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].

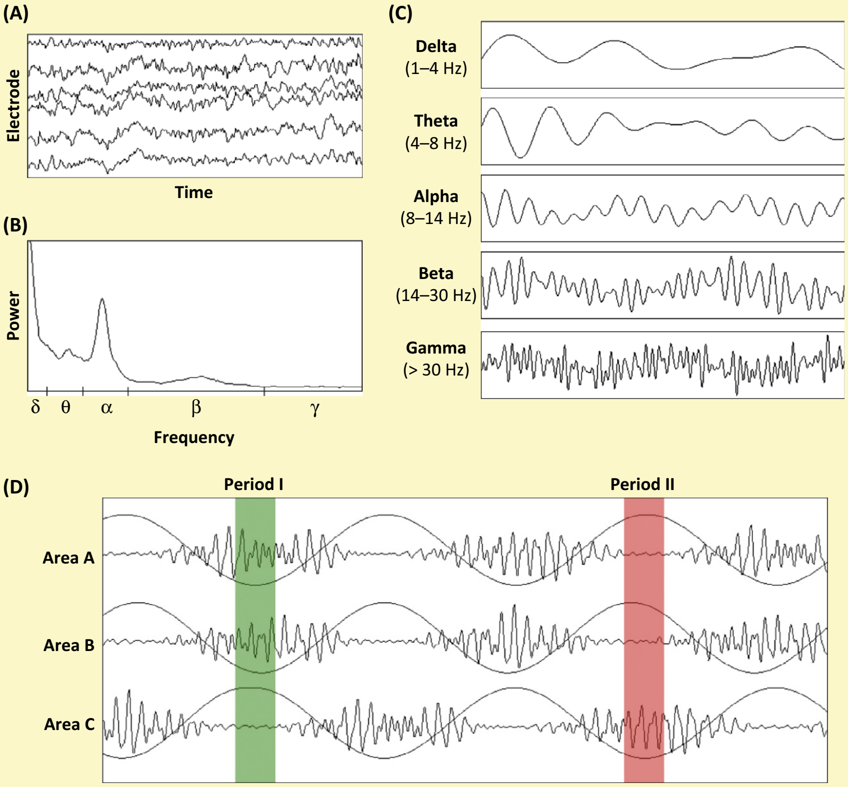

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Figure I. Illustration of what cortical oscillations are, how they are analysed, and how they interact with each other. **(A)**_EEG data recorded from six electrodes positioned on the scalp. **(B)**_A plot of the power of specific oscillatory frequencies 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