

# EEG, MEG and neuromodulatory approaches to explore cognition: Current status and future directions

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## ABSTRACT

Neural oscillations and their association with brain states and cognitive functions have been object of extensive investigation over the last decades. Several electroencephalography (EEG) and magnetoencephalography (MEG) analysis approaches have been explored and oscillatory properties have been identified, in parallel with the technical and computational advancement. This review provides an up-to-date account of how EEG/MEG oscillations have contributed to the understanding of cognition. Methodological challenges, recent developments and translational potential, along with future research avenues, are discussed.

## 1. Introduction

The study of cognition has fascinated humankind for centuries, and it still is of major neuroscientific interest. New instruments and novel approaches have been devised over the last decades, including electroencephalography (EEG) and magnetoencephalography (MEG). Nowadays, non-invasive recording of brain activity and neuromodulatory approaches are continuously expanding research areas, with promising potential as therapeutical tools. This review will provide an up-to-date account of how EEG/MEG oscillations have contributed to the understanding of cognition. We will review how the signal is obtained and how different oscillatory properties can be quantified, comparing the advantages and limitations of different analysis approaches. We will examine how event-related potentials (ERPs) and frequency-specific oscillatory patterns probe different cognitive states and processes, and highlight the importance of dynamic cross-frequency interactions and synchronisation patterns within large-scale circuits in more complex

functions. Finally, current methodological challenges and future opportunities will be discussed in relation to the latest advances within neuro-modulatory approaches.

## 2. EEG and MEG

EEG is an established neurophysiological technique. It is used to record brain activity with high temporal accuracy non-invasively (<ms) (Cohen, 2017; Puce & Hämäläinen, 2017), either at rest (D'Croz-Baron et al., 2019; Damborská et al., 2019; Murias et al., 2007; Rogala et al., 2020; Sponheim et al., 2000; Stam et al., 2005) or during task performance (Gola et al., 2012; Kamiński et al., 2012; Kardan et al., 2020; Molle et al., 1999; Schlichting et al., 2020; Touryan et al., 2016; Zani & Proverbio, 2003). EEG was introduced in the early 1920s by the German psychiatrist Hans Berger, who recorded cerebral activity from the human scalp (Berger, 1929). While doing so, he discovered the alpha (or Berger) rhythm (Berger, 1929), namely oscillatory fluctuations of the

**Abbreviations:** AAC, Amplitude–Amplitude Coupling; CFC, Cross-Frequency Coupling; CNV, Contingent Negative Variation; EP, Electric Potential; EEG, Electroencephalography; EMD, Empirical Mode Decomposition; ERD, Event-Related Desynchronisation; ERPs, Event-Related Potentials; ERS, Event-Related Synchronisation; GABA, Gamma-Amino Butyric Acid; MEG, Magnetoencephalography; MMN, Mismatch Negativity; MS, Multiple Sclerosis; NMDA, N-methyl-D-aspartate; NIBS, Non-invasive brain stimulation/modulation; OPM, Optically Pumped Magnetometer; PAC, Phase-Amplitude Coupling; PD, Parkinson's Disease; PPC, Phase-Phase Coupling; SERF, Spin-Exchange Relaxation-Free; SQUIDS, Superconducting Quantum Interference Devices; tACS, Transcranial Alternating Current Stimulation; tDCS, Transcranial Direct Current Stimulation; TMS/rTMS, (repeated) Transcranial Magnetic Stimulation.

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EEG signal in the 8–12 Hz frequency range. Berger observed the oscillatory EEG patterns in healthy individuals when relaxed with closed eyes, and he delineated the alterations to the EEG produced by the exposure and processing of sensory stimuli (Gloor, 1969; Millett, 2001). He also classified the EEG waves into five major frequency bands: delta [0–3/4 Hz], theta [3/4–7/8 Hz], alpha [7/8–12/13 Hz], beta [12/13–29/30 Hz] and gamma [29/30–300 Hz] (Shibata et al., 2018).

By the second half of the 20th century, his pioneering observations had been followed by a plethora of EEG studies on several cognitive states and neuropsychiatric diseases (Sutter & Kaplan, 2017). In parallel, other non-invasive electrophysiological brain-scanning methods were developed, including MEG. The first MEG signals were recorded by the Canadian physicist David Cohen, in a magnetically shielded room at the University of Illinois in 1968 (Cohen, 1968). The detector, in those days a copper induction coil of limited sensitivity, produced crude and noisy measurements (Cohen, 1968). Upon the development of superconducting quantum interference devices (SQUIDS) by a team of engineers of Ford Motor Company (United States of America), including James E. Zimmerman (Clarke & Braginski, 2004; Zimmerman et al., 1970), Cohen later adopted the SQUIDS as MEG signal detectors, obtaining finer measurements (Cohen, 1972). The MEG recordings gained the interest of many researchers, who followed with a series of investigations on endogenous and evoked MEG signals.

### 3. The source of the EEG and MEG signal

The EEG signal results from the summation of synchronous excitatory and inhibitory inputs (Cohen, 2017; Fries, 2005; Hesprich & Beardsley, 2019; Rangaswamy & Porjesz, 2008). It is simultaneously obtained from several electrodes or channels positioned on the head's surface (Sanei & Chambers, 2007), whose density defines the EEG's spatial resolution (Burle et al., 2015). The signal travels along the dendrites of the parallelly-oriented post-synaptic pyramidal neurons, which are aligned perpendicularly to the cortical surface (Bandyopadhyay et al., 2017; Brienza & Mecarelli, 2019; Fries, 2005; Rangaswamy & Porjesz, 2008). The EEG detects alterations in the electric potential (EP [volts]) at a given electrode by deducting the voltage at the reference electrode, which has a constant and known EP (Schomer & Lopes da Silva, 2012).

Compared to the EEG electric fields, the MEG magnetic fields are less distorted, thus offering a superior spatial resolution (Baillet, 2017; Hämäläinen et al., 1993; Shiv et al., 2005). MEG records magnetic fields at the scalp produced by endogenous electrical signals of the brain via specific magnetometers placed around the head (Boto et al., 2018). These sensors often consist of cryogenic SQUIDS (Boto et al., 2017), although spin-exchange relaxation-free (SERF) magnetometers with higher magnetic field sensitivity are also in use (Li et al., 2018). More recently, an optically pumped magnetometer (OPM) helmet system (<1 kg) for MEG has been designed. Instead of relying on superconducting technology, it applies quantum sensors placed closely adjacent to the scalp surface and comprises a system that cancels background magnetic fields. As such, OPM-MEG permits free and natural movements (e.g. nodding, stretching, drinking) during the brain recording (Boto et al., 2018), preserving a high temporal resolution (ms). Analysing the magnetic fields allows to visualise the constitution and the disruption of functional neural circuits in real-time (Beniczky & Sharma, 2019), with the excellent temporal resolution of about 1 kHz (Borst et al., 2016).

While MEG mainly detects tangential signal sources, EEG is sensitive to both radial and tangential components and can record potentials originating within the sulci, if sufficiently strong to be detectable at the scalp (Ahlfors, 2019; Puce & Hämäläinen, 2017). Compared to MEG, the EEG thus provides a more complex signal. However, MEG can be more advantageous if the uppermost and tangential signal source is targeted (Antonakakis et al., 2019; Hunold et al., 2016; Srinivasan et al., 2006), as the signal would be less affected by potentially interfering sources.

### 4. Approaches for EEG/MEG data analysis

During the 1930s, the EEG proved to be a valuable technique for recording brain activity. In the following decades, researchers in the area of cognitive neuroscience focused on new methods to interpret and analyse the EEG signal to understand the brain's activity in relation to individual cerebral processes.

#### 4.1. Time domain analyses: event-related potentials

The ERPs are one of the earliest approaches of EEG/MEG signal decomposition; simple to compute, and temporally accurate, they have a decades-long history in the study of brain activity during specific cognitive and motor functions (Fabiani et al., 2007; Sokhadze et al., 2017). An ERP is an alteration in EP over time; it reflects changes in the firing patterns of neural cells and is obtained by averaging EEG data over several trials (Luck, 2014). The ERP response is 'time-locked' to a reference event, such as a sensory stimulus or an internal process (Blackwood & Muir, 1990; Nieuwenhuis & De Rover, 2014; Rangaswamy & Porjesz, 2008). The ERP waveform is characterised by positive or/and negative deflections, which define its polarity at different time points, and by their event-relative onset, which indicates underlying cognitive processes (Blake et al., 2015; Rangaswamy & Porjesz, 2008).

