



# New vistas for $\alpha$ -frequency band oscillations

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The amplitude of  $\alpha$ -frequency band (8–14 Hz) activity in the human electroencephalogram is suppressed by eye opening, visual stimuli and visual scanning, whereas it is enhanced during internal tasks, such as mental calculation and working memory.  $\alpha$ -Frequency band oscillations have hence been thought to reflect idling or inhibition of task-irrelevant cortical areas. However, recent data on  $\alpha$ -amplitude and, in particular,  $\alpha$ -phase dynamics posit a direct and active role for  $\alpha$ -frequency band rhythmicity in the mechanisms of attention and consciousness. We propose that simultaneous  $\alpha$ -,  $\beta$ - (14–30 Hz) and  $\gamma$ - (30–70 Hz) frequency band oscillations are required for unified cognitive operations, and hypothesize that cross-frequency phase synchrony between  $\alpha$ ,  $\beta$  and  $\gamma$  oscillations coordinates the selection and maintenance of neuronal object representations during working memory, perception and consciousness.

## Introduction

Hans Berger was among the first to witness electroencephalogram (EEG) rhythms in the  $\alpha$ - (8–14 Hz) and  $\beta$ - (14–30 Hz) frequency bands [1]. During the following four decades, the parieto-occipital  $\alpha$  rhythm was found to be attenuated by eye opening, visual stimuli and by increased attentiveness. These findings inspired the idea of  $\alpha$  oscillations functioning as an ‘idling’ rhythm that characterizes an alert-but-still brain state [2]. Today, the idling hypothesis has been largely overtaken by a framework where the amplitude of  $\alpha$  oscillations reflects a level of cortical inhibition [3–7]. Accumulating data on  $\alpha$  phase dynamics [8–12], however, add a twist to the story; endogenous as well as stimulus-locked  $\alpha$ -band phase correlations seem to have a direct role in the neuronal machinery underlying behavioral-level phenomena, such as attention, STM and sensory awareness. These findings challenge the inhibition hypothesis, as well as the prevailing interpretation of  $\alpha$  amplitude dynamics.

## Do large-amplitude $\alpha$ oscillations reflect cortical inhibition?

Early on, the  $\alpha$ -band oscillations were observed to be strengthened during internal tasks, such as mental

arithmetic and visual imagery, which was interpreted by Ray and Cole [3] to reflect rejection of sensory information intake. This idea was advanced into an  $\alpha$ -inhibition hypothesis by Klimesch [4] and Pfurtscheller [5,6], who proposed that small  $\alpha$  amplitudes are a signature of regions of active neuronal processing, whereas large-amplitude  $\alpha$  oscillations reflect the inhibition and disengagement of task-irrelevant cortical areas. The core phenomenon supporting this hypothesis is the  $\alpha$ -amplitude suppression, also known as event-related desynchronization (ERD), that follows sensory stimuli in the corresponding sensory areas [13] (Figure 1a). In addition, in some experimental paradigms,  $\alpha$  amplitude is enhanced in EEG electrodes surrounding those where the ERD is observed [5–7]. Although changes in the amplitude of  $\alpha$  oscillations indeed seem to be involved in the continuation of sensory stimulus processing [14], we argue here that it is unfeasible to deduce in a one-track fashion that large  $\alpha$  amplitudes correspond to inhibited or disengaged cortical states.

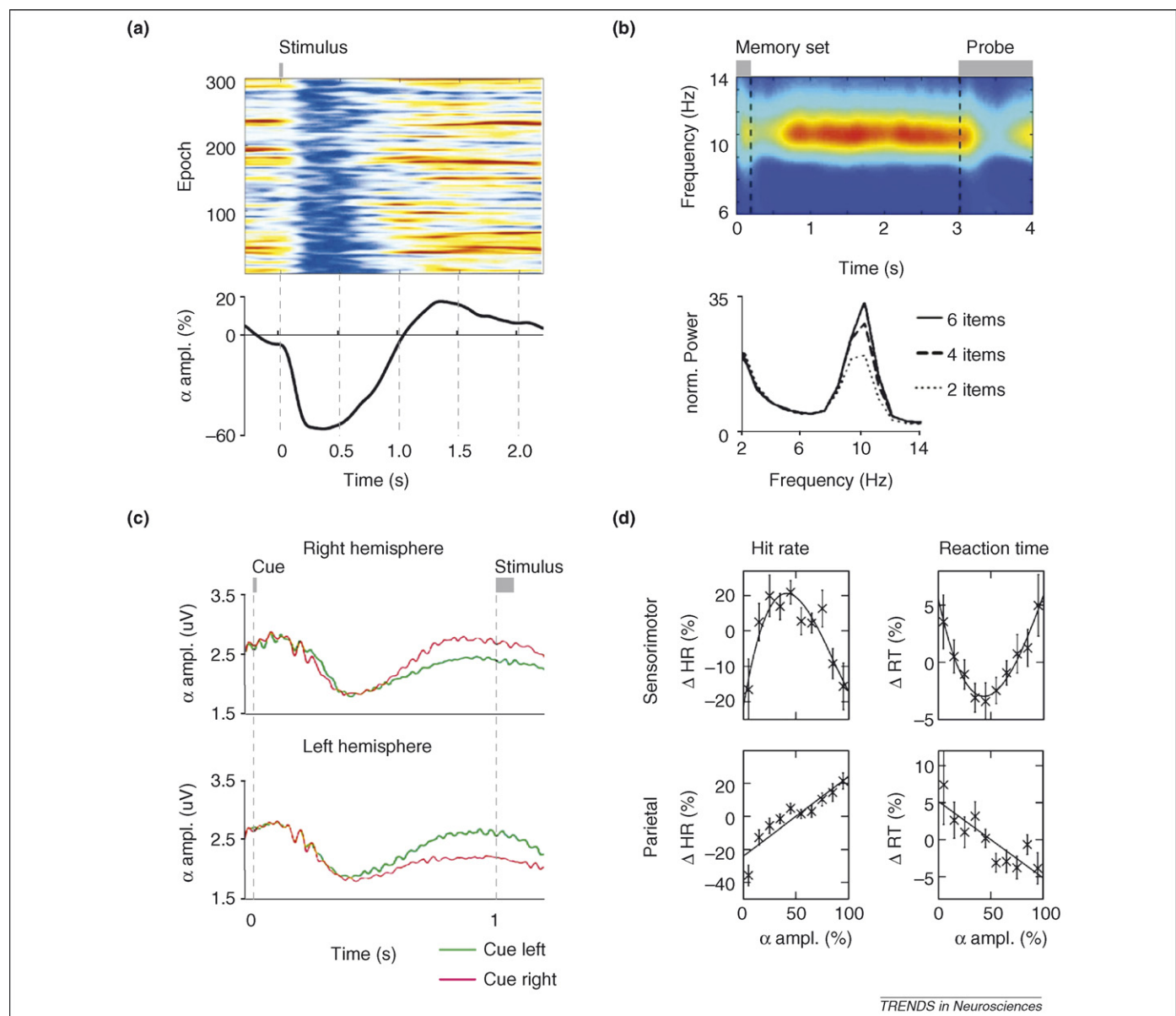
A large body of recent data confirms that  $\alpha$  oscillations are strengthened by internal tasks, such as mental calculation [11] and mental imagery [15–17]. In addition,  $\alpha$ -band amplitude is also enhanced during the short-term- (STM) and working memory (WM) retention period, and is suppressed thereafter [18–20] (Figure 1b). Klimesch *et al.* [7] suggest that these large-amplitude oscillations during memory retention inhibit the retrieval of memorized items, and that this is then reflected in the subsequent amplitude suppression. We propose that the STM- and WM-related  $\alpha$  oscillations in the frontoparietal network [10,11,18] during the memory retention period are an essential constituent of the network activity that sustains the neuronal representations of memorized items. In this light, the retrieval-associated  $\alpha$  suppression [18] (Figure 1b) reflects, in part, the termination of the memory process itself. This view is supported by the positive correlation of the  $\alpha$  amplitude with the STM and WM load [18,19] (Figure 1d) and task difficulty [20].

