Opinion

The roles of cortical oscillations in sustained attention

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We rely on sustained attention to protect task performance against fatigue and distraction. Time-related variations in attention correlate with amplitude changes of specific cortical oscillations. However, the ways in which these oscillations might support sustained attention, how these oscillations are controlled, and the extent to which they influence one another remain unclear. We address this issue by proposing an oscillatory model of sustained attention. Within this framework, sustained attention relies on frontomedial theta oscillations, interareal communication via low-frequency phase synchronisation, and selective excitation and inhibition of cognitive processing through gamma and alpha oscillations, respectively. Sustained attention also relies on interactions between these oscillations across attention-related brain networks.

The problem of sustained attention

The capacity to sustain one's attention is of great practical importance. Nevertheless, we struggle to maintain our focus [1], often with grave consequences. Fatigued clinicians commit medical errors [2], inattentive lifeguards permit drownings [3], and unfocused train drivers cause major collisions by ignoring stop signals [4]. It is therefore imperative to understand the neural mechanisms of sustained attention such that we may ultimately develop effective methods for identifying and preventing attentional declines.

Neuroimaging research has shown that sustained attention tasks elicit activations in a distributed network of brain areas [5]. These findings have recently been integrated with cognitive theories to generate proposals about the contribution of specific brain regions to the constituent processes of sustained attention [5]. Electrophysiological research has further shown that time-related variations in attention correlate with the amplitude, or power, of various cortical oscillations (Box 1) [6]. However, the functional roles of these oscillations, the ways in which they are controlled, and the extent to which they interact across attention-related brain networks, remain largely unknown.

In this article, we take a first step towards addressing this issue by integrating recent electrophysiological and neuroimaging findings with current theories of sustained attention. In so doing, we present an integrative model of how cortical oscillations may support sustained attention and provide a framework for future debate about the roles of oscillatory brain activity in high-level, cognitive functions. If appropriately validated, this framework has the potential to guide the development of attention-monitoring EEG systems and thereby improve the identification of attentional lapses in real-world settings. This discussion begins with an overview of how sustained attention is studied, the cognitive functions thought to be crucial for sustained attention, and the suggested neuroanatomical substrates of these functions.

Supervisory systems of sustained attention

Sustained attention is defined as the self-directed maintenance of cognitive focus under non-arousing conditions [1]. It is commonly studied using tasks that require subjects to monitor infrequent and temporally unpredictable signals over extended periods of time (i.e., more than 10 minutes) [7,8]. Changes in sustained attention are measured as both fluctuations [9,10] and deteriorations [7,11] in performance on these tasks. These different measures of performance have been suggested to reflect dissociable cognitive processes [12]. However, because it remains unclear whether fluctuations and deteriorations in attention reflect dissociable neural processes, this article gives equal focus to each.

Influential early models of cognitive control (see Glossary) proposed that sustained attention relies on activity within so-called anterior and posterior attention systems. In particular, prefrontal regions were suggested to exert prolonged control over perceptual processing via relays in parietal cortex [13,14]. These models have received support from lesion studies [15,16]. However, it has been argued that

Glossary

Cognitive control: the ability to promote thoughts and behaviours that are relevant to current goals in the face of distraction and interference from other cognitive processes.

Cognitive monitoring: the moment-to-moment comparison of current with intended thoughts and actions to detect departures from task goals.

Energisation: promotion of a cognitive process.

Oddball: a target stimulus that occurs rarely during a continuous stream of standard, non-target stimuli. In sustained attention tasks, participants are often required to remain vigilant for the presentation of these 'oddball' stimuli.

Response conflict: simultaneous activation of incompatible response tendencies.

Transcranial magnetic stimulation: application of single pulses of rapidly changing magnetic fields that cause depolarisation of neurons through electromagnetic induction.