The first ERPs were recorded at Harvard University in 1939 by the American physician and physiologist Hallowell Davis and his wife Pauline Allen, to explore the effects on brain activity of acoustic stimulation in individuals in awake (Davis, 1939) and sleep states (Davis & Davis et al., 1939). After World War II, seminal works on sensory processes were resumed. The 1960s marked the contemporary age of the ERP research, with the discovery of what nowadays are well-known ERP components: the positive 'P300' response (Chapman & Bragdon, 1964; Sutton et al., 1965), and the contingent negative variation (CNV) (Walter et al., 1964), which we will later explain in more detail. The importance of these studies resides in the realisation that consistently elicitable patterns of EP changes can be reliably extracted from the considerable background noise and that these relate to cognitive aspects of expectancy.

The increasing popularity of ERP research in the following decades, along with the technological advances in informatics, favoured an incremental growth of experimental studies (Hajcak et al., 2019; Handy, 2005; Sur & Sinha, 2009). Nowadays, the ERPs still constitute one of the most widely used techniques for the study of the neurophysiological underpinnings of cognitive and motor functions. Different ERP components have been defined, depending on characteristic morphological features of the averaged response and on the properties of the triggering event.

The physical aspects of a sensory stimulus affect the ERP response within the initial hundred milliseconds after its occurrence (Eimer & Holmes, 2007; Luck et al., 2000). This early response is usually characterised by a small negative (N) voltage deflection and a shortly-following positive (P) component, known as "N100" and "P100" responses, respectively (Saavedra & Bougrain, 2012). ERP deflections occurring later, instead, putatively reflect individual-specific cognitive processes (Saavedra & Bougrain, 2012). The late-onset positive P300 deflection can be predominantly observed over the parietal cortices at about 300 ms in reaction to 'oddball events' (Choi et al., 2014; Johnson, 1993; Knight & Scabini, 1998; Picton, 1992), namely when the presentation of a sequence of identical stimuli is interrupted by a deviant (i.e. oddball) stimulus, causing surprise in the observer (Citherlet et al., 2020; Devaney et al., 2019). Multiple small negative deflections characterise the typical ERP response to such unexpected events, preceding the P300, which index early sensory-processing (Javitt et al., 1993). The earliest of these deflections is known as mismatch negativity (MMN).

The CNV is another late-onset negative deflection. In the original study, Walter et al. (1964) presented their subjects with two brief stimuli of distinct sensory modality, such as auditory (clicks) or visual (flashed

light), coupled at intervals of about 3–10 s. The subject was instructed to respond to the second stimulus with a button-press. The authors observed that the EP is attenuated if the first stimulus is presented repeatedly and can be restored to its baseline amplitude, if the first stimulus is followed by a second stimulus of different nature (Walter et al., 1964). The interval separating the first (*warning*) stimulus and the second (*imperative*) is known as *foreperiod*, while the *reaction time* (RT) defines the time required by the subject to respond to the imperative stimulus, as soon as it is presented. Walter et al. (1964) additionally observed that the ERP response to the first stimulus is characterised by three components: a short positive deflection, followed by a short negative one, and finally a sustained negative deflection, for which the term CNV was coined. While the sensory modality of the stimuli affects the short-lasting components, the contingent relationship between the two stimuli shapes the sustained (CNV) component. The CNV's onset occurs 260–470 ms following the warning stimulus (Tecce, 1972).

Importantly, the ERP morphology varies depending on the corresponding EEG/MEG channel, since different cortical areas have different responses to the event of interest. Early and distinguishable occipital ERP deflections can be identified when visually processing different facial expressions, coordinating with the parallel sub-cortical limbic evaluation of the emotional content (Eimer & Holmes, 2007). In auditory perception, the ERPs are sensitive to fine-grained stimulus attributes, including its frequency, intensity and duration (Jeantet et al., 2019; Mugruza Vassallo & Potter, 2019). These ERP components can accurately predict behavioural measures such as the RT to sensory events, even at the single-trial level (Antonova et al., 2016; Bender et al., 2015).

The ERPs have been valuable in the cognitive neurosciences, but also in clinical contexts, as they can show abnormalities in psychiatric and neurological disorders. For example, the most consistently reported ERP anomaly in schizophrenia is a less pronounced auditory P300 response (Diez et al., 2018; McCarley, 1993; Neustadter et al., 2016; Souza et al., 1995). In depression, larger P300 responses indexing behavioural inhibition in the stop-signal task (SST) have been found (Palmwood et al., 2017; Ruchow et al., 2008; Zhang et al., 2007). Furthermore, recent reports indicate that P300 responses, compared to healthy controls, are delayed in mild-cognitive-impairment and Alzheimer's patients (Hedges et al., 2014; Morrison et al., 2018), as well as in those affected by Parkinson's (Maidan et al., 2019; Tokic et al., 2016), correlating with their degree of cognitive and motor dysfunction. However, several works on schizophrenia suggest that MNN aberrations may constitute a better functional correlate of clinical symptoms compared to P300 alterations (Hamilton et al., 2017; Koshiyama et al., 2020; McCleery et al., 2019).

The CNV amplitude is diminished in Parkinson's disease (Georgiev et al., 2016; Hamed & Maabady, 2020) and has been used to assess recovery after different clinical manipulations (Bočková & Rektor, 2019), including dopaminergic medication (Amabile et al., 1986; Lukhanina et al., 2006), surgical treatment (Gironell et al., 2002) or deep brain stimulation (Gerschlagler et al., 1999). The CNV has also shown important applications in migraine, where altered central sensory processing as evidenced by higher CNV amplitudes and poor habituation can be restored to normative levels after pharmacological treatments (De Tommaso et al., 2008; Siniatchkin et al., 2007) and behavioural/physical therapy (Meyer et al., 2016; Overath et al., 2014; Siniatchkin et al., 2011). Finally, changes in ERP responses are also employed in longitudinal studies to assess the effect of therapeutic interventions on brain-functioning of clinical populations, including those affected by attention-deficit disorder (Ogrim et al., 2016; Smith et al., 2019), Autism Spectrum Disorder (Okumura et al., 2020) and Traumatic Brain Injury (Dautricourt et al., 2017).

#### 4.2. Spectral analyses: amplitude, phase and coordination changes

The EEG signal can be interpreted using time-domain analyses (i.e., the ERPs), as we have seen, or by performing time-frequency signal

decompositions. Both approaches have distinct advantages and limitations. Spectral analyses are based on the properties of the oscillatory activity: the frequency (cycles/sec), the phase, namely the angle (degrees/radians) at which the sine crosses the 0 point, and the power (squared amplitude) which represents the amount of energy in a given frequency (Cohen, 2014; David et al., 2006; Roach & Mathalon, 2008).

Time-frequency EEG/MEG signal attributes are more easily interpretable compared to the ERPs, as the underlying neurophysiological mechanisms are better understood (Cohen, 2014; Helfrich & Knight, 2019). Although a relatively lower temporal accuracy is to be expected if a short-time Fourier transform is computed over a time window, the temporal resolution can be improved, at least for faster frequencies, by performing a wavelet analysis. Instantaneous signal attributes can be obtained by applying an adaptive time-frequency decomposition, such as the empirical mode decomposition (EMD) (Sweeney-Reed & Nasuto, 2007; Sweeney-Reed, Nasuto, Vieira, & Andrade, 2018).

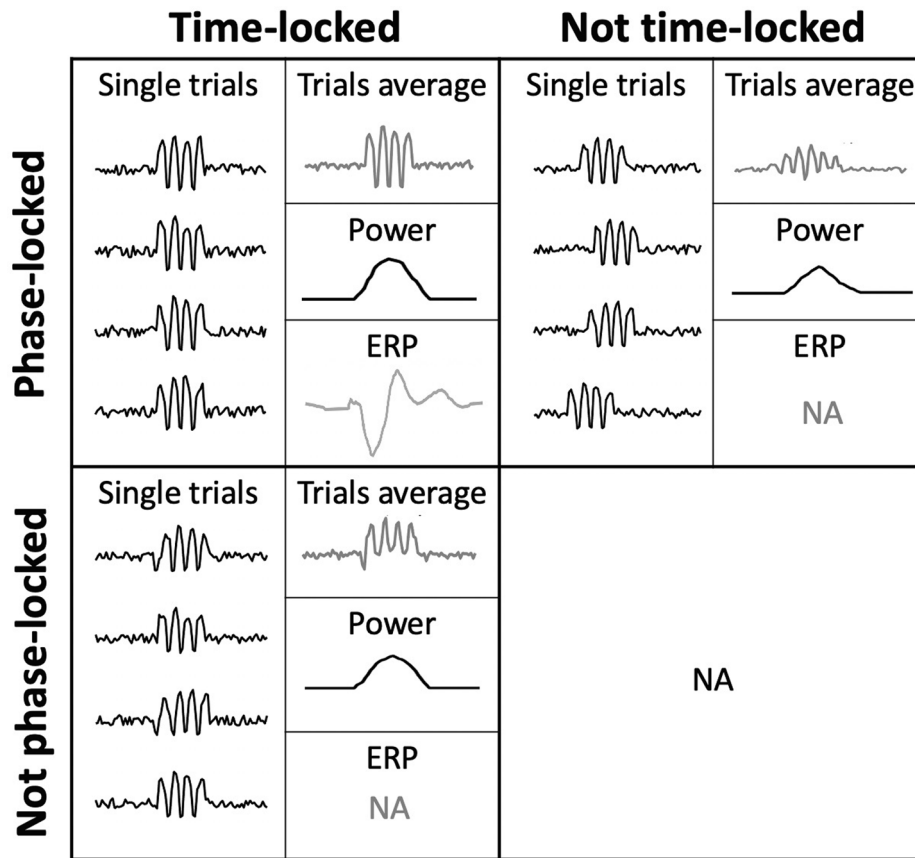
Over the last 20 years, these signal attributes (and their change during specific tasks) have received increasing attention, as they may reveal more fine-grained aspects of neural activity, compared to averaged measures like the ERPs (Başar, 2012; Buzsáki, 2006; Cohen, 2018). As phase-shifts develop on a much faster pace relative to amplitude fluctuations over time, they might be crucial for the understanding of the neural dynamics contributing to specific cognitive processes (Busch et al., 2009; Rivera-Lillo et al., 2018).

