronal correlate of increased functional connectivity (Brežan et al., 2007; Classen et al., 1998; Fries, 2005; Roelfsema et al., 1997).

Interestingly, cortico-spinal and cortico-muscular coherence was measured during movement and has direct functional consequences, as elucidated by using the combination of MEG/EEG- EMG (Baker et al., 1997; Mima and Hallett, 1999; Salenius et al., 1997; van Elswijk et al., 2010). It represents another argument for strong direct coding of brain functions by oscillations, also influencing the transfer of relevant signals to the peripheral targets.

2.2.3 Attention

Complex information that is represented at higher stages of processing influences simpler processes occurring at preceding stages. The function of any area of the cortex is subject to such a top-down influence of attention, which is dynamically established during ongoing processing (Gilbert and Sigman, 2007). Attentional mechanisms help select the behaviourally relevant stimulus by restructuring cortical activity to sensory inputs, amplifying the influence of neuronal groups conveying behaviourally relevant information, while attenuating the irrelevant ones.

Studies on monkeys and humans generally show that attended uni-or multisensory stimulus triggers stronger oscillatory responses than unattended stimulus, typically in the gamma frequency band (Jensen et al., 2007; Senkowski et al., 2008; Womelsdorf and Fries, 2007; Womelsdorf et al., 2007). The strength of synchronisation, depending on whether it is induced by an attended or unattended stimulus, has been shown to be able to predict the speed of learned behavioural response, thus having a direct functional relevance for attention (Womelsdorf et al., 2006). It was suggested that biased competition, a hypothetical mechanism for selective attention based on competition between different stimuli corresponding to different neuronal assemblies, and which feed-forwards only the behaviourally relevant ones while suppressing the non-relevant ones (Desimone and Duncan, 1995), operates through enhanced gamma-band synchronisation by ensuring an exclusive communication link between the selected and the higher-order neurons

(Fries, 2009). Thus, selective neuronal interactions mediated by synchronisation may underlay selective attention.

2.2.4 Memory

Learning and memory are closely related to attention. Working memory, defined as the capacity to retain and manipulate information that is no longer accessible in the environment (Baddeley, 1992) is based on sustained neuronal activity – the persistent firing of "delay-period" neurons (Funahashi, 2006; Fuster, 2008; Fuster and Alexander, 1971; Goldman-Rakic, 1995) and cooperation among many cortical and subcortical areas (Carpenter et al., 2000; d'Esposito et al., 1998; Veltman et al., 2003). Evidence shows that this persistent firing has an oscillatory character with frequencies in theta and gamma bands, and that firing of individual cells tends to occur at a particular phase of theta oscillation (phase locking) (Lisman, 2010; Rutishauser et al., 2010). Several studies have measured increased theta synchronisation between prefrontal and temporal/parietal cortices during encoding and retrieval, or maintenance of information in working memory (Benchenane et al., 2010; Sederberg et al., 2003). Sustained synchrony enhancement in the beta and gamma frequency bands, as well as phase-locking of higher-frequency (beta, gamma) oscillations to theta oscillations, has also been observed during maintenance of working memory (Fell and Axmacher, 2011; Lisman and Buzsáki, 2008; Sauseng et al., 2010). It was recently confirmed that the strength of coherence could predict memory load and individual working memory capacity, strongly pointing to a causal role of oscillations (Palva et al., 2010).

In a very illustrative model of working memory (Jensen and Lisman, 1998; 2005; Lisman and Idiart, 1995) it is proposed that theta and gamma oscillations interact to form a neuronal code for multiple ensembles to represent an ordered sequence of different memory items in sequentially "nested" gamma cycles at different phases within each theta cycle (each theta contains about 7 gamma cycles, corresponding to a well-known working memory limited capacity buffer) (Sternberg, 1966). The neuronal ensemble was defined as a group of active cells with distinct spatial connectivity pattern, firing within a given temporal window in the gamma band, that represents a particular cognitive construct. Such gamma-coded constructs are temporally offset via afterdepolarisation phenomena at a cell/ensemble level, which causes the same cells to fire again after a delay, sequentially in different gamma cycles. Theta serves as an external drive that resets the start of each serial memory scanning operation during recall after the probe

presentation, comparing the probe stimulus to a stored sequence, to provide the temporal frame for maintenance of working memory.

For learning, working or short-term memory must be transferred into long-term memory and neuronal synchronisation plays a role in memory consolidation by modifying synaptic strengths (Section 2.3.3). Human studies show enhanced long-range coherence from delta to gamma frequency range between anterior and posterior brain regions during encoding into, or retrieval from, declarative memory of visually presented objects (Fell and Axmacher, 2011; Jensen et al., 2007). Hippocampus is crucial for the formation of declarative as well as nondeclarative long-term memory – both correlating with an increased synchronisation in broad frequency ranges within the hippocampus and related structures. As the hippocampus has recently been demonstrated to support working memory as well, it is hypothesised that it coordinates the flow of information between both types of memory (Fell and Axmacher, 2011). Cross-frequency synchronisation, especially between the gamma and theta bands also increases, and is thought to support cooperation of both rhythms in the transfer of information maintained in working memory into long-term memory (Canolty et al., 2006; Fell and Axmacher, 2011; Jutras and Buffalo, 2010; Sirota et al., 2008).

2.2.5 Consciousness

Finally, consciousness has been related with neuronal synchrony (Crick and Koch, 1990b; Tononi and Koch, 2008; Uhlhaas et al., 2009). Transient global enhancement of gamma synchrony between occipital, parietal and frontal cortices across the hemispheres has been detected for perceived stimuli, but not for non-perceived, in a human study using brief presentations of words (Melloni et al., 2007). According to the authors, the observed large-scale synchronisation triggers (reflects) a cascade of processes, such as perceptual stabilization, maintenance of working memory, and anticipatory attention, which are plausibly related with perceptual awareness. As consciousness enables access to phenomenal awareness, or subjective experiencing, another paradigm to study correlations between consciousness and neuronal synchrony is the use of physically identical stimuli that lead to different subjective interpretations across trials. Several experiments on humans with various multisensory illusions indeed demonstrate significant changes in gamma synchrony with respect to perceived (illusory or nonillusory) stimuli (Senkowski et al., 2008).

Consciousness might also be studied indirectly, by means of observing and comparing states with lack of consciousness, such as coma, anesthesia or sleep. During sleep, slow thalamocortical oscillations prevail, as arousal brainstem systems remain silent. Different sleep stages are highly distinct in their oscillatory patterns, regulated by specific circuit and intrinsic mechanisms, both modulated by different neuromodulatory effects (Bazhenov et al., 2002; Niedermeyer and Da Silva, 2005; Steriade et al., 1993a). The slow global sleep oscillations may however have an active role: besides reflecting a functional inhibition of sensory input processing via thalamic mechanisms, shutting down the consiousness, they may support memory consolidation by synchronizing thalamo-cortical spindles and hippocampal sharp wave-ripples, regulating transfer of re-activated memories between hippocampus and neocortex, where long-term memory is finally stored (Diekelmann and Born, 2010; Steriade and Timofeev, 2003).

2.2.6 Decision making and reward

Decision making on choice alternatives involves defining goals based on preferences/reward and the prediction of expected outcomes, followed by goal-directed actions based on information accumulation, and finally selecting the alternative that is most valuable to us (Pesaran et al., 2008; Wang, 2008). At the neuronal level, decision processes might depend on neuronal recurrent positive and negative feedback circuits, where strong excitation generates multiple self-sustained stable states of neural populations (attractors) from which categorical choice evolves (Heinzle et al., 2007; Wang, 2008). In “decision neurons”, long ramping of individual neural activity over time is primarily correlated with specific decision choice, includes integration of sensory evidence over time, and ends with a winner-take-all competition (Donner et al., 2009; Gold and Shadlen, 2007; Scherberger and Andersen, 2007; Wong and Wang, 2006). Decision choice is made at a certain firing rate threshold of neurons selective for that choice response, displaying the stochastic, highly irregular neuronal spiking inherent to neuronal networks. Thus, the source of variability in decisions may not be in the sensory stimuli alone, but also in the neuronal system itself (Brunel and Wang, 2001; Wang, 2008).

