Neural Oscillation

In the subject area: Neuroscience

Neural oscillation refers to the rhythmic patterns of activity in the brain that have been associated with various cognitive processes. These oscillations can occur in different frequency ranges and brain regions, and can play a role in cognitive phenomena such as episodic memory.

AI-generated definition based on: Neuroscience & Biobehavioral Reviews, 2010

Functional role of gamma and theta oscillations in episodic memory

Authors, Erika Nyhus, Tim Curran

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Abstract

The primary aim of this review is to examine evidence for a functional role of gamma and theta oscillations in human episodic memory. It is proposed here that gamma and theta oscillations allow for the transient interaction between cortical structures and the hippocampus for the encoding and retrieval of episodic memories as described by the hippocampal memory indexing theory (Teyler and DiScenna, 1986). Gamma rhythms can act in the cortex to bind perceptual features and in the hippocampus to bind the rich perceptual and contextual information from diverse brain regions into episodic representations. Theta oscillations act to temporally order these individual episodic memory representations. Through feedback projections from the hippocampus to the cortex these gamma and theta patterns could cause the reinstatement of the entire episodic memory representation in the cortex. In addition, theta oscillations could allow

for top-down control from the frontal cortex to the hippocampus modulating the encoding and retrieval of episodic memories.

Introduction

Research in cognitive neuroscience thus far has focused on the functional role of particular brain regions. However, to perform the myriad of cognitive tasks that make us human it is recognized that particular brain regions do not work alone, but interact through complex and dynamic neural networks. A major question currently faced by cognitive neuroscientists is: How do the functionally specialized brain areas interact to perform rich cognitive abilities (Başar and Schürmann, 2001, Miller and Wilson, 2008, Varela et al., 2001)? Neural assemblies involve neurons with reciprocal connections that interact at different spatial scales. Neurons in local populations process information whereas larger neural assemblies, including neurons connected across separate brain areas, combine multiple processes that are important for higher-level cognitive tasks. Because cognitive demands change over time, we must not only look at slowly changing anatomical connections but also at quickly changing (transient) interactions between neural assemblies. Both local and global neural assemblies can transiently interact with each other to perform immediate cognitive tasks. Neural oscillations could allow for transient neural network interactions responsible for complex cognitive tasks. Fluctuations in postsynaptic potentials produce local oscillations. In addition, oscillators in one brain region can phase synchronize with oscillators in another region through long-range connections. A mechanism for interaction for both local populations of neurons and large neural assemblies is through phase synchronization of oscillations. As neurons oscillate, they effectively open and close their window to both send and receive information (Buzsáki and Draguhn, 2004, Womelsdorf et al., 2007). For information to be transferred from one neuronal group to another, the sending neuron must be excitable at the same time that the receiving group is excitable. This requires the coupling of oscillations between sending and receiving neurons through phase synchronization (Fries, 2005). This pattern of neural interaction allows for efficient neural communication through the transient coupling of neurons firing synchronously forming functional neural networks. It has been shown that the temporal coincidence of postsynaptic potentials has a greater impact on postsynaptic firing than non-coincident firing (Salinas and Sejnowski, 2001). In addition, this pattern of interaction causes

precise timing of input and output from sending and receiving neurons (Mainen and Sejnowski, 1995). Therefore, neurons must bundle their signal by firing together synchronously to effectively send their signal to a target neuron. Neural assemblies interact at different temporal scales. In local neural assemblies, with close connections between neurons, communication can happen during faster, higher frequencies. In large-scale brain assemblies, with long-range connections between neurons, communication happens during slower, lower frequencies (Fries, 2005). There is also evidence that different bands of activity can multiplex such that slower oscillations provide a framework for other faster oscillations to operate such that fast oscillations communicate content while slow oscillations mediate transient connectivity (Buzsáki and Draguhn, 2004, Fries, 2005, Varela et al., 2001, Ward et al., 2006).

Research has shown that synchronized neural firing can allow for the transient interaction between visual areas for visual perception. It is proposed here that neural oscillations not only allow for synchronized neural firing for the transient interaction between brain areas for perceptual tasks but also for complex cognitive tasks. The following provides a general model of how neural oscillations can allow for synchronized neural firing for the transient interactions important for complex cognitive tasks. During a cognitive task oscillations can allow for local neurons to fire synchronously at high frequencies to process information. Multiple processes can then be combined through large-scale brain networks whose oscillations become phase synchronized causing neurons within these large-scale brain networks to fire synchronously. Transient linking through synchronous firing provides a mechanism to amplify relevant processing (synchronously firing neurons) and filter out irrelevant neural firing (asynchronously firing noise). When processing is complete, phase dysynchronization of oscillations can cause neurons to stop firing synchronously. New brain networks whose oscillations become phase synchronized can then cause the same neurons to synchronously fire with other neurons to form a different neural assembly to perform a different cognitive task. Therefore, oscillations provide a robust mechanism for neurons to effectively form transient neural networks depending on the demands of the present cognitive task.