A given stimulus may induce changes in the coordination of neural oscillations over specific brain areas, resulting in augmented/decreased EEG/MEG signal amplitude or power (Tariq et al., 2018). Specifically, stimulus-locked increases and decreases in synchronisation between neural oscillations are known as event-related synchronisation (ERS) and event-related desynchronisation (ERD), respectively (Lee et al., 2020; Tarasova et al., 2020). Importantly, these events are sensitive to the functional role of specific brain areas such that within the same time frame, opposite synchronisation patterns may be observed in different channels (De Vries et al., 2019; Román-López et al., 2019; Van Wijk et al., 2012).

#### 4.3. Event-related phenomena in comparison: phase-locked vs time-locked

Event-related activity occurring at the same or a similar phase relative to the reference event (endogenous or exogenous) at each trial is said to be *evoked* activity. It is distinguished from *induced* activity, which is not phase-locked, yet still time-locked to the trial event (Cohen, 2014; Gurariy et al., 2017). Phase-locked and non-phase-locked signals undergo different analysis procedures. Evoked responses have a latency of 50–150 ms and are averaged over several trials before undergoing time or spectral analysis (Kalcher & Pfurtscheller, 1995). Conversely, as induced signals have variable onset (150–400 ms), their decomposition is performed on each trial, and the obtained attribute (e.g. power) is then averaged across trials (David et al., 2006; for a schematic summary, refer to Fig. 1). Furthermore, evoked and induced signals have different neural underpinnings and putative functional roles (Tanaka & Miyakoshi, 2019; Zubarev et al., 2019). The first is assumed to mirror the bottom-up processing of incoming sensory information. At the same time, non-phase-locked activity seems to capture high-level control and top-down adjustments through short- and long-range cortical projections (Chen et al., 2012).

The ERPs and the ERS/ERDs are both neural phenomena associated with the onset of an endogenous (internal) event or an external (sensory) stimulus. However, while the ERPs constitute focal time-locked and phase-locked neural responses, power or ERD/ERS changes can be time-locked activity regardless of whether it is evoked or induced (Cohen, 2014). Oscillatory patterns are mostly not phase-locked in an enclosed frequency (Diers et al., 2020; Pantazis et al., 2018; Ross et al., 2017). Moreover, while the ERPs reflect neural activity in response to a given stimulus, ERS/ERD dynamics stem from changes in the interaction between neural cells affecting the frequency attributes of the signal. The



**Fig. 1.** Possible representations of a simulated oscillatory signal as time-locked or/and phase-locked brain activity. Within each square, four panels (from left to right) expose signal amplitude at single-trial level, the trials' average, time-frequency power and event-related potential.

ERPs reflect the post-synaptic activity of pyramidal neurons (McWeeny & Norton, 2020; Müller-Putz, 2020), whereas (de)synchronisation patterns related to a reference event are caused by alterations to multiple properties of neural function, including physical aspects of the cell membrane, ion influx and chemical transmission, as well as, the functional relationship within short- and long-range cortico-cortical and thalamocortical networks (Bauer et al., 2020; Müller-Putz, 2020). Changes to these parameters cumulatively affect the oscillatory dynamics within a given cortical area.

## 5. EEG frequency bands – Power and (de) synchronisation changes

EEG has extensively contributed to the understanding of the relationship of brain oscillations in different frequency ranges with brain states and cognitive processes. Frequency-specific oscillations incur local alterations in amplitude and synchrony with characteristic spatial and chronologic distributions depending on the cognitive requirements of a given task.

### 5.1. Theta rhythm

The theta rhythm predominantly arises from the communication between the excitatory glutamate and inhibitory Gamma-Amino-Butyric acid (GABA) neurons of the hippocampus (Leung & Law, 2020; Lu et al., 2020; Vertes & Linley, 2020) and the modulatory cholinergic projections from the septum pellucidum (Ma et al., 2020). The theta rhythm has been associated chiefly with spatial memory and navigation (Miller et al., 2018; O'Keefe & Recce, 1993; Watrous et al., 2013). A prominent theta activity from the hippocampus (Miller et al., 2018; O'Keefe & Recce, 1993; Watrous et al., 2013) has been probed in rodent

experiments (Hernandez et al., 2018; Theodoni et al., 2017) as well as in humans (Bohbot et al., 2017; Reddy et al., 2019), although less prevalent and lower in frequency.

The firing of individual hippocampal pyramidal neurons follows a topographic pattern (Morris et al., 1982; O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978) where action potentials are timed to the phase of neural oscillations in the neighbouring neurons (França & Monserrat, 2019; Pavlides et al., 2019). In hippocampal place cells, phase precession mediates the encoding of positions in space (Buzsáki & Moser, 2013). Hippocampal theta oscillations reflect sequential dependencies during spatial planning (Kaplan et al., 2019) and state-dependent information processing in decision-making (Amemiya & Redish, 2018). Recently, functionally distinct hippocampal contributions in the high- and low- theta band have been observed in humans (Goyal et al., 2020). Higher oscillations (up to 8 Hz) are prominent posteriorly and correlate with movement speed, implicating their role in spatial navigation. Slower oscillations (~3 Hz) are instead more prevalent anteriorly, and their frequency does not vary with movement speed, which suggests an involvement in non-spatial cognitive processes (Goyal et al., 2020).

Theta oscillations dominate in the hippocampus, but are evident also in other subcortical areas, including the thalamus (Sweeney-Reed et al., 2014) and in widespread cortical circuits (Zhang et al., 2018), serving important contributions to encoding and working memory (WM) functions (Crespo-Garcia et al., 2010; Gruber et al., 2013; Herweg et al., 2020; Hsieh & Ranganath, 2014; Jones et al., 2020; Klimesch, Doppelmayr, Stadler, et al., 2001; Klimesch, Doppelmayr, Yonelinas, et al., 2001; Klimesch, 1999). Theta activity in sensory areas, such as the occipital lobes and the superior temporal gyrus, contributes to the memory processing of visual (Moreau et al., 2020) and acoustic stimuli (Hyafil et al., 2015; Teng & Poeppel, 2020). At the same time, the additional involvement of frontomedial and anterior-cingulate cortices supports



multisensory attention (Keller et al., 2017), WM and episodic memory functions (Herweg et al., 2020; Wang et al., 2018). Strikingly, theta activity positively correlates with the demands of information processing, memory load and manipulation (Meyer et al., 2019). Moreover, it improves hippocampal contextual processing for memory integration (Backus et al., 2016) and recall (Wirt & Hyman, 2019), supporting decision-making (Rajan et al., 2019; Swart et al., 2016).

### 5.2. Alpha rhythm

Alpha waves were the first to be discovered (Berger, 1929) and have been extensively studied. The alpha rhythm reflects short-range supragranular feedback, propagating from the cortex to the pulvinar thalamus (Crunelli et al., 2018), but also from higher-order (associative) areas to primary sensory cortices, including the visual and somatosensory ones (Halgren et al., 2019). Thalamo-cortical high-threshold bursting cells synchronise themselves at the maculae communications (Lörincz et al., 2008; Zeldenrust et al., 2018) and their function can be modulated by GABA/glutamatergic inputs (Joffe et al., 2019; Salt & Copeland, 2017), as well as acetylcholinergic (Dasgupta et al., 2019; Huerta-Ocampo et al., 2020; Rho et al., 2018) and serotonergic signalling (Andrade & Haj-Dahmane, 2020; Vertes & Linley, 2020). A pronounced alpha signal is also observable from deep structures such as the hippocampus (Goyal et al., 2020) and the reticular formation (Buffalo et al., 2011), which has direct projections to the cortex and the thalamus, and plays an essential role in awareness, vigilance and sleep (e.g. Kim et al., 2013).