Decisions are importantly modulated by value signals, such as reward, loss, or risk. Coherent interactions within and between such reward pathways and higher decision making centers in the brain (prefrontal cortex, orbitofrontal cortex, lateral intraparietal area, cortico-striatal loops etc.) could enable parallel processes, such as reward expectation, action value, prediction error and decision choice to communicate between one another and with other relevant contexts (e.g. memory) in reciprocal loops (Fuster, 2008; Miller and Cohen, 2001; Rushworth and Behrens,

2008; Wang, 2008). For example, decision making aspects and its performance correlated with the power of theta oscillations within many different brain regions, with interareal theta coherence (Benchenane et al., 2010; Sederberg et al., 2003; Womelsdorf et al., 2010) and with phase-locking of higher-frequency (beta, gamma) oscillations to theta oscillations (Sauseng et al., 2010). Selective theta synchronisation could reflect selective communication of top-down and bottom-up information (Engel et al., 2001; Womelsdorf and Fries, 2007; Womelsdorf et al., 2007) and may underlie the retrieval of choice-relevant information around decision points (van Wingerden et al., 2010; Womelsdorf et al., 2010). Choice-predictive beta-band oscillations may also reflect decision related processes within and among visual, frontoparietal and motor cortices (Decharms and Zador, 2000; Donner et al., 2009; Engel and Fries, 2010; Wang, 2002), whereas gamma-band synchronisation via attentional networks may mediate attentional selection of the behaviourally relevant visual input (Siegel et al., 2011).

2.2.7 Neurologic and psychiatric pathology

Tremor, epilepsy, schizophrenia, Parkinson disease, dementias, depression and autism, among others, have been strongly connected to dysfunctional neuronal connectivity. Different measures of synchrony were found to be aberrant (Herrmann and Demiralp, 2005; Uhlhaas and Singer, 2010), suggesting a possible explanation of various symptoms. Besides correlations, different focussed therapeutical interventions (e.g., transcranial magnetic stimulation, deep brain stimulation, drugs) may improve symptoms by inducing direct changes to specific, otherwise pathological, oscillatory patterns (Engel and Fries, 2010; Hardesty and Sackeim, 2007; Schnitzler and Gross, 2005; Thut and Pascual-Leone, 2010b; Timmermann et al., 2007). The details are beyond the scope of this article, but it is clear that this line of investigation provides an additional argument for the causal role of synchronised oscillations in functional brain processing.

2.2.8 Synchrony and technology applications: brain-computer interfaces and "mind reading"

Neuronal oscillations can be exploited as a control/input signal for various brain- computer interfaces (BCI) (Andersen et al., 2010; Hatsopoulos and Donoghue, 2009; Kipke et al., 2008; Pfurtscheller et al., 2000). Using different decoding approaches, BCI allows users to control an external device, e.g., by learning to self-change one's own amplitude of oscillatory activity in specific frequency bands (e.g., beta rhythms) at specific regions (a type of neurofeedback learning). For example, beta is inhibited by motor imagery (De Lange et al., 2008), which is exploited in such designs (Bai et al., 2008). New decoding techniques may enable a more precise regulation of BCI by taking into account those oscillations that are naturalistically responsible for

coding a certain desired action and by recording with a more precise spatial resolution. On the other hand, similar methods have been used for the intent of "mind reading", for example to be able to decipher one's thoughts, feelings, perceptions, reveal memories, determine truth vs. lies or predict subjects' responses and choices in advance, without the need for subjective reports (Bles and Haynes, 2008; Haynes and Rees, 2006; Haynes et al., 2007).

2.3 Functional roles in information processing

As discussed above, neuronal synchrony clearly correlates with various cognitive processes, and could in some situations even predict behavioural outcome, which implies its functional significance. In recent years, much evidence has accumulated to firmly support its mechanistic role in information coding, neuronal communication and synaptic plasticity.

2.3.1 Information encoding and decoding by oscillatory phase (phase coding)

Information in the brain is thought to be carried by neuronal spikes (AP) and many aspects of firing patterns, e.g. average firing rate, occurrence of specific interspike intervals, bursts, or the degree to which different cells fire in coincidence (Eggermont, 1998; Engel et al., 1992; Lisman, 1997; Rieke et al., 1999) could potentially encode information and therefore represent the "neural code", as reflected by systematic variation of neuronal activity with respect to a behavioural variable. In oscillatory networks, where the timing of spikes is under the combined influence of external inputs and the internal dynamics of the network, the phase at which a neuron fires relative to an oscillatory cycle (LFP) also carries information (Buzsaki, 2006; Hopfield, 1995).

The first evidence for phase coding came from O'Keefe and Recce (1993) where theta phase precession (a gradual phase advance of spikes over time) in hippocampal "place cells" was observed as the rat walks through the receptive field of a recorded pyramidal cell, possibly representing cued 'prospective' recall of the coming positions from long-term memory, where theta provides an absolute phase reference (Jensen and Lisman, 2000; Lisman, 2005; Tsodyks et al., 1996). Specifically, theta and delta oscillations may enable phase coding and temporal segmentation, e.g. as indicated in the theta phase-locked spike output (Jacobs et al., 2007; Klausberger and Somogyi, 2008), conveying specific information beyond the firing rate (Hyman et al., 2010; Jensen and Lisman, 2000; Panzeri et al., 2010). On the other hand, gamma oscillations could mediate content decoding and representation by coupling specific spatial combinations of simultaneously active neurons (Jacobs et al., 2007; Jensen and Lisman, 2005).

Furthermore, the phase precession of spiking relative to depolarising peak of oscillations is a direct measure of input intensity, which enables transformation of rate coding into a temporal code of spike timing in target neuronal groups (Fries et al., 2007; Singer, 2007). As the coupling strength between the neurons reflects the level of depolarising input, it is proportional to the magnitude of phase advancement, which may also be exploited for short-term storage of information (Buzsáki and Draguhn, 2004).

Next, "encoder-decoder" networks in a phase-sensitive detector model (Jensen, 2001) allow different neuronal populations in different regions to integrate firing patterns, if in coherence, and transfer only specific information dependent on the adjustable phase of the common oscillatory drive input, because of excitability dependent on a depolarising peak phase of the cycle, which can be modulated independently in both regions by among others the theta pacemaker and phase shifting (Jensen and Lisman, 2005; Lisman, 2005).

The phase coding working memory theta-gamma model (Jensen, 2006; Jensen and Lisman, 1998; 2005) predicts that multiple memories held in short-term memory become active at different phases of theta oscillation, supported by evidence that theta oscillations emerge and synchronise in cortex during short-term memory tasks (Gevins et al., 1997; Jensen and Tesche, 2002; Raghavachari et al., 2001; Sarnthein et al., 1998; Sauseng et al., 2004) and that spiking occurs preferentially at a certain theta phase (Lisman and Buzsáki, 2008; Siapas et al., 2005). Interestingly, it was shown that it is possible to decode and predict different states of working memory based on "phase demodulation" processing of EEG signals (Logar et al., 2008a), which also points to a coding potential of the phase content in oscillatory networks.