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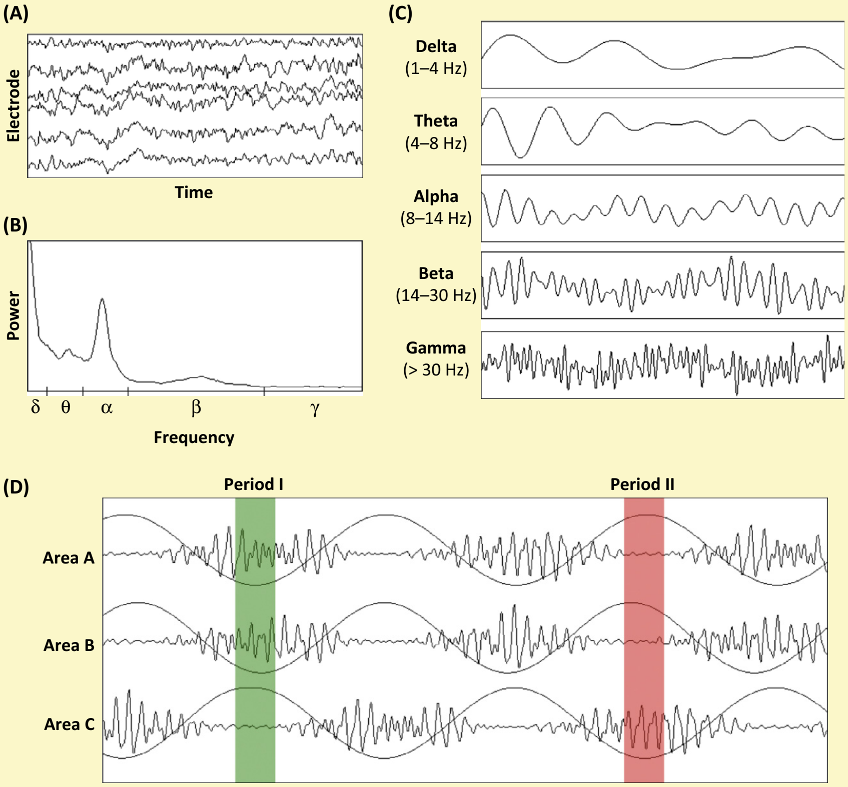
Box 1. What are neural oscillations?

Neural oscillations are observed in all animals and are thought to reflect rhythmic activity of large populations of neurons [79]. This rhythmic firing causes fluctuations in cortical local field potentials that can be measured using implanted electrodes (e.g., intracranial EEG) or scalp detectors (e.g., EEG/MEG) (Figure IA). The spectral composition of these fluctuations, and therefore the characteristic rhythmicity of neural activity, can be determined by transforming recorded electrophysiological data into the frequency domain using techniques such as the Fourier transform. This approach allows estimation of the contribution of individual frequencies to the analysed signal (Figure IB). In the case of cognitive electrophysiological research, frequencies are divided into spectral bands with distinct functional associations: delta (1–4 Hz), theta (4–8 Hz), alpha (8–14 Hz), beta (14–30 Hz), and gamma (>30 Hz) (Figure IC).

Oscillations are thought to be prevalent in neural systems in part because they facilitate communication between neural populations [78]. One way they could do this is through phase synchronisation. Phase synchronisation involves the adjustment and maintenance of the phase relationship between oscillating neural populations. As shown in Figure ID, neural populations can oscillate in phase or out of phase with one another. When in phase, communication between two areas is facilitated because action potentials from one area (Area A) arrive during the excitable phase of the other (Area B) and thus have enhanced postsynaptic impact (Period I). When oscillating out of phase, however, communication is prevented because action potentials from one area (Area C) arrive when the other (Area A) is inhibited (Period II). Owing to conduction delays in long-range transmission of neural impulses, communication between brain regions is suggested to be optimal when partner areas are synchronised at low frequencies [64,78].

Such low-frequency oscillations have been shown to modulate the power of high-frequency oscillations [36,64,65]. This is also shown in Figure ID. Here, the power of gamma oscillations depends on the phase of ongoing theta oscillations. Specifically, gamma power is greatest during theta troughs and lowest during theta peaks. This effect is known as power–phase coupling. Given the suggested role of low-frequency oscillations in long-range neural communication [64,78], and of high-frequency oscillations in the synchronisation of local neural activity [78], power–phase coupling between high and low frequencies provides a mechanism for the control of localised neural processing by distributed brain networks [64,65].



TRENDS in Cognitive Sciences

Figure I. Illustration of what cortical oscillations are, how they are analysed, and how they interact with each other. **(A)** EEG data recorded from six electrodes positioned on the scalp. **(B)** A plot of the power of specific oscillatory frequencies in a sample of eyes-closed, resting state EEG data (δ, delta; θ, theta; α, alpha; β, beta; γ, gamma). **(C)** Electrophysiological data band-pass filtered into the delta, theta, alpha, beta, and gamma bands. **(D)** Electrophysiological data recorded from three different cortical areas demonstrating both the modulation of gamma power by low-frequency oscillations and the mechanisms by which oscillatory phase synchronisation between regions can facilitate and inhibit long-range neural communication (as in Periods I and II, respectively).

frontoparietal systems do not support sustained attention by performing unitary operations, but instead engage in multiple cognitive functions simultaneously [17]. This elaborated model is supported by neuroimaging evidence showing that, during sustained attention task performance, activation is distributed across numerous functionally separable brain networks [5].