Besides being modulated by sensory stimuli and movements, the  $\alpha$ -frequency band amplitude is also modulated by attention. In visual attention tasks, visual [21] and auditory [22] cue stimuli are followed by an  $\alpha$  suppression that is larger in the occipital cortex contralateral than ipsilateral to the attended visual hemifield (Figure 1c). According to the inhibition framework, this post-cue and pretarget stimulus  $\alpha$  suppression, as well as the

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**Figure 1.** Event-related  $\alpha$ -band amplitude dynamics in the human brain. **(a)** In the sensorimotor cortex, the amplitude of ongoing  $\alpha$ -frequency band oscillations, as recorded by MEG, is consistently suppressed by suprathreshold electrical stimuli to the median nerve. Amplitude of single trials is color coded (blue, small; red, large). Amplitude ('ampl.') is averaged across trials and expressed relative to the baseline amplitude. Modified, with permission, from Ref. [13]. **(b)** Subjects were presented visually with six items ('memory set'), of which two, four or six had to be memorized until the probe stimulus was presented and the subject indicated whether the 'probe' item was one of memorized items. Parietal EEG  $\alpha$ -frequency band amplitude is enhanced throughout the STM retention period (yellow and red colors correspond to large amplitudes). During the retention period,  $\alpha$ -frequency band amplitude dependent on the number of memorized items. Modified, with permission, from Ref. [18]. Abbreviation: norm., normalized. **(c)** A symbolic 'cue' (an arrow) pointing to the to-be-attended hemifield was followed by a 'stimulus' in the left or in the right hemifield. The subject was instructed to react to specific target stimuli in the attended hemifield. After the cue, EEG  $\alpha$ -frequency band amplitude, averaged over trials, is smaller in the occipital cortex contralateral to the attended visual hemifield. Modified, with permission, from Ref. [21]. **(d)** The subjects' finger tips were stimulated electrically at the threshold of sensation. The subjects were instructed to react to perceived stimuli. In MEG recordings, the intermediate (but not the small or large) prestimulus  $\alpha$ -frequency band oscillations in the sensorimotor cortex facilitate stimulus detection. In the parietal cortex, by contrast, large amplitude oscillations are associated with best behavioural performance. Modified, with permission, from Ref. [23].

post-target-stimulus ERD, reflects the 'spotlight of attention' that is physiologically implemented indirectly by releasing the task-relevant areas from inhibition, through  $\alpha$  ERD, and by suppressing task-irrelevant regions with large-amplitude  $\alpha$  oscillations [7]. However, the effect of attention on mean  $\alpha$  amplitude in the visual cortex is relatively minor ( $\sim 10\%$  of the baseline level [21,22]) in comparison with the trial-by-trial variation in  $\alpha$ -frequency band amplitude, which is, in general, considerable [13,23] (Figure 1a). Interestingly, in a somatosensory detection task, small and large prestimulus  $\alpha$ -frequency

band amplitudes in the sensorimotor region led to equal psychophysical performance [23]. In fact, in this study, intermediate prestimulus  $\alpha$  amplitudes were associated with facilitated detection and the fastest reaction times (Figure 1d). These observations are not in line with the concept of the  $\alpha$  amplitude having a linear relationship with cortical inhibition, and nor would these results be seen in amplitude estimates averaged across trials. Unfortunately, this type of a single-trial analysis has not been published for the attention-task data [21,22]. Moreover, in the study by Linkenkaer-Hansen *et al.* [23], the

best behavioral performance was preceded by the largest parietal  $\alpha$  oscillations (Figure 1d). This can be seen to reflect the inhibition of (task-irrelevant, visual) cortical areas but, equally well, the finding might show task-relevant  $\alpha$ -frequency band network activity in parietal regions that contribute to the attentional control of the detection task.