The phase of theta oscillations also controls long-term potentiation (LTP) or long-term depression (LTD) of the synapse (Hölscher et al., 1997; Huerta and Lisman, 1993; Pavlides et al., 1988). Phase-coding may be used to separate the processes underlying long-term memory encoding and retrieval operating in distinct phases of the ongoing theta (Hasselmo et al., 2002; Judge and Hasselmo, 2004). Phase reset could be a mechanism of neuronal networks to reset their oscillations when they are recruited to process information, e.g. after memory-related stimulus probe (Givens, 1996; Rizzuto et al., 2003). In recognition memory, slow wave (4–12 Hz) phase reset entails serial scanning operations after probe onset (Jensen and Lisman, 1998).

All of the above considerations support a temporal coding hypothesis that may represent a possible general coding scheme in the brain, where oscillations serve as a temporal ordering frame for organising different processes in different phases of an ongoing rhythm (including future probabilities), and hence provide one of the answers as to why the brain oscillates (Buzsáki and Draguhn, 2004; Jensen, 2006; Judge and Hasselmo, 2004; Lisman, 2005). In such a framework, oscillatory synchronisation (coherence) can mediate the exchange of phase-coded information (Fries, 2005; Jensen, 2001; Jensen and Lisman, 2005; Lisman, 2005; Mizuhara and Yamaguchi, 2007; Varela et al., 2001; Womelsdorf et al., 2007).

2.3.2 Neuronal communication

In an attempt to generalise the binding by synchrony hypothesis into a wider theory of communication through coherence, Fries (2005) emphasized that the higher, top-down cognitive control over perception and behaviour – as manifested e.g. through selective attention, or any other fast and efficient cognitive processing – demands flexibility of communicational structure between the neurons that goes beyond the static anatomical connections, appearing fixed on the timescale of cognitive dynamics, and such effective communication could only be achieved through coherently oscillating neuronal assemblies[12]. Phase synchrony of oscillatory signals establishes high functional connectivity, because interacting neurons can exert a stronger impact on one another if they are depolarised at the same time (Fries, 2005; Womelsdorf et al., 2007). A study by Womelsdorf and co-workers (2007) gave a strong support to this theory with the finding that the strength of mutual influences among neuronal assemblies oscillating in the gamma frequency band is a direct consequence of the phase relations between them – the strongest interaction being exerted when in phase.

This finding has been supported at the cellular level. Coincidence-sensitive neurons predominantly discharge action potentials if simultaneously activated by multiple presynaptic neurons, defining a narrow time window for activation. Cortical neurons were found to have a dynamic firing threshold that depends on summation of transient depolarisations, enhancing fast and synchronous synaptic inputs, while suppressing slow (low slope) depolarisations (Azouz and

[12] In terms of graph-theoretical or network modelling, this is the difference between the functional connectivity that emerges from dynamic, moment-to-moment activity fluctuations of an integrated network as a whole – which supports much richer informational processing capabilities as well as being more responsive to perturbations – and structural, or anatomic connectivity (or the network topology) alone, which is primarily modulated by synaptic plasticity (Bullmore and Sporns, 2009).

Gray, 2003). Moreover, these synchronous inputs can then reliably transform into temporally precise output action potentials by initiating fast local dendritic spikes despite the background synaptic and dendritic noise, thus acting as coincidence detectors (Ariav et al., 2003). These studies suggest that, in addition to passive coincidence detection, which is classically considered to entail communication via synchrony, additional active mechanisms could substantially enhance feed-forwarding of synchronised assemblies. Taken together, neuronal input–output changes (e.g. gain modulation), regulated by transmission of synchronised activity could represent a fundamental neuronal mechanism for controlling behaviourally relevant stimuli (Azouz, 2005).

For functional communication between neuronal assemblies, interaction mechanisms must be selective, and hence there must be some general rules for such selectivity. As with all oscillating systems, information is encoded in the phase and the frequency of the oscillation. Because the mechanism of gamma oscillations itself entails frequency-dependent gain modulation, this will have immediate network consequences in the sense that interaction will be enhanced between those assemblies that receive strong input when their synaptic gain is maximum, and suppressed otherwise; the coupling itself will then proceed through the coincidence detection mechanism (Fries, 2009). Interactions could be further refined by the mechanism of phase shifting (Fries et al., 2007): the more excited neurons in a given assembly would fire earlier in an oscillation cycle and thus suppress the less excited ones due to the fast inhibitory system, consequently entraining the phase of an entire assembly and re-defining the phase relations with other assemblies. Recently, the phase shifting mechanism has been experimentally observed in monkey visual cortex (Vinck et al., 2010a). Long-distance functional communication has also been recently elucidated by a study that showed individual local spiking responses modulated by distant phases and LFP phase coupling between multiple regions, in such a way that their distinct patterns translate into corresponding changes in spike rate and correlate with specific functional involvement of a given neuron or a assembly (Canolty et al., 2010).

2.3.3 Neuronal plasticity

Synchronisation of neuronal firing already plays a role during brain development, promoting synaptogenesis and providing efficient anatomic connectivity patterns for later coding via synchrony (Jermakowicz and Casagrande, 2007; Volgushev et al., 1997). Changes in synaptic strength are collectively known as synaptic plasticity, which is considered a fundamental neuronal mechanism modulating neuronal connectivity and thus learning, memory and adaptive behaviour. Spike timing-dependent plasticity (STDP) means dependence of synaptic plasitcity on the

temporal order of pre- and postsynaptic spikes within a critical time delay window of tens of milliseconds. When a presynaptic spike precedes a postsynaptic spike within this time window, synapses undergo long term potentiation (LTP), and they undergo long term depression (LTD) if the situation is reversed (Dan and Poo, 2004; Markram et al., 1997). A diversity of critical time windows for different types of synapses has been discovered recently. Because STDP has been demonstrated on various types of neurons and synapses, and in different animal phyla, it is considered today a generalisation of Hebbian learning (Caporale and Dan, 2008). As mentioned above, correlative functions between neuronal synchrony and long-term memory are already firmly established. In a study by Wespatat and co-workers (2004) a direct link between gamma neuronal synchrony and STDP was established. It was demonstrated that synapses underwent long term potentiation when presynaptic discharges coincided with the peak of the postsynaptic membrane potential oscillations in the gamma band, and long term depression when coinciding with the trough.

Gamma synchronisation is considered optimal for modifying synaptic plasticity, because it focuses neuronal activity in sufficiently short time windows that coincide with the time windows of STDP (Fell and Axmacher, 2011). However, simple co-firing of presynaptic and postsynaptic neurons within too short time windows would not lead to a systematic STDP (Vinck et al., 2010a). Rather, STDP typically requires that the presynaptic neuron is either leading or lagging the postsynaptic neuron by a few milliseconds, and this might be achieved through the phase shifting mechanism.

To summarise the functional role of neuronal synchrony, neuronal communication and plasticity naturally support each other and coevolve via coherent oscillatory dynamics. Synchronisation between two communicating assemblies will generally enhance communication and strengthen their synaptic connections, whereas desynchronisation will lead to weakening. On the other hand, a pre-existing memory trace may enable a faster synchronisation, processing, and behavioural response (Fell and Axmacher, 2011; Fries, 2009; Singer, 2009; Womelsdorf et al., 2006).

3 TOWARDS THE LONG-RANGE MODES OF SUBNEURONAL INFORMATION PROCESSING

3.1 The need for a dynamic order in brain information processing

Neuronal synchronisation correlates with all basic cognitive processes. Its concomitant impairment in common neurological disorders, and its functional role in neuronal communication and plasticity, imply a generic function in brain information processing. For the same reason, it remains unclear how diverse cognitive functions could emerge from synchronised firing *in se*, as they would interfere among each other, should the relevant information be encoded exclusively on the basis of neuronal oscillations (Fell and Axmacher, 2011). Rather, oscillations in the first place represent the reference timeframe for neuronal communication (Axmacher et al., 2006) and the nervous system likely utilises specific context- and information type-dependent coding strategies (Jermakowicz and Casagrande, 2007), leaving the question of cognitive representation and the "hard" problem of subjective awareness, open to discussion (Cook, 2008; Engel et al., 1999; Koch, 2004; Llinás and Ribary, 2001).