Within this framework, sustained attention is argued to depend upon three cognitive control functions: (i) monitoring and evaluation of ongoing cognitive processes, (ii) energisation of task-relevant processes, and (iii) inhibition of task-irrelevant processes (Figure 1) [17]. Sustained attention in the visual domain, for example, would thus rely on monitoring of current attentional focus, enhanced

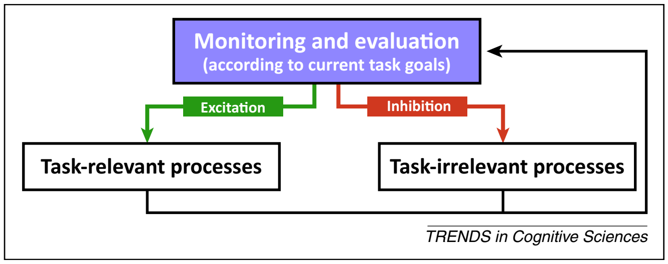


Figure 1. Core cognitive functions of sustained attention. Ongoing cognitive processes are monitored and evaluated according to current task goals. If required, attention is selectively adjusted through the excitation of task-relevant cognitive processes and the inhibition of task-irrelevant cognitive processes. The outputs of these processes are then fed back to monitoring and evaluation systems, enabling the continuous assessment and control of attention.

processing of relevant visual inputs, and inhibition of distracting stimuli (e.g., peripheral, auditory noise). Neuroimaging research has commonly implicated posterior medial frontal cortex (pMFC) in these functions. pMFC, including dorsomedial prefrontal and anterior cingulate cortex, is thought to monitor ongoing mental processing and signal the need for increased attentional control upon detection of inadequate cognitive focus [18,19]. This pMFC signal triggers adaptive modification of ongoing processing by communicating with lateral prefrontal cortex (LPFC), which in turn transmits excitatory and inhibitory signals to lower-level sensorimotor areas [18,19]. These interactions between pMFC and other control regions are crucial for attentional control. Adaptive adjustments of attention (e.g., following errors) are strongly associated with synchronisation of activity within the so-called executive control network [20] – which includes dorsomedial prefrontal, dorsolateral prefrontal, and superior parietal cortices [21]. Furthermore, prolonged control of task-related processing is associated with synchronised activation in the cingulo-opercular network [20], including the anterior cingulate cortex and anterior insulae [21]. These networks are continuously active during extended cognitive engagements [5,22], and regulate activity in the default-mode network during visual attention tasks [23,24]. Composed of medial temporal, posterior cingulate, and ventromedial prefrontal cortices, the default mode network is strongly implicated in introspective thought, and exhibits increased activation before attentional lapses [25].

Neuroimaging studies have thus revealed strong associations between haemodynamic activity in specific brain regions and the core functions of sustained attention. However, despite recent developments in wireless imaging of cerebral blood flow [26], it is currently impossible to measure such localised haemodynamic changes with sufficient reliability outside the laboratory to enable their reliable use in real-world attention-monitoring systems. Moreover, as haemodynamic measures depend on slow changes in blood flow and oxygenation, they are uninformative about rapid neural dynamics. By contrast, electrical brain activity can be recorded easily in applied settings with high temporal resolution using EEG [27]. Furthermore, deteriorations in attention are strongly associated with specific changes in oscillatory EEG features (e.g., the ratio of theta to alpha power [28,29]). Understanding cortical oscillations can thus be of both great practical significance and substantial theoretical interest, facilitating the development of attention-monitoring EEG systems and neuroscientific models of attentional control. However, there remains notable uncertainty over the contributions of cortical oscillations to sustained attention. It even remains unclear for many oscillatory frequencies whether their activity reflects the engagement or disengagement of sustained attention.