Alpha oscillations are prominent when resting with closed eyes (Li, 2010; Toscani et al., 2010). Alpha power decreases when opening the eyes (Britton et al., 2016) and with increasing demands of alertness and attention (Bollimunta et al., 2011; Rajagovindan & Ding, 2011), likely reflecting processes of selection of task-relevant information (Düzel et al., 2005). Suppression of alpha amplitude can, moreover, be observed upon sensory stimulation (Ikkai et al., 2016; Mo et al., 2013; Nishifuji et al., 2010; Pfurtscheller & Aranibar, 1977) as a function of processing load (Rajagovindan & Ding, 2011), and during movement tasks (Pfurtscheller & Da Silva, 1999). Spontaneous resting-state EEG fluctuations of alpha frequency are inversely associated with the visual BOLD activity, and higher alpha frequency preceding a cue/probe is associated with weaker cue/probe-evoked neural responses and longer RTs (Samuel et al., 2018). Altogether, these findings suggest that alpha-band activity may index cortical excitability, contributing to sensory-gating.

While alpha power decreases in stimuli-contralateral (attending) sensory areas (Ikkai et al., 2016), it increases over the “stimuli-ipsilateral” hemifield, predicting memory accuracy (Chen & Huang, 2016; Heinz & Johnson, 2017). The hemispheric lateralisations of alpha amplitude seem to mirror dissociated synchronisation patterns (Pfurtscheller & Da Silva, 1999). Increased alpha synchronisation (or ERS) over the stimuli-ipsilateral hemisphere and alpha desynchronisation (or ERD) in the stimuli-contralateral lobe are observed during attention (Van Moorselaar & Slagter, 2020), WM encoding and maintenance (Van Ede, 2018) in both visual (De Vries et al., 2019; De Vries et al., 2019; De Vries, van Driel, & Olivers, 2017; De Vries, van Driel, Karacaoglu, & Olivers, 2018; Popov et al., 2018; Román-López et al., 2019; Schneider et al., 2019; Van Ede et al., 2019) and auditory (Klatt et al., 2019; Pavlov & Kotchoubey, 2020; Woestmann et al., 2020) modalities. Alpha power decreases, and ERDs are also observed in the sensorimotor cortex during somatosensory and motor planning/execution tasks (Fumuro & Matsushashi et al., 2015, 2018; Pfurtscheller & Da Silva, 1999).

The spatial patterns of synchronisation and desynchronisation may index brain sites that are, respectively, contributing to or uninvolved in information processing. However, despite being lateralised relative to the attentional focus and sensory-load-dependent, alpha activity does not track task-irrelevant cue- or probe-load (Poch et al., 2018; Schroeder et al., 2018), disproving its putative role in the active suppression of

distracting information. Moreover, while alpha frequency decreases (ERD) during memory encoding, it increases (ERS) during memory retention and retrieval in a load-dependent fashion (Samuel et al., 2018; Wianda & Ross, 2019). This finding highlights that preparatory functions of attention, encoding and planning follow alpha synchronisation patterns that are dissociated from later processes of memory consolidation and retrieval, which seem to benefit from the alpha contribution (Makada et al., 2016).

### 5.3. Beta rhythm

Beta waves can be recorded from several cortical areas (Scheeringa & Fries, 2019; Sherman et al., 2016), including the motor (Athanasioiu et al., 2018; Barratt et al., 2018; Khanna & Carmena, 2017), somatosensory (Bartoli et al., 2016), visual (Michalareas et al., 2016) and olfactory ones (Fourcaud-Trocmé et al., 2019). Beta oscillations primarily originate in the basal ganglia to then, through the thalamus, reach the cortex (Holgado et al., 2010; Liu et al., 2020, 2018; McCarthy et al., 2011). Beta waves can be detected within other deep structures including the hippocampus (Rangel et al., 2015; Sakimoto & Sakata, 2020), the basal ganglia, including the subthalamic nucleus and motor thalamus (Basha et al., 2014; Liu et al., 2020; West et al., 2020) and the olfactory bulb (Bagur et al., 2018).

Beta-band activity is regulated by GABA, glutamate and N-methyl-D-aspartate (NMDA) neurotransmission (Osinski et al., 2018; Rebollo et al., 2018; Traub et al., 2004; Yamawaki et al., 2008). Cortical beta activity may be controlled by interacting spiking pyramidal neurons (Bitzenhofer et al., 2017; Lee et al., 2013; Liu et al., 2020; Sherman et al., 2016; West et al., 2020), coordinating at the gap junctions (Roopun et al., 2006), along with other cortical and subcortical (thalamic) modulations (Schmiedt et al., 2014; Sherman et al., 2016). Beta activity from the basal ganglia is controlled by dopaminergic signalling (Sharott et al., 2005), which is strikingly dysfunctional in Parkinsonian patients (Cole et al., 2017; Fischer et al., 2019; Humphries et al., 2018; Reis et al., 2019).

Functionally, a prominent postcentral beta power can be detected in individuals at rest, with peak frequencies correlating with endogenous GABA concentrations (Baumgarten et al., 2016). Beta power has historically been associated with vigilance and attention, as indexed by the faster reaction times when target stimuli are presented during spontaneous beta activity (Dustman et al., 1962). Enhanced beta-band activity is associated to sensory processing and learning, including top-down speech perception (Ou & Law, 2019), audio-visual temporal-perception learning (Theves et al., 2020) and multisensory olfactory-auditory integration (Gnaedinger et al., 2019), predicting pitch discrimination sensitivity (Chang et al., 2019). Altered beta oscillations explain detail-oriented visual processing in autism (Ronconi et al., 2020).

The beta rhythm is thought to have a “sensorimotor” function. During tactile stimulation, sensorimotor beta oscillations show a robust ERD and power-decrease relative to baseline, to then synchronise (ERS) and increase in power upon stimulus-termination (Barratt et al., 2018; Bauer et al., 2006; Spitzer et al., 2010; Van Ede et al., 2010). Similar beta dynamics can be observed in motor studies. Contralateral action-planning in the cortical motor complex is accompanied by beta desynchronisation and powerreduction, which decreases further, also extending to the ipsilateral side during action-execution (Grent-’t-Jong et al., 2014; Heinrichs-Graham & Wilson, 2016; Zaepffel et al., 2013). The power decrease during planning may reflect the dynamic change from a resting to an active state of the motor system, and the degree of beta-modulation correlates with individual trait impulsivity (Tzagarakis et al., 2019). Beta re-synchronises immediately after the movement (Heinrichs-Graham et al., 2017; Niedermeyer & Lopes da Silva, 2005), according to the confidence in the internal model of movement (Tan et al., 2016) and delays of about 100 ms upon an error in motor control and evaluation (Little et al., 2018).

#### 5.4. Gamma rhythm

The gamma activity is prominent over the frontal, parietal (Misselhorn et al., 2019; Samuel, 2019; Tan et al., 2019) and occipital lobes (Orehova et al., 2019), and subcortically, including the amygdala (Feng et al., 2019) and hippocampus (Mann et al., 2019; Samuel, 2019). The gamma rhythm is regulated by the interplay between the excitatory glutamatergic signalling of pyramidal neurons and the modulatory GABAergic inputs by interneurons such as parvalbumin-positive basket cells (Buzsáki & Wang, 2012; Sohal et al., 2009; Vodovozov et al., 2018). The regulation between the glutamate/GABA signalling represents a homeostatic control mechanism that is crucial for cortical functioning (Elzohairy et al., 2019; Le Roux et al., 2006).

A functional description of the gamma rhythm requires a major sub-classification of its low-band (30–100 Hz) and its high-band (100–200 Hz) components, the latter of which is known as high-frequency oscillations (HFOs) (Crone et al., 2006; Lee et al., 2017) and are better detected with intracranial recordings (Gardner et al., 2007; Gliske et al., 2018). The HFOs function is yet to be elucidated, although their coupling with hippocampal ripple waves during rapid-eye-movement (REM) sleep suggests a plausible function in memory processing (Aussel et al., 2018; Colgin, 2016; Tort et al., 2013). Recent reports also indicate a role for prefrontal high-gamma in WM (Alekseichuk et al., 2016; Carver et al., 2019). The low-gamma signal is local and has been associated with attention and memory in both sensory and non-sensory areas (Jensen et al., 2007). Specifically, activity within prefrontal and parietal cortices is also involved in the maintenance of sensory information in WM in tasks spanning different sensory modalities, including visuo-spatial (Lundqvist et al., 2016, 2018; Medendorp et al., 2006; Roux et al., 2012) and audio-spatial (Kaiser et al., 2017, 2008, 2009, 2003; Lutzenberger et al., 2002) and somatosensory (Haegens et al., 2010; Von Lautz et al., 2017). Interestingly, cortical gamma MEG activity seems to covary with WM load (Roux et al., 2012), as confirmed by cortical and subcortical electrocorticographic recordings of the frontal lobe (Howard, 2003) and the hippocampus (Van Vugt et al., 2010).