At the processual level, an important issue concerns the problem of the dynamic spatio-temporal modulations of the synchronised oscillations to meet behavioural demands. For example, the basic mechanism of gamma cycle, which is most relevant for encoding representations, is well understood at the systems level in terms of rhythmic inhibition of excitatory neurons via the $GABA_A$ receptor-mediated inhibitory system of fast-spiking interneurons. Strong and fast inhibitory postsynaptic potentials, rapid signal transfer via electrical synapses, and shunting inhibition are important electrophysiological properties of the inhibitory system, responsible for establishing narrow time windows in which the excitatory neurons can generate action potentials (Bartos et al., 2007; Cardin et al., 2009). Realistic models of gamma synchronisation (Bartos et al., 2007; Vida et al., 2006) can successfully explain the robustness of oscillations even in the presence of heterogenous excitatory input, as is the case in cortical networks. Nonetheless, it remains unclear how the neurons undergo very transient episodes of synchrony in the range of tens of milliseconds, as well as the rapid switching between the coherent and incoherent states observed during different cognitive processes such as attention and perceptual awareness (Breakspear et al., 2004; Melloni et al., 2007; Taylor et al., 2005; Uhlhaas et al., 2009), and which in addition may extend orders of magnitude across the spatio-temporal domains in real cortical

networks (Freeman, 2003b; Freeman and Vitiello, 2006; Petermann et al., 2009; Van De Ville et al., 2010).

A partial explanation of how the brain could achieve such modulatory potential is via stochastic background activity. Individual cortical neurons generally exhibit highly irregular spiking, which contributes a large tonic and only a small sinusoidal component to the network dynamics, even when engaged in synchronous oscillations (Wang et al., 2010). Stochasticity is inherently generated by the circuit dynamics with balanced synaptic excitation and inhibition even in the absence of external stimuli (Barbieri and Brunel, 2008; Compte et al., 2003; Mattia and Del Giudice, 2004; Renart et al., 2007). It is conjectured that dynamic modulation of excitability through stochastic synaptic bombardment in highly recurrent local and distant networks causes an elevated level of depolarisation that can enhance neuronal responsiveness rapidly and in a multiplicative manner to a variety of inputs (Haider and McCormick, 2009). Balance between excitatory and inhibitory interactions, emerging from such dynamic activity is important for the rapid modulation of functional connectivity and sensitivity to synchronised synaptic inputs, even on a cycle-by-cycle basis (Atallah and Scanziani, 2009; Haider and McCormick, 2009). However, the predominantly stochastic fluctuations of membrane potentials would impose systematic problems to long-distance communication and information encoding based *exclusively* on the oscillatory information (Demir et al., 2000). Without proposing some higher-order organisation of brain activity, the specific information would quickly dissolve in synaptic noise, because stable oscillations are highly sensitive to phase perturbations, and more so the high-frequency oscillations (Wang, 2010), whereas precise and reliable phase relations are considered fundamental for meaningful (de)coding (Section 2.3.1). In sum, the complex balance between oscillatory robustness required for consistent coding and long-range communication, and the flexibility of functional connectivity, must be somehow reconciled for brain information processing to be meaningful.

A more integrative approach is to treat the stochastic background activity as a scale free dynamics that maintains itself close to criticality, as indicated by the power-law distribution ($1/f^{\alpha}$) of power spectral density of oscillations as a function of frequency (Freeman, 2005; 2009). Scale-invariant (fractal) avalanches of neuronal activity – a hallmark of self-organised criticality[13] (Bak et al.,

[13] A property of complex dynamic systems whereby the system spontaneously maintains itself at the critical border between ordered and chaotic dynamics, with no intrinsic time or length scale (Bak et al., 1988; Kauffman, 2008).

1988) – have been demonstrated in human and animal cortex, and they are considered an important factor allowing for the rapid transitions of cortical activity at multiple spatio-temporal scales (Freeman, 2005; Petermann et al., 2009; Stam and De Bruin, 2004; Thatcher et al., 2009; Van De Ville et al., 2010). Freeman (1990; 2000; 2003b; 2009) has shown that stochastic background activity reorganises in response to sensoric stimuli into distinct spatio-temporal structures (Section 3.5.1) of cortical activity in different sensory cortices, constrained by a macroscopic order parameter. The wave packet is considered a perceptual carrier, encoded *homogenously* by the (context-dependent) phase- and amplitude-modulated carrier oscillation throughout the whole spatio-temporal domain.

Freeman also observed that the state transitions of different wave packets between basins of attraction occur unusually rapidly, exhibiting a phase velocity that exceeds the group velocity of oscillations, which implies that some long-range neuronal interaction may be required for the transition, independent of synaptic transmission (Freeman et al., 2003; Freeman and Vitiello, 2006). We already mentioned that local neuronal assemblies can also interact by ephaptic (EM) coupling, which could provide very rapid communication between them and contribute to entrainment of neuronal oscillations (Section 2.1.2). In recent years, however, a variety of models of highly cooperative signal propagation and integration have emerged, revealing a potentially even richer level of information processing that may additionally reveal a dynamic order behind the complex spatio-temporal patterns of neuronal oscillations. We shall briefly review those models and then discuss how the cortical dynamics could be functionally modulated through coherent states at different organisational levels.

3.2 The emerging role of neuronal cytoskeleton

The classical role of the cytoskeleton, reduced to structural scaffold supporting cellular shape, growth, motility and the transport of molecular cargo, has been drastically expanded in the last decades. It is established that the cytoskeleton integrates converging signalling pathways, influences the gene expression, coordinates membrane receptors and ionic flows, and localizes many cytosolic enzymes and signalling molecules, while at the same time representing an immense catalytic surface for metabolic interactions (Bounoutas et al., 2011; Clegg, 1984; Gardiner et al., 2011; Ingber, 2003; Janmey, 1998; Shepherd, 2006). As the cytoskeletal filaments, most notably the microtubules (MTs) and actin filaments (AFs), are polyelectrolytes, they plausibly entail electrically non-trivial biological functions in addition to their structural-

mechanical role. Electrical properties of cytoskeletal elements have been the focus of theoretical and experimental research, and are hypothesised to be specifically important for neuronal information processing (Craddock et al., 2010; Jaeken, 2007; Lin and Cantiello, 1993; Priel et al., 2010; Woolf et al., 2009).

The neuronal cytoskeleton is particularly complex and well differentiated. It comprises an integrative intraneuronal network by binding to ion channels and neurotransmitter receptors, scaffolding proteins[14] and their adaptors, motor proteins, microtubule-associated proteins (MAPs), and other linking proteins (Sheng and Pak, 2000; Woolf et al., 2009). AFs and MTs form interconnected networks[15] extending from synaptic spines – where AFs link the ion channels and other postsynaptic proteins – to the MTs in dendritic shafts, which form a network continuum throughout the soma and the axon. Thus, the neuronal cytoskeleton, together with its interconnecting modulatory proteins, such as MAP2 and MAP tau, physically connects ion channels within synapses and synapses throughout the neuron into a structurally and functionally integrated system, or the intraneuronal matrix (Ingber, 2003; Woolf et al., 2009).