For example, frontomedial theta power has been linked with both attentional fatigue [30] and enhanced attention task performance [11]. Similarly, alpha power reflects reduced attention when localised to posterior regions [8], but reflects improved attention when averaged across the scalp [31]. In addition, despite the aforementioned importance of distributed brain networks in attentional control [19], the contribution of long-range interactions between cortical oscillations to sustained attention remains unclear. In particular, recent findings on the roles of phase synchronisation and cross-frequency coupling in long-range neural communication (Box 1) have had limited impact on models of sustained attention. This article addresses these issues by linking specific patterns of oscillatory brain activity to the core neurocognitive functions of sustained attention. In doing so, it describes how these functions may be supported by spatially localised oscillations interacting across attention-related brain networks.

Cortical oscillations and sustained attention

Frontomedial theta: monitoring and control

A robust oscillatory correlate of prolonged cognitive performance is frontomedial theta (fm-theta). Fm-theta power grows substantially during sustained attention tasks, together with error rates and reaction times [11,32]. It is thus an indicator of deteriorated attention [30]. However, despite this negative association, there is evidence that fm-theta may in fact play a positive role in attentional control.

For example, fm-theta power has been shown to increase significantly following the presentation of rare oddball stimuli [33,34], during reorientations of auditory attention [35], and before accurate performance on prolonged cognitive tasks [11,36]. Fm-theta power also increases following both negative task feedback [37] and the commission of errors on a range of tasks [38,39]. Such power increases predict subsequent enhancements in post-error reaction-time slowing [40] and post-error reductions in inhibitory alpha power in task-relevant cortical areas [41]. These experimental findings are correlational and thus give limited insight into the causal roles of such activity in cognitive functions. Nevertheless, they strongly implicate fm-theta in cognitive monitoring and control processes thought to be crucial for sustained attention [42].

Consistent with this hypothesis, magnetoencephalography (MEG) [43] and intracranial EEG studies [36] have localised fm-theta oscillations to dorsomedial prefrontal and anterior cingulate cortices – key hubs of the executive control and cingulo-opercular networks, respectively. Furthermore, theta oscillations in superficial layers of mPFC have recently been suggested to support cognitive monitoring and control processes by promoting integration of thalamocortical inputs and the detection of conflict between current and intended behaviours [44]. Together, this evidence provides a partial explanation for why fm-theta has been associated with both increased cognitive control over short time-scales and reduced attention following prolonged cognitive engagements [33,34]. Specifically, it suggests that increased fm-theta power during fatigue-related declines in sustained attention may reflect detection of mismatch between current and desired levels of attention. This detection causes reactive engagement of cognitive control processes. However, when cognitive resources are depleted, these processes are unable to refocus attention and performance does not improve. Put simply, increased fm-theta power during prolonged cognitive engagements may be analogous to the revving noises of a tired motorcar trying to climb a steep hill.

Low-frequency phase synchronisation: long-range transmission of information

For theta-driven cognitive monitoring systems to exert significant control over attention, they must communicate within attention-related brain networks. As previously described, pMFC is hypothesised to exert such control by coordinating its activity with LPFC which, in turn, transmits modulatory signals to low-level, sensorimotor areas [18,19]. Recent evidence suggests that this pMFC–LPFC coordination is facilitated by theta-band phase synchronisation. For example, EEG studies have commonly observed increased theta-band phase synchronisation between medial and lateral prefrontal areas following both negative task feedback [37] and the commission of errors during sustained attention tasks [39,45]. Similar results were also reported in a human intracranial EEG study in which pMFC and LPFC activity was recorded invasively while patients performed a response conflict task [36]. Here, theta phase synchronisation between pMFC and LPFC increased significantly on correctly classified trials and during periods of high response conflict. In addition, the phase of pMFC theta oscillations modulated gamma power in LPFC (an example of power–phase coupling; Box 1), and the strength of this gamma–theta coupling predicted improved performance on subsequent trials. Together, this evidence supports the role of theta-band pMFC–LPFC communication in the direction of cognitive control.