Nonetheless, the homeostatic glutamate/GABA control hypothesis of the gamma rhythm challenges its implication in cognition. The biochemical mechanisms supporting the homeostatic excitatory-inhibitory signalling equilibrium in the cortex are mediated by changes, over successive oscillatory cycles, in frequency, amplitude and phase attributes (Abey Suriya et al., 2018; Adesnik, 2018; Guo et al., 2017; Peterson & Voytek, 2019; Velazquez et al., 2019). The engagement of the gamma rhythm in such cortical regulation may leave no residual degrees of freedom in its spectral dimensions that could account for further information-processing, thus impeding its implication in additional cognitive functions (Merker, 2016). Accordingly, any previously-reported functional association of gamma oscillations with specific cognitive processes might only represent a spurious association due to cortical activation (Merker, 2013). However, temporal and spatial changes in synaptic gain can still impact oscillatory coordination-patterns in any frequency-range, and in turns influence their cognitive function (Wright & Bourke, 2016; Wu et al., 2013). The nature of gamma-band responses to given sensory features and their relationship with perceptual and cognitive processes is still elusive. Isolating the effect of the synaptic dynamics with their geographical distribution and temporal sequence, and of intrinsic cell properties (i.e., excitability) on the oscillatory coordination patterns, may shed light on the current debate on the putative role of gamma oscillations in cognition.

#### 6. The importance of synchrony: From local to distributed networks

When processing information and engaging in cognitive tasks, clusters of neurons within brain circuits become transiently and dynamically connected (Schack et al., 2005; Varela et al., 2001). Neurons of the network that display stronger and closer connections with one another

are more markedly specialised for supporting a given mental process, such as the selectivity for face-perception of some neurons of the fusiform gyrus, in the inferior temporal cortex (Kanwisher et al., 1997; Keller et al., 2017). During a given process, if neural activity from different geographical sources is correlated or if the oscillatory phases from different scalp sources become synchronous, these brain locations are said to be ‘functionally connected’ (Hutchison et al., 2013; Karwowski et al., 2019; Singer, 1999; Wang et al., 2020; Yu et al., 2008).

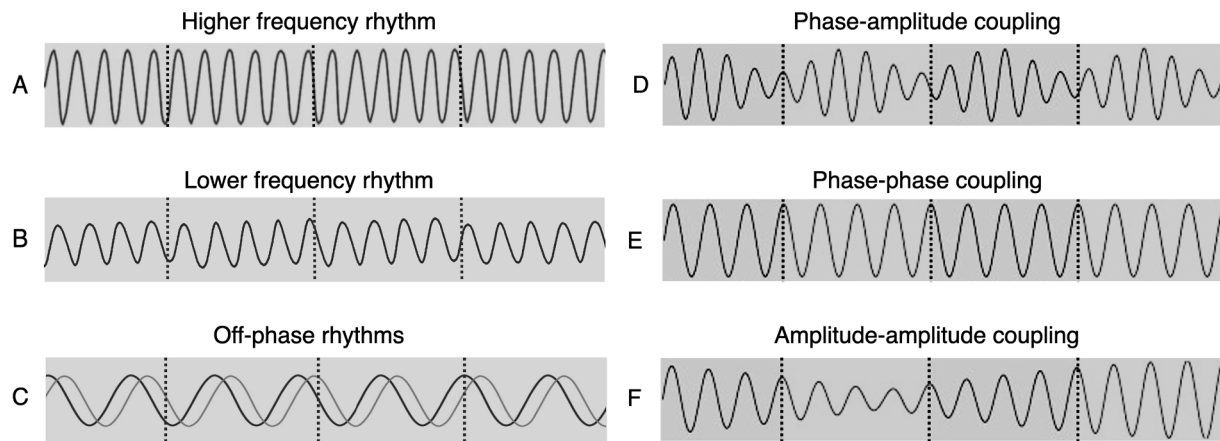
There is extensive evidence that increased local increases/decreases in synchronisation (i.e., ERS/ERD) within specific frequency bands accompany and support different cognitive processes, including sensory-processing, memory maintenance, encoding, manipulation and retrieval (Roohi-Azizi et al., 2017). However, it is becoming clear that more complex cognitive tasks, involving a temporally and quantitatively dynamic contribution of different brain structures, require a fast and flexible communication within circuits (Hampshire et al., 2012; Polanía et al., 2012; Violante et al., 2017). The coordination processes between networks of larger scale and the mechanisms that underlie them are thus receiving increasing attention (Bauer et al., 2020; Beppi et al., 2020).

Large-scale synchronisation can be assessed by recording neural activity in parallel from different locations, determining whether a signal from given locations (voxels or regions of interest) alter in synchrony with one another over time (Harris & Gordon, 2015; Nowak et al., 2017). In EEG/MEG, synchronisation patterns can occur between different attributes of the electrophysiological signal (amplitude or phase) within the same frequency, or between different frequencies. Coordination patterns between different frequencies are called cross-frequency coupling (CFC) (Aru et al., 2015; Canolty & Knight, 2010; Canolty et al., 2006; Cohen, 2008; Tass, 1999; Wilson & Foxe, 2020). CFC between a low-frequency rhythm with a higher-frequency rhythm can be further classified as phase-phase coupling (PPC) (Belluscio et al., 2012; Rings et al., 2020) or phase-amplitude coupling (PAC) (Ohki et al., 2020; Tort et al., 2010; Voytek et al., 2010).

The cross-frequency amplitude–amplitude coupling (AAC) instead defines the correlation between the amplitude envelopes of oscillations of different frequencies (Yeh et al., 2016). Despite its physiological importance (Shirvankar et al., 2010), it is a relatively less studied form of CFC, in part because signals with nonstationary nonlinear oscillations can result in spurious AAC (Yeh et al., 2016). The effects of nonlinearity and nonstationarity can be contained by applying the EMD (Hu et al., 2008; Wang et al., 2015), which can reduce the detection of artificial AACs compared to classical Fourier-based methods (Yeh et al., 2016). A summary illustration of different types of CFC is displayed in Fig. 2. Phase-coordination patterns facilitate the exchange of information within distributed circuits, increasing synaptic plasticity and efficiency (Constantinidis & Klingberg, 2016; Daume et al., 2017; Fries, 2015; Parkin et al., 2015; Violante et al., 2017). Synchronisation patterns can be studied based on different computational models/frameworks, among which *graph theory* is one that has reached widespread popularity (Box 1).

Long-range synchronisation patterns, largely in the alpha band, have been shown to organise resting-state networks during internal mental processes (Jann et al., 2009; Knyazev et al., 2011). Event-related cross-frequency phase-synchronisation patterns seem instead to dynamically (in a time-varying manner) orchestrate the activity of different brain structures devoted to attention, WM and inhibitory control (Beppi et al., 2020; Daume et al., 2017) to fulfil complex cognitive tasks, as we will see in the following sections.

Visuospatial attention load is indexed by alpha-beta cross-frequency PPC within parieto-occipital cortices, which instead reduces during attentional re-orientation (D’Andrea et al., 2019). Internally-guided attention-shifting produces enhanced frontal theta and frontoparietal medial alpha activity, and its spatial orientation is predicted by the occipital alpha lateralisation (Bengson et al., 2020). The enhanced frontoparietal theta coherence in willed attention is bidirectional (Rajan et al., 2019), suggesting that frontal cortices may not only guide parietal



**Fig. 2.** Two types of CFC between a higher frequency rhythm (A) and lower frequency rhythm (B): Unsynchronised oscillations of the same frequency (C). The amplitude of a higher frequency rhythm is modulated by the phase of a lower frequency rhythm resulting in PAC (D). PPC (E) and AAC (F) between the higher frequency and lower frequency rhythms.

### Box 1

Graph theory for the analysis of synchronisation patterns.