3.2.1 Role in neurotransmission and memory

It is increasingly clear that ion channels and receptors of common neurotransmitters and neuromodulators functionally interact with the intraneuronal matrix in a bidirectional way. The matrix functions as a downstream target of neurotransmitters predominantly through calcium signalling, which can modify the matrix stability directly, or via signal transduction pathways by modifying phosphorylation status of binding molecules (e.g., MAP2, CaMKII), which in turn affect its structure and connectivity (Gardiner et al., 2011; Woolf et al., 2009). On the other hand, evidence has accumulated of the matrix exerting a direct control over neurotransmission. Exposure to agents that affect the integrity of various matrix components consistently causes changes such as channel conductance and desensitisation in the gating properties of voltage- and ligand-gated ion channels, indicating that the function of ion channels could be modulated directly and independently of the filaments' transport role. Channels specific for Na^+, Ca^{2+}, K^+ and Cl^- conductances in neurons and other cell types have been considered in these studies (e.g.,

[14] The proteins attached to the postsynaptic membrane that connect the receptors to the effector proteins responsible for signal transduction cascades, and to the cytoskeleton, e.g. postsynaptic density protein-95 (Sheng and Pak, 2000; Woolf et al., 2009).

[15] There are at least three ways in which AF and MT interact: through direct binding, via cross-linking proteins such as MAP2, and via the signal transduction cascades (Woolf et al., 2009).

Janmey, 1998; Mironov and Richter, 1999; Schubert and Akopian, 2004; Shcherbatko et al., 1999; Strege et al., 2003; Sun et al., 2008). Some experiments have suggested that loss of cytoskeletal integrity could directly reduce membrane excitability and propagation of action potentials (Gardiner et al., 2011; Sakai et al., 1985), however without conclusive mechanisms.

The bidirectional interplay between neurotransmission and matrix reorganisation appears to be essential for learning and memory consolidation. Long-term potentiation has been recognised as a surrogate for the cellular processes that encode and consolidate memory, and it is necessarily accomplished by polymerisation and structural reorganisation of actin network in dendritic spines, as reflected in their highly dynamic morphology (Lynch et al., 2008). On the other hand, evidence has accumulated that points to the substantial role of matrix reorganisation in the subsynaptic zones below the synapses for permanent memory storage[16]. Many correlative as well as interventive studies, employing colchicine[17] consistently demonstrated that dendritic MT reorganisation is essential for memory consolidation. Moreover, studies on rats employing different learning paradigms demonstrate that MAP2 is proteolysed at brain regions corresponding to the type of learning, which is thought to promote MT reorganisation as new memories are formed. On the contrary, genetically induced overexpression of MAP tau has been found to impair learning, an effect thought to arise as a consequence of an over-stabilised MT network that reduces the potential for reorganisation. For a detailed discussion, see recent reviews (Priel et al., 2010; Woolf et al., 2009).

In addition to MAPs, another layer of stability regulation in the MTs – with possible implications for memory – is represented by the composition of tubulin isoforms and post-translational modifications (Craddock et al., 2010; Woolf et al., 2009). Both types of regulation express most variability in their modifications of the C-termini tubulin tails, which have also been hypothesised to participate in intraneuronal electric signalling (Priel et al., 2005). In sum, an intricate balance between stability and instability appears to coordinate the neuronal cytomatrix architecture, which has a role in memory consolidation and in turn it feeds back to modulate neurotransmission.

[16] Consistently with the fact that synaptic strength itself could not reflect permanent memory storage, because synaptic plasticity must be globally constrained by homeostatic mechanisms in order to maintain long-term system stability and plasticity (Davis, 2006; Turrigiano, 2008).

[17] A MT toxin that completely blocks MT polymerization and also interferes with their depolymerization (Vandecandelaere et al., 1997).

3.2.2 Electric signalling by actin filaments and microtubules

So far, very little is known about how the intraneuronal matrix modulates neurotransmission. The hypothesised mechanisms are predominantly based on structural interactions imposed by the matrix components that may influence molecular transport, clustering of ion channels, or binding of channel-associated proteins (Casini et al., 2010; Schubert and Akopian, 2004; Sun et al., 2008). While these mechanisms might account for slower neuromodulatory processes whose modifications are dependent on matrix reorganisation, they are insufficient to contribute to dynamic changes of functional neuronal connectivity.

One promising line of research indicates that microtubules and actin filaments act as biological conduction "wires" for charged particles. As MTs and AFs are negatively charged polyelectrolytes, they condense counterions in the proximity of their surfaces (Wong and Pollack, 2010). The counterions are arranged in ripple-like layers concentrated around charged groups, as directly observed in the case of AFs, and it was demonstrated that they exhibit highly coordinated dynamics (Angelini et al., 2006; Angelini et al., 2003). Upon application of a voltage gradient at physiological ionic strength, both types of filaments display conductive capability that depends on the adsorbed counterions (Cantiello et al., 1991; Lin and Cantiello, 1993; Priel et al., 2006a).

In a hypothesised model of electric signalling (Lin and Cantiello, 1993; Priel and Tuszyński, 2008; Priel et al., 2006b; Tuszyński et al., 2004), conductivity is mediated by counterionic propagation along the filaments in the form of nonlinear, soliton-like ionic waves. Molecular modelling indicates that electrostatic perturbations of counterions between adjacent MTs could couple via the MAP2, thus potentially integrating the whole matrix into an electrically coupled network (Priel et al., 2006b; Priel et al., 2005). Since the intraneuronal matrix effectively connects synapses throughout the neuron, the initial electric perturbation (i.e., cations entring the postsynaptic density upon channel opening) would propagate throughout the matrix, and the output signal (resulting from collective input integration by the network) may then affect the neuronal response by electrically modulating the activity of voltage-depended ion channels, or by inducing cytoskeletal reorganisation via the signal transduction pathways. Thus synaptic activity could be integrated via the matrix in as many combinations as is mathematically possible. However it might be skewed by the previous memory-dependent structural constraints favouring activation of specific dendrites, or release of specific neurotransmitters and neuromodulators (Priel et al., 2010).

Could the hypothesised intraneuronal electric signal propagation have a role in neuronal synchrony? Priel and co-workers (2010) indeed suggest that electric signalling may participate in coincidence detection, which is considered fundamental for communication by synchrony because it enables temporal focusing of synaptic inputs (Fell and Axmacher, 2011; Fries, 2009). In this respect, electric signalling can complement current models of adaptive coincidence detection and input integration that are based predominantly on active dendritic conductances through voltage-gated channels (Ariav et al., 2003; Azouz and Gray, 2003). Another possible implication of electric signalling is its interaction with endogenous EM fields. The "strategic" position of counterions at the filamentous surfaces suggests antennae-like properties which could enhance the susceptibility of, and amplify the physiological response to, EM fields of exo- or endogenous origin (Funk et al., 2009; Gartzke and Lange, 2002). As described in the next sections, the emerging concept of molecular coherence could afford this system the required long-range coordination.

3.3 Overview of molecular coherence

As an integrated part of a living organism, the brain must ultimately obey the same organisational principles that apply to biological systems. In the introductory section, we pointed out that synchronisation is a general form of self-organisation harnessed by organisms to boost their efficiency. Since Erwin Schrödinger (1944), one of the founders of quantum physics, pointed out that statistical mechanics alone is not sufficient to explain the remarkable efficiency of living organisms, the idea of a long-range order in biological systems that "escapes" the dictum of Brownian (statistical) molecular motion, has gradually expanded. The phenomenon of spontaneous synchronisation of weakly coupled oscillators with random frequency distribution has been mathematically proven by Winfree (Winfree, 1967). Herbert Fröhlich (1968) has shown for the first time how spontaneous synchronisation could be established within biological macromolecules by modelling them as a system of thermally driven electro-elastically coupled electric dipole oscillators. At some critical level of energy input, a phase transition occurs whereby thermally distributed excitation energies are funneled into a single (coherent) oscillation mode, resulting from the phase synchronisation of electromechanical oscillations. Fröhlich (1978; 1975) has further predicted that such a system would have important implications for molecular dyna mics, allowing highly selective molecular recognition and long-range interactions based on resonant frequency coupling.