For these prefrontal activities to modulate sensorimotor processing, they must then be communicated to posterior brain areas. This communication may also be facilitated by long-range, low-frequency ($<$14 Hz) phase synchronisation. Increased low-frequency phase synchronisation between frontal and posterior areas is commonly observed during the orientation of attention [46–48], and has been found to predict improvements in attention following momentary attentional lapses [49,50]. Furthermore, during sustained attention tasks, fronto-posterior phase synchronisation in the alpha band has been found to decrease with cognitive fatigue [51,52] and to increase during periods of participant-assessed ‘on-task’ performance [53]. Simultaneous EEG–fMRI recordings have revealed a positive association between this alpha-band, fronto-posterior phase synchronisation and haemodynamic activity in the executive control network [54]. Global alpha power has also been linked with increased activity in the cingulo-opercular network [55]. Collectively, this evidence implicates large-scale, oscillatory synchronisation in the coordination of attention-related brain networks. As a result, it also suggests a novel explanation for why global alpha oscillations have been positively associated with sustained attention [31,56]. Although global alpha has been said to reflect a rhythmic refreshing of cognitive processing that enhances sensitivity to upcoming stimuli [55], it may instead reflect coordinated activity in frontal and posterior control regions.

Gamma ($>$30 Hz) oscillations: promotion of task-relevant activity

According to the neurocognitive theory outlined above, sustained attention depends on continuous activation of task-relevant activity. This function may be achieved via the generation of localised gamma oscillations in task-relevant cortical areas. Gamma oscillations in sensory cortices have often been linked with enhanced attention to sensory inputs. Increased gamma power in occipito-parietal cortex has been associated with improved visual oddball task performance [57,58]. Similarly, gamma power in auditory areas is increased during extended auditory attention tasks [35,59]. These gamma modulations in sensory cortex are strongly influenced by the activity of cognitive control systems. One study found that, although gamma power increased in macaque visual cortex during deployment of attention to visual inputs, removal of LPFC significantly attenuated this gamma enhancement [60]. Transcranial magnetic stimulation of LPFC was recently shown to modulate occipital gamma power during a visuospatial attention task [61]. Furthermore, posterior gamma power is strongly modulated by the phase of low-frequency oscillations ($<$14 Hz) [62,63]. This low-frequency, power–phase coupling is known to facilitate long-range neural communication and may reflect the application of cognitive control by attention-related brain networks [64,65]. Consistent with the role of low-frequency modulation of gamma power in sustained attention, the strength of gamma–theta power–phase coupling across frontal and posterior areas has been shown to correlate positively on a trial-by-trial basis with performance on a visual attention task [63].

Gamma oscillations have also been strongly associated with activation of non-sensory cortices. For example, enhanced cognitive control following identification of response conflict is associated with increased gamma activity (as well as gamma–theta power–phase coupling) in LPFC [36]. Furthermore, in an intracranial EEG study, increased gamma power was observed during a visuomotor task in a range of frontal and posterior brain areas previously identified as being positively involved in this task [66]. In summary, localised gamma oscillations seem to promote the activation of task-relevant processes across the brain. They are also strongly modulated by the phase of low-frequency oscillations, possibly reflecting the influence of distant brain regions on local cortical activity and the importance of such cross-frequency coupling for sustained attentional control.

Alpha (8–14 Hz): inhibition of task-irrelevant processes

In addition to facilitating task-relevant processes, cognitive control systems must also inhibit task-irrelevant processes that might otherwise interfere with task performance. This function may be achieved via generation of alpha oscillations in task-irrelevant cortical areas. Alpha oscillations have been linked consistently with inhibition of task-irrelevant sensory modalities. For example, alpha power in visual cortex has been positively associated with both somatosensory attention [67] and auditory oddball task performance [68,69]. Conversely, increased alpha power in auditory areas has been associated with the initiation of visual attention [70]. Alpha oscillations have also been linked with targeted inhibition of task-irrelevant activity within sensory modalities. For example, shifting attention to one side of visual space is strongly associated with increased alpha power in areas of visual cortex dedicated to the opposite side [71]. Furthermore, shifting attention to visual properties processed in the ventral visual stream (e.g., colour) has been linked with increased alpha power in dorsal visual cortex [72].

As with gamma oscillations, these inhibitory alpha modulations appear to be driven by the activity of frontal control regions. Studies using EEG in combination with optical imaging [73] and fMRI [74] have shown that occipital alpha power correlates significantly with the activity of pMFC and LPFC. Transcranial magnetic stimulation of LPFC can attenuate both the strength of fronto-posterior alpha phase synchronisation [75] and the lateralisation of occipital alpha power during shifts of visuospatial attention [41,76]. Furthermore, occipital alpha power during sustained visual attention tasks has been found to correlate negatively on a trial-by-trial basis with fm-theta power [41,76], suggesting a key role of theta-driven pMFC activity in the control of alpha oscillations in sensorimotor areas.