All things considered, investigations of amplitude dynamics, as such, are inconclusive on the functional role of  $\alpha$ -frequency band oscillations. In the majority of the amplitude data,  $\alpha$  oscillations might be seen to reflect active processing in task-relevant networks or active inhibition of task-irrelevant regions, or both. Notably, many of the conclusions have been based on EEG recordings that involve considerable spatial smearing and are therefore difficult to exploit in the identification of the task-relevant or -irrelevant cortical regions. More importantly, it is problematic, if not impossible, to interpret the neurophysiological underpinnings and consequences of changes in field oscillation amplitude (Box 1). Therefore, the functional significance of  $\alpha$ -amplitude dynamics in task execution remains unclear.

### Alpha-frequency band phase correlations

Compared with the large body of data on  $\alpha$ -amplitude dynamics, investigations on  $\alpha$ -phase dynamics have remained infrequent, although this line of research is now rapidly gaining popularity. Phase synchrony is essential in the formation of transient neuronal assemblies [24], in communication therein [25] and, consequently, in large-scale integration [26]. Phase interactions thus define

functional networks in the cerebral cortex. Therefore, we propose here that it is the phase (Box 1), not amplitude, dynamics that reveals the functional significance of  $\alpha$ -frequency band rhythmicity.

Using magnetoencephalography (MEG), we observed that ongoing  $\alpha$ -frequency band oscillations in human sensorimotor, as well as frontoparietal regions known to be relevant for attention [27] and consciousness [28,29], phase lock selectively to weak somatosensory stimuli that become consciously perceived [12] (Box 1, Figure 1a, b). Also,  $\gamma$ -frequency band (here, 30–50 Hz) phase locking was selective for perceived stimuli but was very local, perhaps present only in the primary somatosensory area (Box 1, Figure 1b). However, although the phase locking of large-scale  $\theta$ - (4–7 Hz) and more local  $\beta$ - (14–30 Hz) frequency band oscillations was clearly correlated with conscious perception, this phase locking was highly significant also for the unperceived stimuli. Thus, perception-selective  $\alpha$ -frequency band phase locking in sensorifrontoparietal networks indicates a direct role for  $\alpha$ -frequency band phase correlations in neuronal processes supporting consciousness. In these data, the phase locking in not only  $\alpha$ -, but also in  $\beta$ - and  $\gamma$ -bands was followed by an amplitude suppression that was greater for the perceived than for the unperceived stimuli. Nevertheless, this amplitude suppression (or ERD), especially in the  $\alpha$ -frequency band, is unlikely to reflect active stimulus processing because the most pronounced suppression takes place after the behavioral responses of the subjects (Box 1, Figure 1c).

The relevance of  $\alpha$ -frequency band phase dynamics has also been recognized in several other studies. Gail *et al.* [30]

### Box 1. Event-related phase and amplitude dynamics

We describe here the data-analysis approaches that have been most widely used in the investigations on  $\alpha$  oscillations presented in here.

For several decades, averaging across several stimulus presentations has been used to isolate information on event-related neuronal processing from recordings of ongoing neuronal activity. Traditionally, peristimulus epochs of recorded data are 'cut' and averaged to obtain an 'evoked' response [Figure 1(a)(i)]. Evoked responses contain time domain signal components that are locked to the stimulus, whereas activities uncorrelated with the stimuli are lost in the averaging procedure.

It is possible to identify components that are not stimulus-locked by averaging estimates of the signal amplitude instead of the signal itself [Figure 1(a)(iii)]. This approach reveals 'mean amplitude dynamics' or 'induced' oscillations [51]. In many studies on  $\alpha$ -frequency band oscillations, the amplitude is estimated by squaring or rectifying a conventionally filtered signal before averaging, as in the 'ERD' [6] or 'temporal spectral evaluation' [15] methods, respectively. Alternatively, the continuous 'analytical' amplitude [as in Figure 1(a)(iii)] can be obtained with complex wavelets [12,51], as well as with conventional filtering utilized with the Hilbert transform [12].

Classical time-domain averaging is an acceptable approach in a scenario in which activities of interest are evoked by stimuli but buried in ongoing, uncorrelated background 'noise'. However, it has been realized that the evoked responses in EEG and MEG might also arise from a phase reset of ongoing oscillations. Because conventionally filtered signals contain both phase and amplitude information, the magnitude of evoked responses does not index the extent of such phase locking. The phase locking of ongoing activity to stimuli can be quantified by first obtaining the continuous phase [Figure 1(a)(ii)] and averaging as earlier, but by utilizing a measure of phase dispersion, such as the PLF [12], across the epochs for each point in time [Figure 1(a)(ii)]. The continuous phase can be obtained with both

wavelet and Hilbert-transform approaches [12,51]. Finally, it should be noted that, in addition to phase reset, evoked components are also visible in phase-locking analyses.