Fröhlich's model of molecular coherence has been further elaborated within the framework of quantum field theory, which provides the most fundamental physical description of condensed matter currently available (Del Giudice et al., 2005; Del Giudice et al., 1985; Del Giudice et al., 1988; Preparata, 1995; Vitiello, 2001; 2009). This theory can describe several well-known macroscopic quantum systems which display high stability despite their orderliness (and which is not the case in classical systems where order requires energy expenditure), such as crystals, ferromagnets, lasers, etc. The coherent state is described in terms of spontaneous symmetry breaking – that is, *ordering* – of specific molecular degrees of freedom due to their dynamic interaction with the long-range correlation quanta that mediate coherent condensation. For example, dipole wave quanta mediate breaking of rotational symmetry of dipole oscillations and hence their phase synchronisation. A peculiar property of the theory is that it can describe phase transitions and the coexistence of multiple inequivalent phases of a coherent system, making it directly applicable to biological systems (see Vitiello (2001) for a qualitative discussion). The theory has been specifically applied to model the two-phase liquid state of water (Arani et al., 1995) and later extended to the dissipative dynamics of biochemical cycles (Del Giudice et al., 2005; Del Giudice et al., 2010; Del Giudice and Tedeschi, 2009). Its application to neurobiology was pioneered by Ricciardi and Umezawa (1967) and later further elaborated by Jibu and Yasue (1995) and Vitiello (Section 3.5.1).

The recent groundbreaking experiments on photosynthetic systems (Collini et al., 2010; Engel et al., 2007; Lee et al., 2007) represent a proof-of-principle that macroscopic molecular coherent states exist in “warm and noisy” biological environment and exert a biologically meaningful function. Oscillations of light-induced electronic excitation energy in these systems preserve stable phase relationships throughout the whole molecular complex – composed of several proteins and light pigments – for a short, but sufficient period to allow simultaneous sampling of an entire energy phase space to find the most effective sink for excitation transfer to the reaction center. As the energy is shared among the excited molecules, this mechanism is fundamentally different from the semi-classical “hopping” through which the electronic excitation would move stepwise between different excited states, dissipating energy at each step, and where only one state could be occupied at any one time (Engel et al., 2007).

Apart from photosynthetic systems, strong indications of macroscopic quantum phenomena have been observed in various animal sensory systems, such as avian navigation (Gauger et al., 2011), odour recognition (Brookes et al., 2007; Franco et al., 2011) and vision (Prokhorenko et al.,

2006). Other non-trivial (i.e., of biological significance) coherent phenomena include resonant vibrational energy transfer in proteins and water (Kobus et al., 2011; Woutersen and Bakker, 1999; Yang and Skinner, 2010), hydrogen tunneling in enzyme catalysis (Nagel and Klinman, 2009), and long-range transport of electrons in proteins (Bandyopadhyay, 2010; Sahu et al., 2011; Skourtis et al., 2011). These findings initiated a general interest in "quantum biology" and in the role of coherence in various aspects of life (Abbott et al., 2008; Arndt et al., 2009; Bischof, 2008; Fleming et al., 2011; Lloyd, 2011; Plankar et al., 2011; Trevors and Masson, 2011; Tuszyński, 2006). The theoretical frameworks under which they are interpreted remain, however, disputed[18].

3.4 Coherence and the intraneuronal matrix

3.4.1 Coherent electromagnetic fields

As already pointed out, actin filaments and microtubules are polyelectrolytes with high density of electric polarisation. In the MTs, electric dipoles are arranged into helical tubular lattice composed of tubulin heterodimers. MTs exhibit interesting biophysical properties, such as ferroelectricity (spontaneous dipole alignment upon transient application of an external electric field) and piezoelectricity (mechano-electrical coupling), which implies their potential for electrodynamic interactions (Mavromatos et al., 2002; Mershin et al., 2006; Tuszyński et al., 1997; Tuszyński et al., 2008).

Theoretical analyses of electro-mechanical dipole oscillations in MTs indeed predict a wide range of longitudinal coherent modes with frequencies ranging from the kHz to the THz (Cifra et al., 2010; Pokorný, 2004; Pokorný et al., 1997). Coherent oscillations collectively produce a dynamic electromagnetic field with a complex spatial geometry around the filament and of sufficient strength to influence the motion of charged or polarisable neutral (via dielectrophoretic force) particles in their vicinity (Cifra et al., 2010). Evidence of endogenous coherent EM fields has been obtained by examining the external frequency-dependent growth rate of bacteria, by studying dielectrophoretic behaviour of particles around cells, and by direct measurements of EM fields emanating from different cells, with some studies indicating MTs as the field generators

[18] The vast majority of research on coherent phenomena is interpreted quantum mechanically. However, important distinctions between quantum mechanics and quantum field theory have been pointed out and suggested that the latter is exclusively applicable to organisms, because it can describe complex systems exhibiting phase transitions, which is not the case in quantum mechanics (see Vitiello (2001) and Del Giudice et al. (2010) for a discussion).

(e.g., Cifra et al., 2011; Giladi et al., 2008; Grundler and Kaiser, 1992; Hölzel, 2001; Kirson et al., 2007; Pokorný et al., 2001).

Coherent EM field produced by the longitudinal dipole oscillations in the MTs could exert biological effects through a plethora of biophysical mechanisms, in much a similar manner as externally applied EM fields (Cifra et al., 2011; Funk et al., 2009), by adding a non-brownian (directional) term to particles' kinetics (Pokorný et al., 2005). Resonant interaction of the field with condensed counterions surrounding the filaments is plausibly one of the most direct consequences (Gartzke and Lange, 2002), suggesting a modulatory effect of the coherent field on voltage-dependent ion channels (Sections 3.2.2 and 3.5.2).

3.4.2 Microtubule as an information processing device

Tubulin dimers can exist in at least two stable conformational states, which differ in the alignment of electric dipoles depend in part on conformational constraints of neighbour tubulins in the filament and partly on GTP hydrolysis (Mershin et al., 2006; Woolf et al., 2009). The idea that a MT could act as an information processing nanostructure by switching conformational states was proposed almost forty years ago (Atema, 1973) and further elaborated upon by many research groups. In one model, electromagnetic interactions between the dipoles of adjacent tubulins occur as input-sensitive two-dimensional lattice of evolving conformational states, analogous to cellular automata. The "output" state of such processing is hypothesised to modulate binding of MAPs and thus influence the structural properties of MTs (Hameroff, 2006; Smith et al., 1984). Another model of dipole interactions predicts the propagation of waves of transient conformational changes along the filaments coupled to the energy of GTP hydrolysis, either as dipole "flip" waves (Mershin et al., 2006) or kink-like solitonic excitations (Satarić and Tuszyński, 2003), that are hypothesised to influence the MTs' conductive properties and mediate long-distance transfer of energy (Priel et al., 2010).

Assuming sufficient thermal isolation, some models predict that tubulin conformational states may sustain quantum mechanical superposition for a sufficient period to support the long-range information processing along the whole MT filament (Hameroff and Penrose, 1996; Mershin et al., 2006). Although such macroscopic coherence is generally considered implausible (McKemmish et al., 2009; Reimers et al., 2009) it received experimental support by the recent detection of ballistic electron conductance at physiological temperature – with temperature and filament length-independent resistance as a direct indication of coherent transport

(Bandyopadhyay, 2010; 2011; Sahu et al., 2011). Hameroff (2006) argues that the coupled chains of polarisable electron clouds in tubulin hydrophobic pockets, and not the whole dimers, are sufficiently isolated from thermal noise and balanced by molecular forces to support long-range pathways of coherent interactions across the filament. Preliminary experiments indicate that these pathways may take the form of topological qubits, which are stable against temperature fluctuations and could allow efficient information transfer and processing (Bandyopadhyay, 2010; Bonderson and Lutchyn, 2011; Das Sarma et al., 2005).