Alpha is also associated with suppression of activity in non-sensory cortices. For example, increases in MEG-measured alpha power in the frontal eye fields has been associated with inhibition of undesired, stimulus-driven attention [77]. Furthermore, human intracranial EEG studies have observed increases in alpha power during visual attention tasks in key nodes of the default-mode network [66]. Overall then, alpha oscillations seem to

Box 2. Testing the predictions of the current model with transcranial alternating current stimulation

The evidence cited in this article is largely correlational in nature. It thus remains unclear whether the cortical oscillations referenced here are merely associated with sustained attention or whether they mechanistically support sustained attention in the ways this model suggests. To provide causal evidence, it is necessary to modulate cortical oscillations selectively and experimentally and to demonstrate how this modulation influences sustained attention performance in ways that are consistent with predictions.

There are many ways in which oscillatory brain activity can be modulated (see [80,81] for discussion of neurofeedback technology). One promising method is transcranial alternating current stimulation (tACS). tACS involves the delivery of rapidly alternating electrical currents to the brain and has been found to enhance EEG activity at the frequency of stimulation [82,83]. It can also be applied during the performance of cognitive tasks, and thus provides an excellent tool for testing the hypotheses of the current model. For example, this model posits that pMFC theta activity plays a central role in cognitive monitoring and control functions that are crucial for sustained attention. It therefore predicts that sustained attention capacities will improve following the application of tACS at central theta frequencies (e.g., 5 Hz) over medial frontal areas. Furthermore, given previous evidence of an anti-correlation between fm-theta and posterior alpha power [41,76], it also predicts that theta-tACS of medial frontal cortex will bring about enhancements in sustained attention by suppressing inappropriate increases in alpha power in task-relevant sensory cortices. In addition, the current model posits a strong role of fronto-posterior phase synchronisation in the implementation of attentional control. Recent research has shown that such phase synchronisation and related cognitive processes can be enhanced through the application of bifocal, synchronised tACS [84,85]. As a result, this model also predicts that sustained attention performance will be improved through the application of synchronised tACS to frontal and posterior areas at low frequencies.

In each of these cases, evidence can only be considered to support the involvement of an oscillation in sustained attention if:

(i) Changes in sustained attention performance are associated with EEG-recorded power modulations at the frequency of stimulation.
(ii) These changes in sustained attention are observed only when stimulation is delivered within the frequency band of interest (i.e., not at higher or lower frequencies).
(iii) The cortical oscillation of interest is recorded maximally at previously determined scalp locations (e.g., fronto-medial electrodes for fm-theta, posterior electrodes for occipito-parietal alpha).