Systems neuroscience is a flourishing and actively developing area of research. Electrophysiological, blood oxygenation level and behavioural data, describing the functional dynamics within neural circuits, is becoming incrementally dense and complex. This calls for the necessity of efficient quantitative techniques for data modelling and analysis (Bassett & Sporns, 2017). *Graph theory* is a conceptual framework that can be used to computationally model pairwise relations between the activity of individual elements of a distributed brain network (Hasanzadeh et al., 2020; Smith & Stacey, 2019; Sporns, 2018, 2003). A mathematical graph is made up of nodes (neurons / regions) and edges (connectors), whose functional connectivity can be quantified by different descriptive metrics (Van Wijk et al., 2010; Wang et al., 2020). The *degree* is an absolute quantity defining the number of edges that are incident to a given node, while the *density* represents the ratio of the degree and the number of possible edges (Karwowski et al., 2019; Sun et al., 2019). The *efficiency* describes the shortest path length between nodes as a local or global measure (Roy et al., 2017; Yu et al., 2008) while the hub-like character of nodes is referred to as *betweenness centrality* (Fletcher & Wennekers, 2018; Makarov et al., 2018). These measures are used to identify smaller “communities” within brain networks and the core elements easing the information exchange. Particularly, dynamic (changing over time) and multi-layered models, as well as mathematical topology methods are becoming of wider use (Sporns, 2018, 2003). Insofar, graph theory has been central for the understanding of brain architecture and its methods and measures have been valuable to identify functional cerebral alterations in diverse neurological, neurodegenerative and psychiatric disorders (Bassett et al., 2018; De Haan et al., 2009; Hallquist & Hillary, 2018).

attentional-control but also receive feedback from there to monitor the attentional state. The results overall suggest that long-range CFC between frontoparietal regions mediates reciprocal communications between the frontal executive and parietal attentional-control areas, which support the top-down control and modulation of primary sensory processing.

Nesting of faster oscillations into a slower rhythm constitutes a CFC-mechanism for supporting WM retention, where parietal theta-gamma PAC increases with memory load, predicting memory capacity (Chaieb et al., 2015; Wolinski et al., 2018). These findings received support in a recent study by Zhang et al. (2020) showing that theta-gamma cross-frequency PAC increases over days of WM-training, enhancing network connectivity and transmission-efficiency measures, including mean degree, shortest path length and global efficiency, but not local and small-world properties. Jones et al. (2020) also observed that sustained theta-gamma PAC between prefrontal and temporoparietal regions accompany working-memory training. Strikingly, the strength and timing of the PAC were predictive of WM performance.

Delta-beta PAC between associative cortices is furthermore associated with audio-visual integration (Ohki et al., 2020). Cognitive control in task-switching is instead supported by CFC between low frequencies (delta-theta) within frontoparietal networks, predicting behavioural accuracy (López et al., 2019). Dissociable fronto-parietal synchronisation foci have been identified for the proactive and reactive kinds of executive control (Beppi et al., 2020; Cooper et al., 2015).

Taken together, these findings indicate that long-range CFC, in the form of PAC and PPC patterns, indexes frontoparietal attentional modulation and top-down control over sensory-processing regions, to support complex or cognitively-demanding tasks. While attention, WM and multisensory-integration processes rely on cross-frequency PAC where a fast rhythm (gamma, beta) nests into slower (theta, delta) oscillations, executive control is instead supported by low-frequency CFC patterns. These synchronisation patterns also accompany and mediate large-scale network connectivity changes associated with learning and memory.

The importance of coordination within distributed networks is highlighted by clinical evidence of disrupted or dysfunctional long-range synchronisation in neuropsychiatric conditions (Uhlhaas et al., 2017), such as autism spectrum disorder (Edgar, 2020; Yuk et al., 2020), schizophrenia (Steinmann et al., 2020) and Alzheimer's disease (Hata et al., 2016), predicting its conversion from mild cognitive impairment (Pusil et al., 2019). Novel methods of investigation of synchrony patterns and neurobiological substrates (e.g. Pesaran et al., 2018; Widge et al., 2019) would be beneficial for the understanding of the aetiology and treatment outcome of clinical conditions.

## 7. From electrophysiological recording to brain stimulation

The functional significance of neural oscillations remains elusive. Oscillatory fluctuations constitute a cyclical critical temporal-window of perceptual sensitivity that depends on shifts in neural excitability



(Klimesch, 2012; Thut, Miniussi, & Gross, 2012). Accordingly, the phase of endogenous oscillatory activity would be informing and predictive of detection probability (Becker & Hervais-Adelman, 2019; Mathewson et al., 2011; Uhlhaas et al., 2008). Indeed, retrospective EEG/MEG spectral trial-by-trial decompositions revealed that visual detection correlates with specific phase-angles of theta-alpha endogenous oscillatory signal (Busch et al., 2009; Mathewson et al., 2009; VanRullen et al., 2011). This theta/alpha phase-related effect of perceptual facilitation has also been probed in auditory (Henry et al., 2016) and somatosensory perception (Palva et al., 2005), memory retrieval (Rizzuto et al., 2006) and temporal discrimination (Milton & Pleydell-Pearce, 2016).

As discussed in the previous sections, functional connectivity EEG/MEG studies have provided mounting evidence for the relevance of phase-coupling on cognition, raising the question about the epiphenomenal or causal nature of this link. Stimulation and perturbational approaches can interact and modulate the timing of the endogenous neural oscillations (Chen et al., 2011, 2012; Vosskuhl et al., 2018) using phase-locked sensory stimulation and non-invasive brain stimulation/modulation (NIBS) methods, such as transcranial magnetic stimulation (TMS), transcranial direct-current stimulation (tDCS) and transcranial alternating current stimulation (tACS), explained and illustrated in Box 2 and Fig. 3. Such intervention approaches have allowed the testing of new hypotheses as to the function of neural oscillations and are a continuously evolving research field (Peruzzotti-Jametti et al., 2013). Evidence of fast and recurrent changes in task performance resulting from the manipulation of oscillatory activity would demonstrate causal relations between brain oscillations and cognitive abilities.

Manipulations of the stimuli onset, relative to the phase of ongoing theta-alpha oscillations by periodic ‘attentional cueing’ (e.g. with flickering stimuli), demonstrated that the phase-stimulus coupling predicts cognitive ability in different domains and sensory modalities, including visual and auditory perception (Somer et al., 2020; Landau & Fries, 2012; Romei et al., 2008), episodic memory (Clouter et al., 2017), and temporal detection accuracy (Benedetto et al., 2018). Moreover, by examining visual-target detection at cued and uncued spatial locations that could be part of the same or a different object, Fiebelkorn et al. (2013) demonstrated that the online reweighting of attentional priorities based on space-object relations are supported by stimuli-phase coherent (4–8 Hz) cortical oscillatory patterns, regulated at thalamic level (Saalmann et al., 2012).

By applying phosphene-inducing TMS-pulses over the visual cortex at perceptual-threshold intensity, Dugué et al. (2011) demonstrated that the pre-pulse phase (<400 ms) of ongoing ~10 Hz EEG oscillations predicted visual detection probability. Importantly, phosphene

perception can vary depending on stimulation intensity, frequency and electrode montage. Bayesian optimisation is an active learning method that can be applied to search through the parameter space to identify the combination (e.g. frequency-phase) that elicits the most robust behavioural performance at the individual level. By applying Bayesian optimisation across two different montages, Lorenz et al. (2017) confirmed that differences in the relative phase between cortical electrodes affect tACS-induced phosphene perception. Somer et al. (2020) further revealed that in-phase (0° stimulus-relative phase-difference), relative to antiphase (180°), tACS stimulation improves visual performance when applied at theta-band over the occipital cortex, but not when stimulating over the medial prefrontal cortex or at alpha-band.

While disrupting frontal or parietal networks impairs declarative memory (Kim et al., 2016), their targeted stimulation can modulate neural encoding states and improve memory performance (Ezzayat et al., 2017). Evidence highlights the critical function of frontoparietal circuits in contextual and declarative memory, likely affecting the ongoing oscillatory activity in connected areas, such as the hippocampus. Right frontoparietal tACS during a verbal WM task can improve behavioural performance, in a phase-dependant manner (Violante et al., 2017). Similarly, Polanía et al. (2012) observed that tACS theta-band pulses applied at prefrontal and parietal cortices with 0° phase-difference during a delayed letter-discrimination task significantly improved visual memory-matching reaction times as compared to sham stimulation. Strikingly, the counter ‘antiphase’ condition (180° phase-difference) deteriorated performance.