In their orchestrated objective reduction theory, Hameroff and Penrose (2006) further hypothesise that upon quantum state reduction, the collapsed state would act as molecular "lever" governing the conformational state of an entire tubulin dimer, thus conveying the output of information processing to the MT exterior. Periodic switching between the classical (incoherent) and quantum (coherent) states is thus inherent to this theory, and its rate is hypothesised to coincide with that of gamma frequency oscillations. However, while the recent experimental progress may have weakened to some extent the usual criticism regarding the relevance of macroscopic quantum phenomena for cognition (Koch and Hepp, 2006), this and other theories of the "quantum mind" (Stapp, 2009) that exploit the measurement problem to explain consciousness (or even qualia as the "units" of subjective experience), face the difficulty of how the proposed mechanism of the wave function collapse might be reconciled with the well-established mechanisms of neuronal oscillations (Sections 2.1 and 3.1); we assert that this criticism may be even more important than the mere (im)plausibility of macroscopic quantum states.

Finally, the MT lumen has been speculated to represent another layer of information processing – optical signalling – by acting as a quantum optical cavity (Jibu et al., 1994; Mavromatos et al., 2002; Vitiello, 2001). Modelled in the framework of quantum field theory, water dipole oscillations in the lumen are predicted to be sufficiently thermally isolated to sustain a highly polarised, electret-like state due to tubulin surface charge. Such ordering could allow highly synchronised interactions with the quantized electromagnetic field entering the filament, and a consequent propagation of coherent excitations along the cavity without energy dissipation (the phenomenon of self-induced transparency), implying a potential for signal integration with an immense capacity. Optical signalling remains the least experimentally tested hypothesis of coherence-based communication along the MT, although indirect support for it is provided by the spectroscopic studies of resonant intermolecular transfer of vibrational energy in liquid water

(Woutersen and Bakker, 1999; Yang and Skinner, 2010), and by the observed optical conductance along sensory and motor nerve roots, obtained by *in situ* biophoton autography (Sun et al., 2010).

3.5 Coherence as a generic property of information processing in the brain

So far, we have addressed the neuronal and molecular coherent oscillations separately. Jibu and co-workers (1994) have already remarked that both types of coherent dynamics might be related. Only recently, however, a synthetic approach to both levels of brain information processing has been elaborated within the dissipative brain dynamics theory, proposed by Freeman and Vitiello (2006; 2008; 2009).

3.5.1 Dissipative brain dynamics

Using high-density electrocorticography on animals trained to specific sensory stimuli, Freeman (1990; 2003b; 2005; 2009) observed distinct spatio-temporal patterns of synchronised neuronal oscillations emerging from the background cortical activity in the sensory cortices of animals responding to conditioned stimuli. Individual stable patterns, or the wave packets, exhibit distinct phase- and amplitude-modulation of specific carrier frequency in the beta and gamma ranges throughout the electrode array, and they appear in a sequential manner that resemble cinematographic frames. The frames remain stable from milliseconds to a second and can span from under a millimeter to an entire hemisphere – conforming to the self-organised criticality of cortical activity (Section 3.1). The size and discernibility of the frames correlate with the state of subject arousal; clearly discernible frames are only observed in subjects fully engaged with the environment, indicating their correlation with perception and meaning (Freeman, 2003a; Freeman and Vitiello, 2006). Related concepts of dynamic spatio-temporal patterns of synchronised activity as the “units” of cognition have been termed transients (Friston, 2000), microstates (Van De Ville et al., 2010), and dynamic cell assemblies (Breakspear et al., 2004).

A specific characteristic of the wave packet is that the border between different frames is marked by a rapid and transient decrease in the order parameter (measured as a decrease of the analytic signal power and a concomitant increase of analytic frequency and phase variances), manifested in the transition of neuronal activity into chaotic (non-synchronised) oscillations, a phenomenon referred to as the null spike (Freeman, 2009; Freeman and Vitiello, 2009). The most elusive property of this transitory instability is an almost instantaneous phase reset (the phase slip) across the entire electrode array which, in a study on humans, spanned up to 19 cm in less than 5 ms,

implying a global state transition of cortical activity occuring with a phase velocity of over 40 m/s (Freeman et al., 2003). A similar phenomenon was observed in the rabbit olfactory bulb, where phase velocity during the state transition was demonstrated to be independent of the group velocity of synaptic propagation (Freeman, 1990; 2000). Such a long-range correlation of neuronal activity and rapid subsequent onset of a new wave packet is difficult to explain exclusively by serial synaptic transmission due to continuous variations (stochasticity) in transmission frequencies (Freeman and Vitiello (2006); see also Section 3.1). Neither can it be sufficiently explained by ephaptic transmission, because electric field emerging from synaptic inputs and postsynaptic potentials is considered inadequate to exert the *long-range* modulatory effects on dynamic synchronisation patterns because of its relatively rapid decay with distance and dependance on relevant geometric restraints (Canolty et al., 2010; Freeman and Vitiello, 2006).

Dissipative brain dynamics theory explains this seemingly instantaneous phase correlation by a spontaneous breakdown of the electric dipole rotational symmetry which entails the state transition of cortical dynamics from a microscopic (Hebbian) assembly to the macroscopic ordered pattern. Spontaneous symmetry breaking is ascribed in the quantum field theoretical approach (Preparata, 1995; Vitiello, 2001) to macroscopic coherent condensation of the long-range correlation quanta, i.e., dipole wave quanta, into synchronised electric dipole oscillations within densely polarised media. It is postulated that the coherent state utilises the transitory oscillatory instability by imposing to the cortex a macroscopic order parameter which initiates the rapid neocortical phase transition propagating radially from localized regions (forming distinct phase modulation patterns, or phase cones[19]), and settles the cortical dynamics into a new emergent pattern-attractor, or a frame. As a specific coherent state represents only one of the many possible physically inequivalent ground states (states with minimum energy), the theory also accounts for the experimentally observed state transitions in the same cortical region between many different modulation patterns with distinct carrier frequencies (Freeman and Vitiello, 2006; Vitiello, 2009). In sum, the role of spontaneous symmetry breaking and the concomitant phase transitions between different coherent states is to subtly "steer" the functional network connectivity and thus enable the rapid spatio-temporal transitions of macroscopic

[19] As the precise location and phase orientation of the phase cones seems to be randomly determined by the system's internal dynamics, it is unlikely that the synchrony can be ascribed to entrainment by an external pacemaker or a central relaying hub, such as the thalamus (Freeman, 2003b).

oscillatory cortical activity between different *basins of attraction* in response to external perturbations, by utilising the high cortical sensitivity maitained through self-organised criticality.

3.5.2 Connecting the levels of coherence?

Dissipative brain dynamics provides the first integrative framework for brain information processing based on the principle of coherence that incorporates both neuronal synchronisation and coherence of molecular dynamics. As shown mathematically by Vitiello (2009), the fractal, scale-free nature of coherent states is indeed inherent to this theory. However, it does not explicitly adress the mechanistic relationship between both levels of coherent dynamics (see also Uzan, 2011). Biological polymers and the polarised water molecules with which they are endowed generally meet the temperature and polarisation density criteria determined by quantum electrodynamics theory to represent plausible carriers of the coherent states (Arani et al., 1995; Del Giudice et al., 2005; Del Giudice et al., 1988; Del Giudice et al., 2010; Vitiello, 2001).