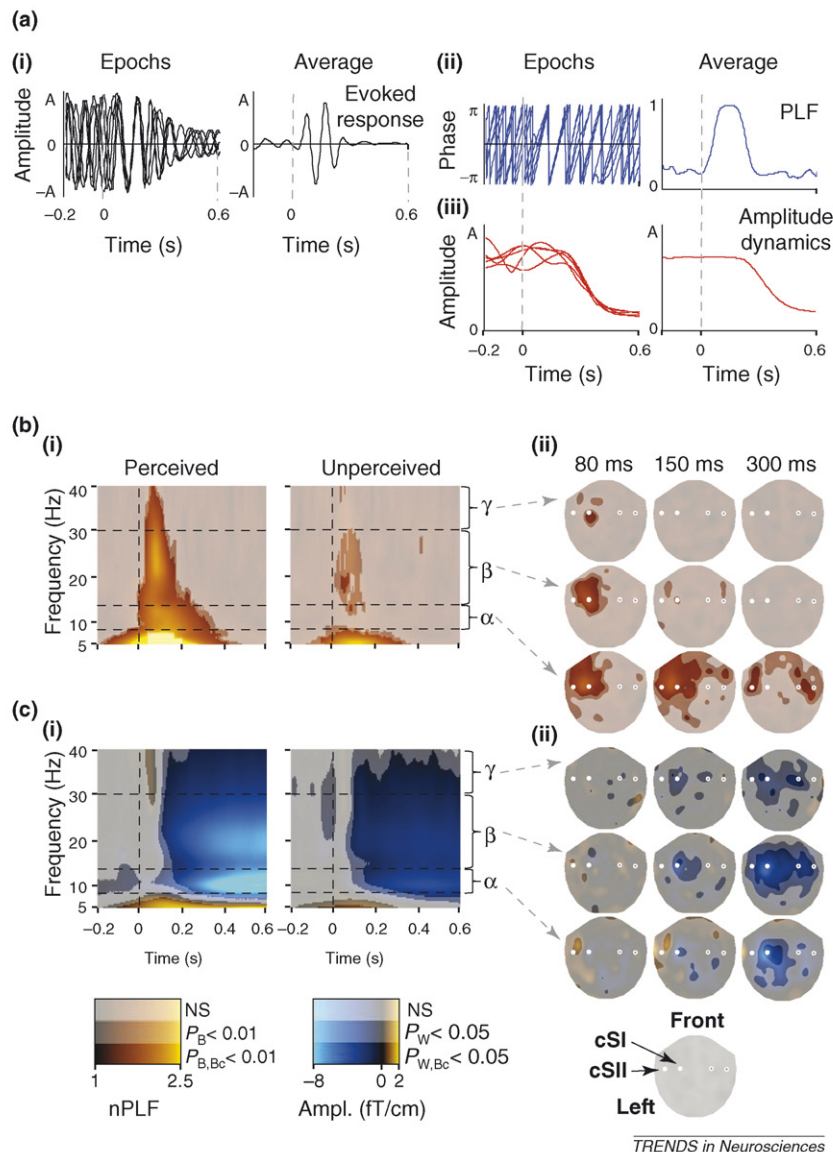
### Interpretation of field amplitude dynamics

The classical assumption underlying the interpretation of EEG and MEG amplitude changes is that the overall neuronal activity level is approximately constant, and the field amplitude changes are caused by changes in neuronal synchrony. Hence, an amplitude decrease is called an ERD and an amplitude increase an 'event-related synchronization' (ERS).

However, in the absence of changes in actual synchrony, the field amplitude might change if the number of neurons entrained to the oscillation is changed. In addition, phase relationships of subpopulations strongly affect the field amplitude. For instance, without changes in the number of active neurons or in the total degree of synchrony, a thalamic  $\alpha$  oscillation waxes and wanes depending on the size of an antiphase subpopulation in the thalamic network [39]. Moreover, considerable phase ordering might take place in the absence of amplitude changes [12] or even during simultaneous amplitude suppression [9,10]. Thus, caution must be exerted when making physiological or functional inferences based on oscillation amplitude.

However, regardless of the recording method and level of inspection, the phase of an oscillation is always, at least approximately, related to spike timing. The presence of field-signal phase synchrony thus indicates the presence of neuronal-level spike synchrony, which is relevant in the light of the crucial role of spike timing in neuronal communication [25,79]. Similarly to the case of amplitude, the estimation of phase dynamics also contains several pitfalls but it is our view that the phase information remains crucial in the identification of functional neuronal networks.





**Figure 1.** (a) Simulated 8–12 Hz ongoing activity (i) with phase (ii) and amplitude (iii) dynamics reminiscent of those observed in MEG data [12]. Note that for visualization purposes, the strength of phase locking (ii), as well as the magnitude of event-related amplitude suppression (iii) have been exaggerated here. (b) (i) Phase locking of ongoing activity over the primary somatosensory cortex to weak somatosensory stimuli. Phase locking in the  $\alpha$ -frequency band is significant exclusively for the stimuli that were consciously perceived. (ii) Unlike the phase locking in the  $\beta$ - and  $\gamma$ -frequency bands, the  $\alpha$ -frequency band phase locking to the perceived stimuli involves a large-scale frontoparietal network. (c) (i,ii) Interestingly, early phase locking in the  $\alpha$ -,  $\beta$ - and  $\gamma$ -frequency bands was not associated with significant changes in mean amplitude, whereas phase locking in the  $\theta$ -frequency band was closely paralleled by an enhanced amplitude. This suggests that  $\theta$ -frequency band phase locking reflects a classical evoked component, whereas  $\alpha$ - and  $\beta$ -frequency band phase locking is produced by a phase reset of ongoing activity [44]. Phase locking (b) and amplitude (c) are color scaled. The transparency scale indicates the statistical significance of the results: Bc, Bonferroni correction with the number of samples (b, 240) or channels (c, 102); cSI and cSII, putative locations of contralateral primary and secondary cortices, respectively; NS, not significant;  $P_B$  and  $P_W$ ,  $P$  value of Binomial and Wilcoxon signed-rank statistics, respectively. Modified, with permission, from Ref. [12].