A recent study applied transcranial current stimulations aligned to the temporal shifts (envelope) of concomitant acoustic speech inputs, observing significant effects on speech-recognition performance in a cocktail-party-like scenario and a listening task (Riecke et al., 2018). It demonstrated that speech-brain entrainment is critical for auditory speech intelligibility, suggesting that transcranial stimulation (with speech-envelope-shaped currents) can be utilised to modulate speech comprehension. However, the semantic facilitation does not necessarily result into an advantage in speech production. A subsequent study applied high-density in-phase theta (4 Hz) tACS over auditory and motor speech areas (i.e., left inferior frontal and superior temporal cortices) to modulate interregional phase-coupling, producing no enhancement in auditory-motor speech mapping compared to antiphase and sham conditions, in a task of nonwords listening and verbal repetition (Preisig et al., 2019). Theta tACS might fail to modulate auditory-motor mapping possibly due to a suboptimal choice of stimulatory parameters, including the electrode positioning (unilateral as opposed to bilateral) or/and stimulatory intensity. While bilateral stimulatory protocols produce an expanded electric field in the area between the two stimulated sites,

## Box 2

### Established NIBS techniques.

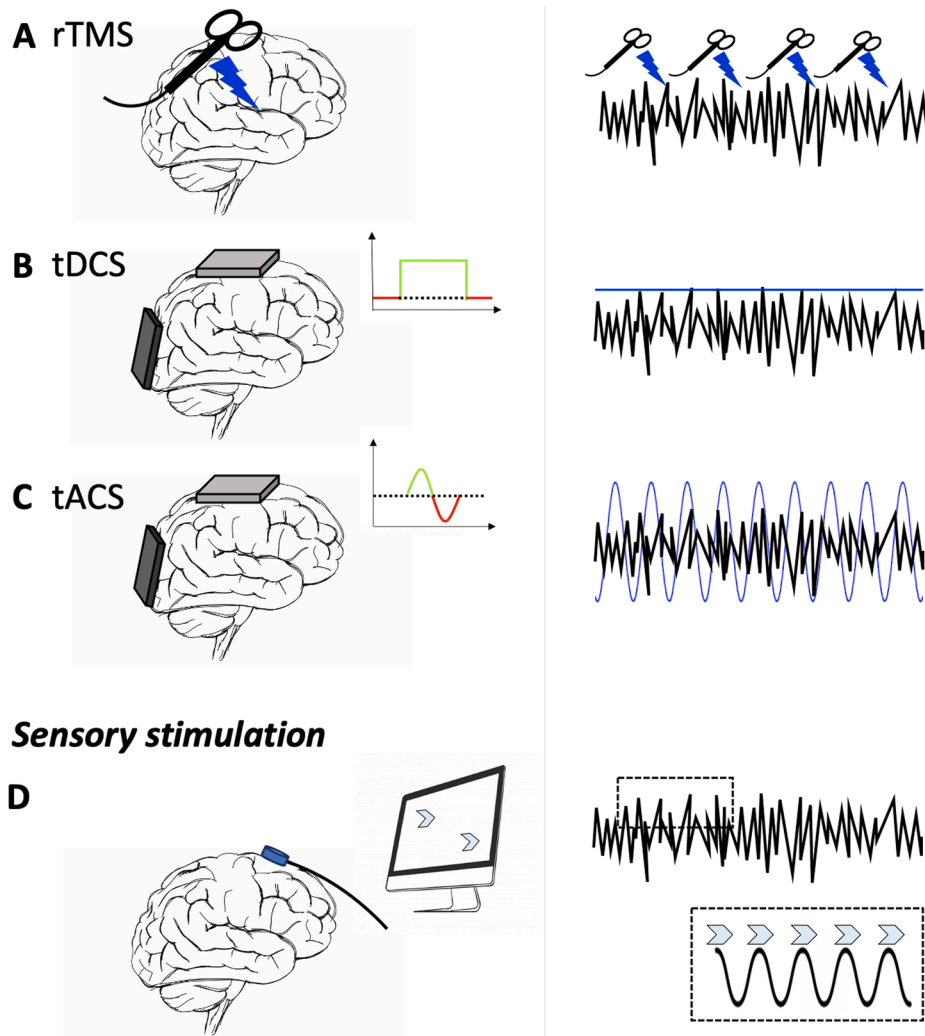
TMS is a well-established non-invasive brain-stimulation technique (Hallett, 2000; Pascual-Leone et al., 2011; Sabel et al., 2020; Thut & Miniussi, 2009). A high-power brief electrical pulse is discharged through the coil, inducing electrical current in the brain by electromagnetic induction (Valero-Cabré et al., 2017). Depending on the stimulation parameters, the current will transiently enhance or disrupt cortical excitability, facilitating or hampering information processing (Iglesias, 2020). TMS can be applied as a single pulse (e.g. to induce small muscle twitching), or as rapid rhythmic pulses (rTMS) (Brunoni et al., 2017). Depending on the frequency, these can hamper ( $\leq 1$  Hz) or entrain and strengthen ( $\geq 10$  Hz) neural oscillations (Milev et al., 2016).

tDCS is an alternative brain-stimulation method that has been gaining increasing interest due to its advantages in terms of safety, flexibility and costs (Filmer et al., 2014; Nitsche & Paulus, 2000; Nitsche et al., 2008; Schoellmann et al., 2019). Like TMS, tDCS can increase/decrease neural activity, although by different principles (Woods et al., 2016). The resting membrane potential of neurons is altered via anodal/positive stimulation (depolarisation) or negative/cathodal stimulation (hyperpolarisation) to modulate the excitability (Sandrini et al., 2015).

tACS is similar to tDCS as a neuromodulatory technique (Antal et al., 2008; Paulus, 2011; Veniero et al., 2015). However, it does not apply direct electrical current, but low-level alternating sinusoidal current (Helfrich et al., 2014; Witkowski et al., 2016). A single constant frequency or several pulsed oscillations can be applied to, respectively, synchronise or desynchronise the endogenous neural oscillations (Antal & Paulus, 2013). A wide range of tACS protocols with different duration, electrode montage, target frequencies (4–70 Hz), phase and amplitude have been probed in distinct cognitive tasks, including attention, perception, WM and motor tasks (reviewed in Tavakoli & Yun, 2017).

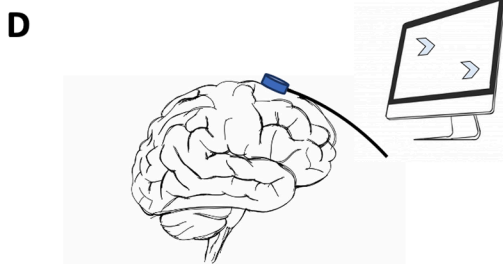


## NIBS



**Fig. 3.** Different stimulation or perturbational approaches. From the top, the three main NIBS methods: rTMS (A), tDCS with external electrodes (B) and tACS (C). The left panel illustrates the respective technique application, with the voltage change over time. The distribution of the electric field, indicating the target area, is represented in grey patches. The right panel depicts the stimulation input (blue) relative to the endogenous EEG/MEG signal (black) from a given channel. On the bottom, a sensory stimulation protocol (D) with a fronto-medial EEG/MEG electrode: the visual stimuli (arrows) are presented in phase (with 0° phase lag) relative to the endogenous brain oscillations, in a given frequency.

## Sensory stimulation



hemilateral configurations induce more focalised electric fields (stimulated area and surrounding tissue), but at the expense of a lower current reaching the brain (Faria et al., 2011). Stronger stimulatory intensities (1.8 mA compared to 1 mA peak-to-peak) are putatively more effective, although more unpleasant.

These brain stimulation studies overall support the retrospective EEG/MEG spectral decompositions (Busch et al., 2009; Henry et al., 2016; Mathewson et al., 2009; Milton & Pleydell-Pearce, 2016; Palva et al., 2005; Rizzuto et al., 2006; VanRullen et al., 2011) validating that the endogenous neural oscillations create, through their phasic fluctuations, periodic ‘windows of excitability’, during which sensory perception is more likely to occur, hence facilitating sensory detection, WM, and speech recognition. Electrode positioning and stimulatory intensity are two important stimulatory parameters that impact the efficacy of NIBS, and must, therefore, be probed (consistent piloting) for obtaining optimal performance (Faria et al., 2011). Mixed results may also relate to small sample sizes and the heterogeneity of outcomes, which cannot be excluded.

### 7.1. Further considerations on NIBS methods

#### 7.1.1. The effects of stimulation intensity

By using a simple cortical computational model of inhibitory and excitatory neurons, Herrmann et al. (2016) showed different types of

rhythmic responses obtainable by NIBS. While with high-intensity stimulations (up to 20 Hz) resonance and entrainment patterns dominate, weaker higher-frequency stimulations (50–100 Hz) induce a mechanism of nonlinear acceleration of the endogenous oscillations, which progressively increases the network’s output frequency (Herrmann et al., 2016).

#### 7.1.2. Adverse effects

No severe negative effects have been reported in tDCS and tACS (Matsumoto & Ugawa, 2017). In TMS, serious adverse effects like seizures and auditory damage are also uncommon (Taylor et al., 2018). Skin problems are the only long-term negative effects of tDCS, while none have been reported for tACS (Matsumoto & Ugawa, 2017). TMS exposes to a ~5% incidence of mild adverse effects, including headache, nausea or local pain over the stimulated area, largely (~78%) post-session, and more predominantly at initial than later sessions (Maizey et al., 2013; Taylor et al., 2018). No correlations between individual-specific factors and TMS frequency or intensity have been observed (Maizey et al., 2013).