In order to modulate local and long-range neuronal firing and the patterns of neuronal synchronisation, coherent molecular states would have to interact with the membrane potential. Based on discussion in previous sections, it is reasonable to hypothesise that dynamic pathways of energy and information transfer along the intraneuronal matrix filaments may be involved in such an interaction within a neuron. As this system is immersed in an ionic atmosphere with a vast surface (Section 3.2.2), the presumed intraneuronal mechanism of membrane potential modulation is by regulating voltage-dependent ion channels in the dendrites and at the axon initial segment via the gradients of electric potential induced by ionic waves (Pereira and Furlan, 2010; Priel et al., 2006b; Priel et al., 2010)[20].We thus predict that endogenously generated electric dipole oscillations in the matrix are strong enough to exert an electrodynamic modulation of the counterions, causing their oscillatory movement around a fixed position or net translational movement according to the frequency and geometry of the electric field, which can be tested by theoretical modelling and experimentally on isolated filaments.

[20] Tsong and co-workers have indeed shown experimentally that periodic electric potentials of low and medium intensity, ranging widely in optimal frequency (from 10 Hz to 1 MHz), can induce conversion of electric field energy into chemical potential energy in the tested membrane proteins (see reviews by Tsong (1992) and Cifra et al. (2011) and references therein).

Components of the brain extracellular matrix[21] are, however, also negatively charged polyelectrolytes that bind water and condense counterions at their surfaces. The counterions are presumed to act as a buffering system controlling for the availability of cations for generating action potentials (Brückner et al., 1993; Dityatev et al., 2007; Härtig et al., 1999). Assuming that the cations are periodically perturbed, either by an external EM source or by endogenously generated coherent longitudinal dipole oscillations, their electrostatic interactions could likewise be modulated in a frequency-dependent manner and thus may, if sufficiently excited (depending on the ion mobility, their vicinity to the EM source and frequency of the field), cause interference with the membrane potential fluctuations. Recent observations of the frequency entrainment of a whole oscillating neuronal assembly to an externally applied frequency of *weak* electric field, i.e. within physiological range, indeed provide a proof-of-principle that similar modulatory role of EM oscillations at the local network level is possible, although much lower frequencies were employed (Section 2.1.2). The highly localised endogenously generated coherent oscillations may provide yet a greater focus on modulating the membrane excitability by acting on ion channels.

The recent experiments also confirm that the loss of structural integrity of perineuronal nets – lattice-like differentiations of extracellular matrix that ensheath specific types of neurons – directly affects the function of voltage-dependent calcium channels (Kochlamazashvili et al., 2010) and excitability of fast-spiking basket interneurons (Dityatev et al., 2007) in hippocampal cultures. As this type of interneuron substantially contributes to establishing synchronised high-frequency neuronal oscillations (Section 3.1), it can be assumed that perineuronal nets are functionally involved in modulating neuronal synchrony (Dityatev et al., 2007). Abnormal oscillations in the gamma and theta frequency band have indeed been observed in the hippocampus of mice deficient in specific glycoprotein *in vivo* (Dityatev et al., 2007; Gurevicius et al., 2009).

Interestingly, close association between the perineuronal nets and astrocytic processes was also described (Derouiche et al., 1996). The modulatory potential of astrocytes in neuronal synchronisation has been already discussed (Section 2.1.2) and could, in the context of perineural nets, contribute to another layer of neuro-glial interactions based on coherence. We may speculate

[21] The extracellular matrix of the brain consists of large molecular aggregates of proteins and carbohydrates, of which the main components are hyaluronic acid, proteoglycans and glycoproteins. It forms a network continuum with the intracellular matrix of neurons and glia by binding to various transmembrane proteins, which participate in signal transduction pathways that modulate synaptic plasticity (for a detailed discussion, see the recent review by Dityatev and Rusakov (2011)).

that the "quantum-like macro coherent process" Pereira and Furlan (2010) envision as a requirement for the collective integration of calcium waves into the astroglial network is embodied in the long-range coherent states within intra- and intercellular matrix filaments.

Taken collectively, theoretical considerations, together with the recently emerging experimental evidence, support the role of filamentous networks of intra- and extracellular matrices in dynamic modulation of functional neuronal connectivity. At the network scale, the long-range interactions within these matrices could help explain – e.g., via resonant coupling with the membrane potential fluctuations and network oscillatory entrainment – the experimentally observed rapid transitions of the phase and the carrier frequency, defining distinct patterns of synchronised neuronal oscillations, which have as yet not been conclusively explained by the classical models of functional connectivity.

4 CONCLUSIONS

Throughout this review, we have explored mechanisms of dynamic order in brain information processing at different organisational levels and from a variety of research disciplines, whose one common denominator is the principle of coherence, or synchronisation. Knowledge from neuronal oscillations and long-range molecular dynamics, together with their potential modulatory interactions, e.g. via electric signalling along the cytoskeletal filaments, ephaptic coupling, or neuroglial interactions, is for the first time collectively discussed in the context of dynamic emergent order, epitomised by coherence. Coherence may represent a dynamic operational principle capable of modulating functional network connectivity, upon which a succession of rapidly arising and transforming neuronal activity patterns could emerge that mediate integration of interneuronal and subneuronal information processing (i.e., its local and long-distance transfer, encoding and storage) into a unified ongoing cognitive synthesis.

Coherent neuronal oscillations have become acknowledged as a fundamental mode of interneuronal information processing and could represent one of the principle neuronal correlates of cognition. Yet, the basic operational principles behind them remain unclear. As Uhlhaas and co-workers (2009) remind us, there currently exists no satisfying explanation of "how different percepts dynamically map into different states, and how the system dynamically selects subsets of neuronal responses for conscious representation". We have tackled this problem from a

multidisciplinary perspective, taking into additional consideration the integrative approach of the dissipative brain dynamics theory, and the so far much neglected properties of filamentous matrices that pervade the brain inside and outside the neurons, endowing it with an immense catalytic and electrically active surface. Because of their information processing potential, the intra- and extraneuronal matrices may represent an integrative functional system, complementing synaptic interactions.

An important intracellular component of this system are the microtubules, supramolecular nanostructures hypothesised to support coherent transport of energy and information at various layers: in their ionic exterior, within the protein filaments themselves, and in their aqueous interior. It remains to be determined which of these layers could actually interact with the synaptic (or non-synaptic) input and contribute to signal integration and neuronal response. Some of the proposed mechanisms demand treatment of biological structures as macroscopic quantum systems, a topic that deserves to be approached with caution and upon which we did not here elaborate.

The structures of the extracellular matrix, on the other hand, represent an analogous extracellular system that could additionally establish and modulate long-range interactions between the neurons. Conspicious structures of the perineuronal nets, connecting specific types of neurons and glia, as well as their functional significance in modulating ionic currents, certainly support such a dynamic role. However, their electrodynamic properties are much less known and need further investigation. It will have to be established whether they are capable of rapid local and long-distance information transfer and what are the underlying molecular carriers of such information. It will also have to be determined how the filamentous matrices are capable of modulating the membrane potential, e.g. by the generation and modulation of ionic waves, or by some other means of acting on charge transport, and finally how such processing will affect the neuronal response. Selectively disturbing and manipulating the coherent states to establish their causal role in generating real-time changes on the membrane and network level will undoubtedly represent a great methodological challenge. Nevertheless the ordered filamentous matrices within and between the brain cells may likely provide, in addition to membranes and synapses as the principle substrates, the structural basis for the emerging theoretical framework required for a systems understanding of the dynamic oscillatory behaviour of the brain; coherence can provide its functional basis.

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