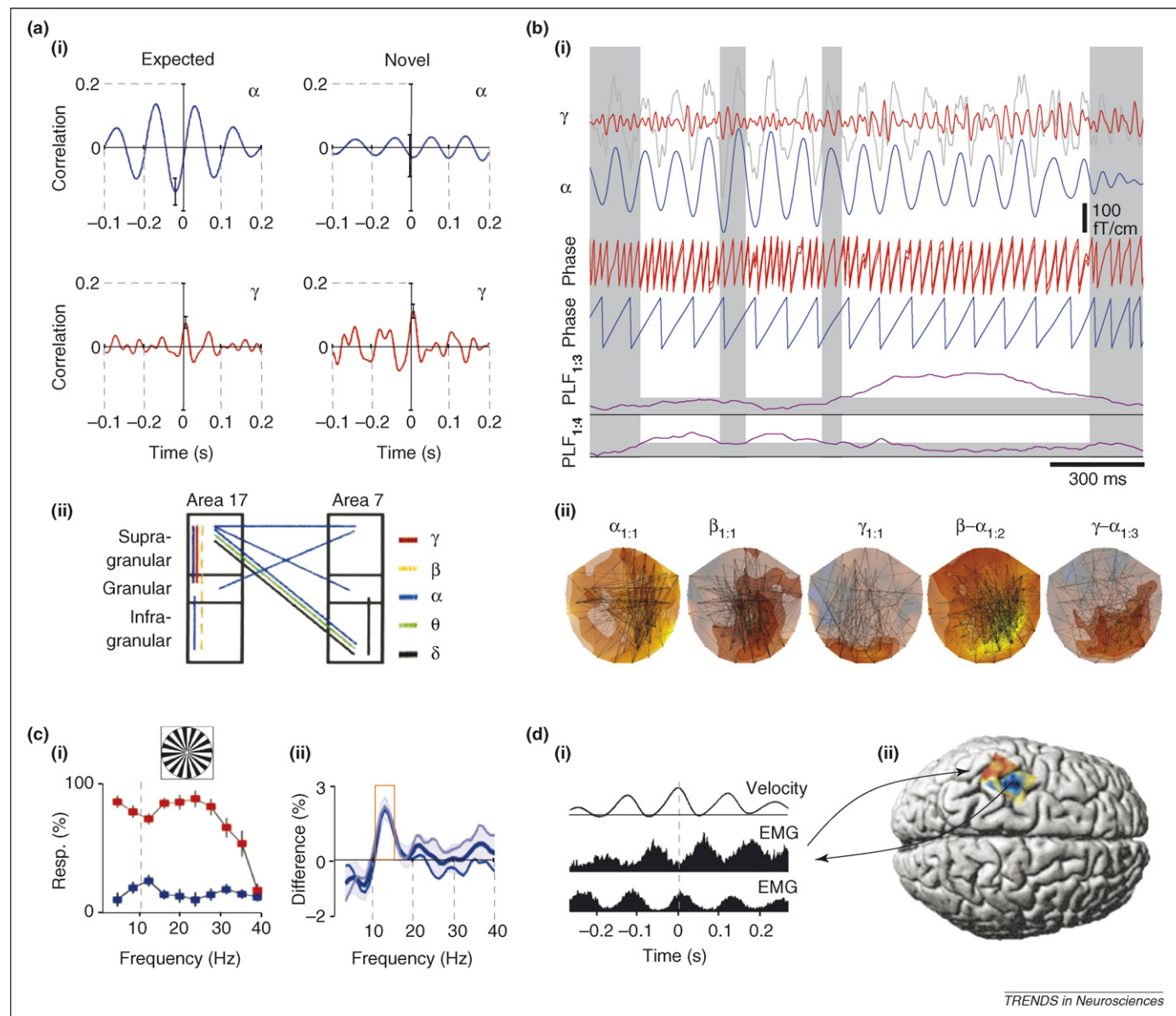
recorded field potentials and multiunit activity from the monkey primary visual cortex and found that the field potential coherence in 4–12 Hz and 12–28 Hz bands was positively correlated with perception in binocular rivalry. Mima *et al.* [9] presented human subjects with meaningful and meaningless visual objects and found that, when attended, meaningful objects strengthened EEG  $\alpha$ -frequency band coherence in the occipitotemporal region. Meaningless or unattended objects were followed by decreased coherence. Hanslmayr *et al.* [31] used a perceptual discrimination task and found stronger phase locking in the EEG  $\alpha$ -frequency band for the good than bad performers. Using depth electrodes in human intracranial

recordings, Halgren *et al.* [10] observed phase synchrony in  $\alpha$ - and other frequency bands in occipital, parietal, frontal and Rolandic regions during periods of mental calculation and WM maintenance. In MEG recordings of human cortical ongoing activity, we found that mental calculation is associated with enhanced frontoparietal  $\alpha$ - and  $\beta$ -frequency band phase synchrony [11]. Taken together, these data show that cognitive tasks involve pronounced large-scale  $\alpha$ -frequency band phase synchrony.

In their seminal work, von Stein and colleagues [8], recorded field potentials from the primary visual cortex (area 17) and from a higher-level association area (area 7)

in cats performing a 'Go-No-Go' task. Their data showed that **interareal  $\alpha$ -frequency band synchrony was prominent during 'Go' trials and negligible during 'No-Go' trials. Moreover, this interareal  $\alpha$ -frequency band synchrony was**

**prominent in the responses to the expected stimuli but absent in responses to occasional novel stimuli (Figure 2a). These data show that  $\alpha$ -frequency band synchrony is involved in top-down modulation of behaviorally**