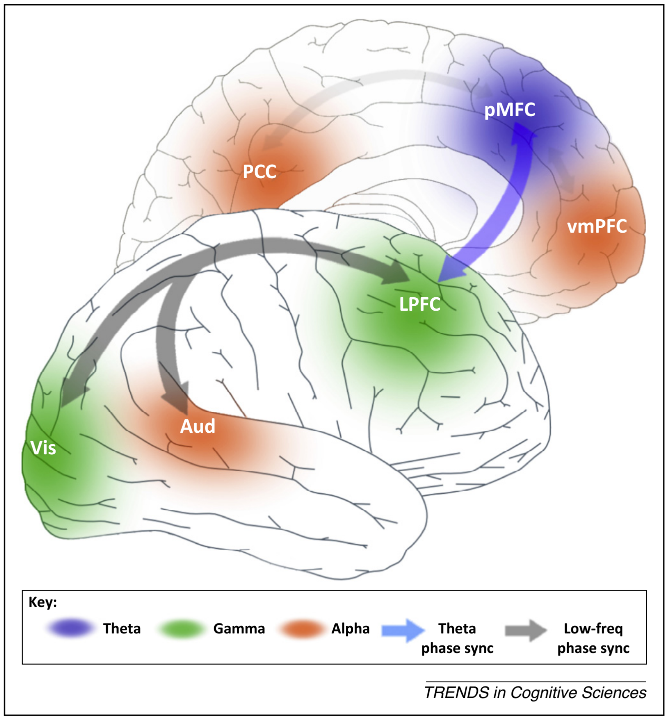


Figure 2. Schematic model of sustained attention (example from a visual task). Monitoring of attention is supported by theta (4–8 Hz) oscillations in posterior medial frontal cortex (pMFC). Communication between pMFC and lateral prefrontal cortex (LPFC) is facilitated by long-range phase synchronisation in the theta-band. Communication between LPFC and posterior, sensorimotor areas is facilitated by phase synchronisation within fronto-posterior networks at low frequencies (<14 Hz). This communication allows prefrontal systems to exert control over low-level, perceptual processes. These systems do this by promoting gamma oscillations (>30 Hz) in task-relevant cortical areas [e.g., visual cortex (Vis) in this example] and alpha oscillations (8–14 Hz) in task-irrelevant cortical areas [e.g., auditory cortex (Aud), posterior cingulate cortex (PCC), and ventromedial prefrontal cortex (vmPFC) in this example]. This model predicts that inhibitory control over activity in the default mode network (PCC, vmPFC) is exerted by pMFC through low-frequency phase synchronisation (light-grey arrow). Abbreviations: low-freq, low-frequency; phase sync, phase synchronisation.

reflect local cortical inhibition driven by cognitive control systems. When present in task-irrelevant cortical areas, these oscillations promote sustained attention by suppressing distracting information. However, when present in task-relevant cortical areas (e.g., visual cortex during a visual attention task), these oscillations can significantly impair attentional focus [8,9]. Nevertheless, given the influence of pMFC and LPFC on posterior alpha power [73,74], these undesirable alpha increases could be prevented through modulation of theta activity in frontal control regions (Box 2).

Concluding remarks

In this article we integrate recent electrophysiological findings with current theories of cognitive control and propose an oscillatory model of sustained attention. Within this framework, sustained attention relies on (i) cognitive monitoring and cognitive control functions mediated by fm-theta oscillations, (ii) communication across brain networks through low-frequency phase synchronisation, (iii) gamma-mediated excitation of task-relevant cortical areas, and (iv) alpha-mediated inhibition of task-irrelevant cortical areas (Figure 2). These localised oscillations interact with one another across attention-related brain networks, as evidenced by gamma–theta power–phase coupling and anti-correlations between fm-theta and alpha power in task-relevant sensory areas.

There are many aspects of the relationship between oscillations and sustained attention that remain unclear (Box 3). Furthermore, as this model is derived primarily from correlational studies, future research into the causal roles of these oscillations in sustained attention is required (Box 2). Nevertheless, this model takes a first step towards explaining why sustained attention has consistently been found to correlate with the power of specific cortical oscillations (e.g., fm-theta and global alpha). If properly validated, this model also has the potential to guide design of attention-monitoring EEG systems (e.g., focused on decreases in gamma–theta power–phase coupling, long-range phase synchronisation, or the ratio of alpha power in task-relevant vs task-irrelevant sensory areas). Given the negative impact of attentional declines in real-world settings [2–4], the possible societal benefits of these methods are significant. However, oscillations are not only associated with attention, and great benefits can be gained from incorporating oscillations into existing models of other cognitive processes. Rhythmicity is a fundamental feature of neural activity [78], and it is only through an integrative understanding of the intrinsic oscillatory nature of the brain that the mysteries of its function can be revealed.

Box 3. Outstanding questions

- Subcortical structures are known to play a role in the organisation of cortical oscillations [86]. How does subcortical activity influence and interact with oscillatory activity related to the maintenance of sustained attention?
- The cingulo-opercular network has been found to exert control over activity in the default mode network [23,24]. Frontal and posterior regions are thought to communicate through low-frequency phase synchronisation. Does such phase synchronisation between cingulo-opercular and default-mode network regions facilitate interactions between these networks (Figure 2)?
- Can sustained attention be enhanced through the application of transcranial alternating current stimulation (Box 2)? Would the behavioural effects of this stimulation be long-lasting, as has been observed in previous electrical stimulation studies focused on other cognitive functions [87]? What would be the neuroethical implications of such findings given the importance of sustained attention in everyday life (from driving to military operations)?
- Sustained attention is commonly found to deteriorate over time [1]. Our model suggests that these deteriorations may be caused by reductions in the control of oscillatory brain activity. What factors might cause such reductions?
- Do cortical oscillations associate differently with fluctuations versus deteriorations in attention? For example, do posterior alpha increases reflect fluctuations in attention whereas fm-theta increases reflect more prolonged deteriorations?
- Sustained attention is strongly enhanced by motivation [88]. How does motivation affect the power of attention-related cortical oscillations? (see [89]).

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