#### 7.1.3. The relative efficacy of different NIBS

One might consider differences among NIBS methods in their efficacy with respect to the cognitive aspects that ought to be improved. While rTMS over the dorsolateral prefrontal cortex during an n-back

WM task improved RTs and accuracy relative to sham, tDCS only resulted in faster RTs (Brunoni & Vanderhasselt, 2014). Focal delivery of theta band electrical current, using high-definition tACS, delivered to the right fusiform cortex during encoding of visual associations improved memory performance, while tDCS and sham had no effect (Lang et al., 2019). Similarly, Röhner et al. (2018) compared the effects of theta tACS (6 Hz) on frontal-parietal loop, sham, and anodal tDCS on dorsolateral prefrontal cortex on WM performance, by mean of a within-subject crossover (time-counterbalanced) design. A larger RT improvement resulted from tACS compared to tDCS. These behavioural differences might stem from the different modulatory actions exerted by the NIBS techniques. While tACS effects on the functional connectivity of WM circuits are driven by activity increases within posterior DMN areas, both during and post-stimulation, tDCS induces a post-stimulation decrease in prefrontal DMN activity compared to during the stimulation, with these activity reductions being associated with faster RTs (Abellaneda-Pérez et al., 2020). Consistently, Kim et al. (2020) observed that the modulatory action of tDCS is focalised frontally, while tACS induces more widespread fronto-central, parietal and temporal modulations. Based on the findings, it can be concluded that tACS and TMS might be more effective than tDCS at optimising associative and WM performance, and should therefore be favoured in future work aiming at improving these specific cognitive aspects.

## 7.2. The translational potential of non-invasive brain stimulation

Capitalising on the understanding of the relation between oscillatory dynamics and their attributes with perceptual and WM processes, brain-stimulation methods have the potential to improve clinical symptoms of different conditions.

Parkinson's disease (PD) is a neurodegenerative disease that impairs motor and cognitive abilities (Sveinbjornsdottir, 2016). With a progressive course and no counteracting remedy yet available, the development of novel therapeutical approaches to alleviate disabling and discomforting symptoms constitutes a priority (Mateus & Coloma, 2013). Schoellmann et al. (2019) recently showed that high-beta tDCS stimulation over the left sensorimotor area modulated the oscillatory synchronisation, improving the clinical motor outcome of PD patients, as measured by the fine motor-control performance of their distal upper-limb. Consistently, a meta-analysis showed an overall positive effect on motor function of rTMS and tDCS compared to sham stimulation, but no significant effect on cognition. No effects of stimulation parameters on motor or cognitive function were observed (Goodwill et al., 2017).

In the context of cerebrovascular diseases, high (>3 Hz) or low ( $\leq 1$  Hz) frequency repeated TMS (rTMS) can be used to, respectively, increase the excitability of the ischemic brain structure or reduce the excitability of the contralateral homonymous area (Kubis, 2016). Such neuromodulatory treatments have demonstrated positive outcomes on the neurological disease scales and a functional disability score of stroke patients (Koch & Hummel, 2017; O'Brien et al., 2018), especially for the upper-limb motor-control recovery (Kubis, 2016).

The same rehabilitative principles of altered cortical excitability and plasticity apply to Multiple Sclerosis (MS), an inflammatory demyelinating disease of the central nervous system, characterised by relapsing-remitting neurological dysfunctions (80–85%) or/and the progressive accumulation of neurological disability (15–20%) (Dobson & Giovannoni, 2019; Lassmann, 2018). Despite the existence of multiple pharmacological interventions, MS symptoms including neuropathic pain, spasticity and psychiatric symptoms remain a challenge, calling for the necessity of novel therapeutical approaches (Baecher-Allan et al., 2018). However, stimulatory parameters and target brain areas differ depending on an individual's specific symptomatology, and the occurrence of structural neural changes in MS hinder the modulatory effects, reducing the efficacy of NIBS therapies (Iodice et al., 2017). Indeed, the applicability of rTMS and tDCS for the treatment of MS symptoms including depression, fatigue, tactile sensory deficit, pain, motor

performance, and spasticity has shown mixed results in several studies (reviewed in Palm et al., 2014).

Individuals with Autistic Spectrum Disorder show decreased ability to phase-lock to sensory stimuli in the low-gamma frequency-range (De Stefano et al., 2019) and multiple sessions of high-frequency rTMS can re-set their oscillatory patterns, improving the executive functioning of both young and older individuals (Ameis et al., 2020). Unilateral and bilateral motor cortex tDCS results in anterior cingulate network modulations and behavioural improvements in semantic fluency and motor speech in both young and old adults, with a higher left-laterality effect in the latter group (Martin et al., 2017). Similarly, Perceval et al. (2020) demonstrated that multi-session tDCS can improve short-term verbal associative learning in older adults, and long-term maintenance in both old and younger individuals, with stronger effects on those with higher learning deficits. The studies support that tDCS can enhance language acquisition and fluency in healthy individuals and potentially improve language reacquisition after stroke-related aphasia.

NIBS can improve memory reconsolidation (reviewed in Sandrini et al., 2018; 2015), presumably by reproducing long-term potentiation (Agboada et al., 2020; Shimizu et al., 2020), despite variability in the results (Guerra et al., 2020; Hordacre et al., 2017). More benefits are obtainable if applying NIBS before or during learning, compared to during an assessment (Simonsmeier et al., 2018). Hence, memory recall may occur at critically restricted temporal-windows, during which they are susceptible to modification (decay/consolidation). NIBS may improve memory impairments resulting from healthy ageing and neurological memory disorders, such as mild cognitive impairment and Alzheimer's Disease (Flöel, 2017; Goldthorpe et al., 2020; Ladenbauer et al., 2017).

In sum, NIBS can modulate brain activity by enhancing the oscillatory coherence and synaptic plasticity, and, hence, has the potential to produce long-term therapeutic effects for different motor, language and memory disabilities. The applicability of NIBS to neuropathologically and clinically heterogeneous disorders (e.g., MS) remains a challenge. To increase the effectiveness and utility of NIBS in clinical contexts, future research should prioritise the exploration of stimulation parameters based on individual-specific symptomatology and resting-state excitability.

## 8. Conclusions

The phasic fluctuation of neural oscillations provides periodic restricted temporal windows of higher perceptual sensitivity and memory lability (for decay/consolidation). This advantage is supported by transient increases in cortical excitability and synaptic plasticity. Phase-synchrony within circuits of large scale has a critical role in the accomplishment of complex functions. Brain-stimulation protocols can target critical large-scale circuits to enhance oscillatory phase synchrony to facilitate the attentional and perceptual processes supporting WM, learning and motor control. The translational value of brain-stimulation methods is a promising avenue for further investigation and development in cognitive and clinical neurosciences.

Further research is needed to shed light onto the role of phase, particularly with regards to its putative causal link to cognitive performance. While previous NIBS studies have already imposed current with different oscillatory phases (e.g. peak, trough, sham) between electrodes, extending this to closed-loop approaches that trigger stimulation at particular endogenous phases of a rhythm might further inform the effect of phase on behaviour. Moreover, future studies might explore the anatomical distribution of relevant large-scale circuits and the temporal/chronological order of their respective contributions during a given complex cognitive or motor task. Neurostimulation aiming at improving short-term and long-term memory should target long-range memory networks to facilitate their exchange of information, rather than targeting an individual brain region. Stimulation parameters such as pulse intensity, frequency and electrode montage, are also critical factors

influencing the outcome of neuromodulation that need to be appropriately targeted. In particular, high-density focal (hemilateral) stimulation and electrode size are currently active areas of investigation (Lang et al., 2019). To these purposes, Bayesian optimisation methods (e.g. Lorenz et al., 2017) can be applied to identify the optimal stimulation parameters, but also to increase the probability and extent of efficacy in specific cognitive domains or/and clinical conditions.

It is becoming clear that the distinct neuromodulatory principles of the various NIBS methods might better apply to certain cognitive functions (e.g., tACS > tDCS for WM). Future work should explore different NIBS in comparison (e.g., Lang et al., 2019; Röhner et al., 2018; Brunoni & Vanderhasselt, 2014) to understand their relative efficacy for improving a given function or task. The efficacy of NIBS in the symptomatic treatment of neuropathologically and clinically heterogeneous disorders (e.g., MS) is still limited. Future work might explore stimulatory settings according to individual-specific symptomatology and resting-state excitability, in the attempt to improve the clinical applicability of NIBS. Larger sample size and power analyses would be required to reduce the incidence of mixed results and unreplicated findings.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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