**Figure 2.** Evidence supporting a direct role for  $\alpha$ -frequency band oscillations in the mechanisms of the global neuronal workspace. **(a)** (i) Cats were trained to perform a Go-No-Go task. The well-learned target and non-target stimuli were then interspersed with novel stimuli. Cross-correlation analyses of local field potentials recorded from the primary visual cortex (area 17) and distant visual association cortex (area 7) show that  $\alpha$ -frequency band synchrony (upper row) is prominent for 'expected' target stimuli (left-hand column) and insignificant for both the 'novel' stimuli (right-hand column) and the No-Go stimuli (not shown).  $\gamma$ -Frequency band synchrony (lower row), by contrast, was stronger for the novel than for the expected stimuli. (ii) Patterns of strengthened (unbroken lines) and attenuated (dashed line) synchrony during 'Go' stimuli.  $\gamma$ -Frequency-band synchrony (red) is predominantly local and is found only in the granular and supragranular layers of area 17.  $\alpha$ -Frequency band synchrony (blue), by contrast, is robust both intra- and interareally, and especially between the infragranular layers of area 7 and supragranular layers of area 17. The data in (i) and (ii) indicate a role for large-scale  $\alpha$ -frequency band synchrony in attentional top-down modulation. Modified, with permission, from Ref. [8]. **(b)** (i) MEG recordings of ongoing neuronal activity in the human brain reveal that  $\gamma$ - (red) and  $\alpha$ - (blue) frequency band oscillations can become transiently 1:3- and 1:4-phase synchronized. The phase-locking factor ('PLF<sub>1:3</sub>' and 'PLF<sub>1:4</sub>') traces above the gray horizontal rectangle indicate periods of statistically significant cross-frequency phase synchrony. 1:3  $\gamma$ - $\alpha$  synchrony is also easily seen in the continuous 'phase' traces of  $\gamma$ - and  $\alpha$ -frequency band oscillations (see red-blue striped arrows). (ii) Compared with active rest, continuous mental calculation tasks enhance both within-frequency (1:1) and cross-frequency (1:2 and 1:3) phase synchrony among  $\alpha$ -,  $\beta$ - and  $\gamma$ -frequency band oscillations. Modified, with permission, from Ref. [11]. **(c)** (i) Continuous wagon-wheel illusion experiments with human subjects show that illusory reversals are most frequent at motion frequencies in the  $\alpha$ -frequency band. The graph shows reported actual (red squares) and opposite (blue squares) motion perception averaged across subjects. These data suggest that human visual perception takes place in discrete frames occurring at  $\alpha$ -frequencies. Modified, with permission, from Ref. [69]. (ii) The difference in EEG amplitude between a perception of real and illusory motion is significant (orange square) only in the upper  $\alpha$ -frequency band and is independent of the temporal frequency of the stimulus. The findings suggest that  $\alpha$ -frequency band neuronal oscillations are involved in perceptual sampling. Modified, with permission, from Ref. [72]. **(d)** (i) Smooth self-paced finger movements are characterized by discontinuities at 6–9 Hz, which indicates that human action, similarly to perception [see (c)], takes place in discrete frames. Finger velocity (upper trace) and electromyography (EMG) of finger agonist and antagonist muscles (middle and lower histograms) were averaged around velocity discontinuities. These discontinuities were associated with clear out-of-phase agonist-antagonist bursting in the EMG. (ii) EMG signals in the 6–9 Hz band were coherent with the ongoing neuronal oscillations in the contralateral sensorimotor cortex so that coupling in the postcentral gyrus (somatosensory cortex) was predominantly afferent (red), whereas the coupling in the precentral gyrus (motor cortex) was predominantly efferent (blue). Thus, similarly to perceptual sampling, discrete motion is also coordinated by cortical  $\alpha$ -frequency band oscillations. Modified, with permission, from Ref. [73].

significant neuronal processing. Two additional lines of evidence strongly support this conclusion. First, synchronized  $\alpha$ -frequency band oscillations in the primary visual cortex lagged behind those in the association cortex, implying that the association area drove oscillations in the primary visual cortex through feedback connections (Figure 2a). Second, in accordance with the known cortical source and target layers of feedback projections,  $\alpha$  coherence was prominent between the deep layers of area 7 and superficial layers of area 17 [8,32] (Figure 2a).

In conclusion, phase interactions seem to be informative in understanding the functional significance [24,26] of the  $\alpha$ -frequency band oscillations. Observations of  $\alpha$ -frequency band phase correlations in task-relevant networks can all be seen to support a direct role for  $\alpha$ -frequency band rhythmicity in the neuronal mechanisms of top-down modulation and attention. However, in studies reporting strengthened  $\alpha$ -phase synchrony, some show a simultaneous amplitude increase [11,30,31], whereas others show an associated amplitude suppression [9,10,12].

### Thalamic burst discharges during $\alpha$ -frequency band oscillations

At the cellular level, the concept of  $\alpha$ -frequency band inhibition has been largely based on an association between sleep-state  $\alpha$  spindles and burst discharges of thalamocortical neurons [6]. Thalamocortical relay neurons have long been known to operate in two distinct modes: in a depolarized state they tonically fire single spikes, whereas following a period of hyperpolarization ( $\sim -70$  mV), long enough to deactivate T-type calcium channels, they discharge spike bursts (interspike intervals 2–5 ms) riding on low-threshold calcium potentials (LTCPs) at rates in the  $\alpha$ -frequency band or below [33,34]. Thalamic burst firing characterizes some sleep stages and many pathological conditions, whereas normal waking behavior was long thought to be exclusively associated with single-spike firing. Moreover, single-spike discharges relay sensory information with high fidelity, whereas burst firing was historically thought to lead to unreliable and imprecise information transmission [33–35]. Hence, single-spike and burst-discharge modes had been concluded to reflect ‘open’ and ‘closed’ thalamic gates, respectively [35,36]. Among others, Pfurtscheller [6] suggested that not just  $\alpha$  spindles in sleep, but also large  $\alpha$  oscillations in the awake brain reflect a ‘closed thalamic gate’, where no information is relayed to the cortex.

$\alpha$ -Frequency band oscillations in an awake brain are, indeed, often associated with thalamic burst firing [37–39]. However, two recent discoveries overturn the notion of a ‘closed gate’. First, occurrence of LTCP bursts in an awake brain is phenomenologically distinct from that during  $\alpha$  spindles or pathological rhythmic activities [34], and, even in the bursting mode, thalamocortical neurons relay sensory information efficiently. Whereas the firing rate in tonic mode is linearly related to the strength of sensory signals and is thereby well suited for detailed signal analysis, the transmission in bursting mode takes place in an all-or-none fashion and might be better suited for signal detection [33,34]. Second, Hughes *et al.* [39] have recently discovered a novel form of thalamic burst firing producing  $\alpha$ -frequency band rhythmicity, which could be

important for neocortical  $\alpha$ -frequency band oscillations. A subset of thalamocortical neurons synchronized by gap junctions discharge high-threshold ( $> -55$  mV) bursts of spikes (interspike intervals  $> 10$  ms) following activation by metabotropic glutamate receptors, and hence also following sufficient corticothalamic modulatory excitation. Thalamic high-threshold bursting is synchronized with EEG  $\alpha$  oscillations [39,40], and it might be more prevalent than LTCP bursting during *in vivo*  $\alpha$  oscillations.

In addition to the reciprocal thalamocortical circuitry, intracortical mechanisms [41] might also be crucial in the generation of *in vivo*  $\alpha$  oscillations (see also the study by Nicolelis and Fanselow [34]). These neocortical circuits might also be important for the interaction [11] of  $\alpha$ -frequency band oscillations with  $\beta$ - and  $\gamma$ -frequency band oscillations [42].

At the behavioral level, it has become well established that large-amplitude awake-state  $\alpha$  oscillations in the primary sensory cortex are not associated with either a ‘closed thalamic gate’ or with inhibited or disengaged cortical networks. The detection of somatosensory stimuli by humans [23] and rats [43] is equally probable for both small and large prestimulus  $\alpha$ -frequency band oscillations in the primary somatosensory cortex (Figure 1d). Taken together, it seems that the available cellular-level data do not suggest that the thalamocortical  $\alpha$ -frequency band oscillations would necessarily be associated with disengaged cortical states or blocked thalamocortical signal transmission.

### Phase reset of ongoing $\alpha$ oscillations

The classical event-related potentials (ERPs) are influenced by both peristimulus amplitude and phase dynamics (Box 1). In contrast with the classical view of ERPs revealing stimulus-evoked components from ongoing ‘noise’, several human EEG studies suggest that some early ERP components, N1 in particular, at least partly emerge from a stimulus-caused phase reset of ongoing  $\theta$  [44,45] and  $\alpha$  oscillations [44–46] (Box 1, Figure 1b, c). These findings place a large body of data on the N1 component into an interesting light. It has long been known that the N1 component of human auditory [47] and visual [48] ERPs, as well as the corresponding component in rhesus monkey somatosensory [49] ERPs, is robustly correlated with conscious detection. Also, the enhancement of N1 by attention is historically well known. Moreover, the principal sources of monkey somatosensory N1 are in the superficial layers of the primary somatosensory cortex, where it is produced by top-down inputs from higher-order areas, such as the secondary somatosensory cortex [50], which is in good agreement with the data of von Stein *et al.* [8] and the concept of  $\alpha$  having a top down role. Although the contribution of phase reset in the generation of N1 still warrants further consolidation, these data support the role of  $\alpha$ -frequency band phase dynamics in attention and consciousness (see also [8,12]).

### Phase synchrony among $\alpha$ , $\beta$ and $\gamma$ oscillations

In recent years,  $\beta$ - and  $\gamma$ -frequency band oscillations have attracted widespread interest. Transient synchronization of neuronal activity seems to be a key mechanism in the



binding of anatomically distributed feature processing into coherent perceptual objects, where it is often associated with  $\beta$  or  $\gamma$  oscillations [24]. Also, the phenomenology of  $\gamma$  oscillations in the human EEG is in line with a role in the formation of neuronal object representations [51], and, accordingly,  $\gamma$  oscillations are present during the WM retention period [52], modulated by attention [53–55] and correlated with conscious perception [56,57]. von Stein [8] proposed that, in contrast with a top-down role for  $\alpha$ -frequency band synchrony,  $\gamma$ -frequency band synchrony would be significant in bottom-up processing.

Thus, it seems that  $\alpha$ -,  $\beta$ - and  $\gamma$ -frequency band oscillations all contribute to the neuronal underpinnings of attention, WM and consciousness. The mechanisms that integrate such spectrally distributed processing are likely to involve cross-frequency interactions [26,58]; however, the latter are a largely uncharted field. In a recent article, we examined the possibility that cross-frequency phase synchrony between distinct frequency bands could be used to integrate spectrally distributed processing. Indeed, we found that 1:2- and 1:3-phase synchrony (Figure 2b) was present among cortical oscillations throughout the frequency range from the  $\delta$ - (1–4 Hz) to the  $\gamma$ -frequency band [11]. Moreover, we found that a WM-intensive mental calculation task enhanced cross-frequency phase synchrony between globally synchronous networks in  $\alpha$ - and  $\beta$ -frequency bands, as well as between  $\alpha$  and more local  $\gamma$  oscillations (Figure 2b). Importantly, in these data, the strength of 1:3  $\gamma$ - $\alpha$ -phase synchrony was positively correlated with WM load. In other investigations, 1:2-phase synchrony between  $\beta$  and  $\alpha$  oscillations [59], as well as verbal memory load-dependent 1:2 synchrony between  $\alpha$  and  $\theta$  (4–7 Hz) oscillations [60], has been observed in the human EEG.

These findings thus support an idea that cross-frequency phase synchrony might coordinate the integration of spectrally distributed neuronal processing [11]. However, the findings of WM load-dependent cross-frequency phase synchronization of global-scale  $\alpha$  with  $\theta$ ,  $\beta$  and  $\gamma$  oscillations support the notion that these oscillations cooperate in cognition.

Spectral integration and coordination might also involve nested oscillations [61–63], which might, in addition to cross-frequency phase synchrony, be important in many cognitive functions. In nested oscillations, the amplitude, but not the phase, of the faster oscillation is modulated by the phase of the slower oscillation. Lisman, Idiart and Jensen [64,65] have suggested that nested  $\theta$  and  $\gamma$  oscillations underlie the retention and capacity limits of WM. VanRullen and Koch [66] postulated that nested  $\alpha$  and  $\gamma$  oscillations produce discrete perception, so that  $\gamma$  waves constitute the contents of each ‘snapshot’, with the entire percept being mediated by the  $\alpha$  waves. Future research is likely to reveal a fundamental role for hierarchical multi-band oscillations and cross-frequency interactions in the system-level mechanisms coordinating scattered neuronal activity into perception, cognition and action.

### Discrete perception and action

When visual objects are presented serially at fixation, humans can recognize and categorize them at rates up

to 8–12 Hz [67,68]. In a continuous wagon wheel illusion experiment, illusory reversals are most probable at wheel-motion frequencies of  $\sim 10$  Hz, which is suggestive of discrete perceptual sampling [69] (Figure 2c). Similarly, rats sample and discriminate odors at a rate of 8 Hz [70] and use active whisking at 7–14 Hz for tactile perception [34]. Hence, perception seems to operate in discrete ‘snapshots’ of  $\sim 100$  ms, which might correspond to consecutive cycles of  $\alpha$  oscillation [66,71]. Indeed, the perception of illusory motion reversals is correlated with  $\alpha$ -frequency band amplitude in the ongoing EEG [72] (Figure 2c).

In parallel with perceptual sampling, smooth movements are also realized in discrete steps (Figure 2d). Movement discontinuities are caused by phasic muscular activity that is 1:1 phase locked to cortical  $\alpha$ -frequency band oscillations [73]. The coordination of such discrete motion is achieved in a large-scale cerebello-thalamo-cortical network that is coupled through coherent  $\alpha$ -frequency band oscillations [73,74] (Figure 2d). Several lines of evidence thus link the temporal segmentation of perception and action with neuronal  $\alpha$ -frequency band rhythmicity.

### Discrete cognition: $\alpha$ oscillations in the ‘global neuronal workspace’

According to the current dogma of neuronal network dynamics, synchronous  $\gamma$ -frequency band assemblies account for ‘active’ neuronal processing, whereas the roles of  $\alpha$  oscillations are in the inhibition and ‘inactivation’ of task-irrelevant cortical regions. However, as discussed here, an accumulating body of evidence emphasizes a direct involvement of  $\alpha$  oscillations in the mechanisms of top-down modulation, attention and consciousness.

Neural correlates of consciousness (NCC) are widely recognized to involve neuronal coalitions [71] and synchronous assemblies [58], recurrent processing [75] and the frontoparietal network [28]. One conceptual model of NCC is the ‘global neuronal workspace’ (GNW) [76,77], in which sensory information enters awareness following an interaction between the sensory and frontoparietal network [29]. It is important to see that the GNW model is applicable not only in perception and attention, but also in STM and movement execution.

We propose here a framework in which a subset of neurons engaged in  $\alpha$  oscillations belongs to the NCC through an  $\alpha$ -frequency band synchronized sensori-fronto-parietal network that defines the GNW. This framework is based on the following six lines of evidence: (i) top-down modulation can be mediated by  $\alpha$ -frequency band phase interactions [8], and thus  $\alpha$  rhythmicity could contribute to recurrent processing [75] and top-down amplification [29]; (ii)  $\alpha$ -frequency band oscillations can phase lock between widely separated cortical regions [8,10,11,74] and thus form functional large-scale networks [26]; (iii) enhanced  $\alpha$ -frequency band synchrony in the frontoparietal network is associated with the execution of cognitive tasks [10,11,74]; (iv)  $\alpha$ -,  $\beta$ - and  $\gamma$ -frequency band oscillations coexist and are colocalized during stimulus processing and task execution [8,10–12,30,74,78]; (v)  $\alpha$  oscillations can be synchronized with  $\theta$ ,  $\beta$  and  $\gamma$  oscillations in response to cognitive demands [11,60], which is likely to be essential for the coordination and communication [25] in

## Box 2. Hypotheses derived from the framework advanced in this article

- Frontoparietal  $\alpha$  synchrony should be found during focused attention, WM and STM, as well as during conscious perception, cognition and action, but it should not phase lock to the stimulus processing when the stimuli are subliminal, unattended or are not consciously perceived for other reasons.
- Those  $\alpha$ -frequency band oscillations that are not phase locked to the synchronous frontoparietal network do not belong to the GNW and thereby might have different functional roles, such as idling or inhibition.
- The interaction between the GNW and the neuronal object representations should influence the dynamic structure of these representations according to variations in the cognitive context (e.g. anesthetized or awake; attended or ignored; one or multiple perceptual objects).
- $\alpha$  Oscillations and  $\alpha$ - $\gamma$  interactions should be related to the attentional enhancement of  $\gamma$ -frequency band synchrony.
- Cross-frequency phase synchrony between the frontoparietal  $\alpha$  network and locally synchronous  $\gamma$ -frequency band assemblies underlies the selection and inclusion of neuronal object representations into the focus of attention and sensory awareness.

multiband networks; (vi) perception and action can proceed in discrete 'snapshots' involving  $\alpha$ -frequency band periodicity [30,66,71,73,74]. This is natural or even mandatory if  $\alpha$  oscillations are involved in the GNW. Some predictions associated with this framework are presented in Box 2.

In conclusion, an elucidation of the functional roles of  $\alpha$  oscillations seems to be mandatory to the understanding of large-scale integration in the brain. Whether  $\alpha$  oscillations mediate idling, inhibition, attention, binding within the GNW or any combination of these, remains a topic for years to come.

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