Episodic memory is a complex cognitive function that involves many interacting brain regions and allows us to store the content of experience that can be retrieved later. Episodic memory is unique from semantic memory in that it stores contextual (spatial

and temporal) information about individual events that can be later retrieved. In addition, episodic memories are robust to interference, allowing us to store and retrieve separate but similar experiences. Although episodic and semantic memories are distinct, semantic memories may be originally encoded through episodic processes and the encoding of episodic memories may rely on semantic elaboration. By this definition all of the studies reviewed employ episodic memory tasks.

Neural oscillations have been linked to various cognitive phenomena in humans. There is not an exact mapping of oscillatory rhythms to specific cognitive processes. Instead, neural oscillations in a specific frequency range in one brain region may function in one cognitive process and in another cognitive process in another brain region. In addition, different neural oscillations can each function in a specific cognitive phenomenon (Başar et al., 1999, Kahana, 2006, Klimesch et al., 2008). The primary aim of this review will be to examine evidence for a functional role of gamma and theta oscillations in human episodic memory systems.

The review will focus on gamma and theta rhythms because recent evidence has suggested a functional role of gamma (25–100 Hz) and theta (4–8 Hz) oscillations in episodic memory. Other rhythms such as delta (1–4 Hz), alpha (8–12 Hz), and beta rhythms (15 Hz) will not be discussed because they have not been consistently reported as being related to episodic memory and the cortical–hippocampal network. Delta and beta rhythms have been reported in only a few studies (Düzel et al., 2003, Düzel et al., 2005, Hanslmayr et al., 2009, Klimesch et al., 2000a, Mormann et al., 2005, Sederberg et al., 2007a, Sederberg et al., 2007b, Weiss and Rappelsberger, 2000), but do not always correlate with episodic memory (Doppelmayr et al., 1998, Hanslmayr et al., 2009, Klimesch et al., 2001b, Klimesch et al., 2008, Osipova et al., 2006).

Separating the neural rhythms involved in semantic and episodic memory is often difficult as episodic tasks often include semantically meaningful items. There is convincing evidence that different neural rhythms contribute to semantic and episodic memory. The alpha rhythm has been related to semantic memory because it consistently phase desynchronizes with the presentation of semantically related items (Klimesch, 1996, Klimesch, 1999, Klimesch et al., 1994, Klimesch et al., 1997, Klimesch et al., 2000b, Klimesch et al., 2004, Klimesch et al., 2008, Mölle et al., 2002). Importantly, neural rhythms have been shown to dissociate when comparing semantic and episodic memory tasks. For example, Klimesch (1999) reviews a series of studies comparing

alpha and theta modulations while subjects performed a semantic or episodic task. In the semantic task subjects were given a concept prime (e.g. eagle) and then a target feature (e.g. claws) and they had to judge whether the target was semantically congruent with the prime. In the episodic task subjects were given a concept and feature and they had to judge whether the concept/feature pair was previously shown at study. Comparing these two designs several studies found a consistent post-target decrease in alpha power for the semantic task and a post-target increase in theta power for the episodic task. Klimesch (1999) posits that the alpha rhythm likely involves the thalamo–cortical network whereas the theta rhythm likely involves the hippocampal–cortical network. These results are consistent with other results indicating that alpha is related to semantic memory whereas theta is related to episodic memory.

First, the methods used to measure rhythmic neural activity will be discussed. Second, the basis of neural oscillations will be discussed. Third, a review of the animal literature will provide the anatomical and physiological basis for understanding the role of gamma and theta oscillations in cortical–hippocampal episodic memory networks. Finally, a review of recent evidence from recording the electrical activity of the human brain will explore the functional role of gamma and theta oscillations in human episodic memory. To date, little work has been done to synthesize the findings from these studies. This review will aim to synthesize these findings by connecting them to what is known about gamma and theta oscillations at a neural and systems level in the animal brain. Integrating these levels of analysis will elucidate the functional role of gamma and theta oscillations in episodic memory.

Section snippets

Measurement methods

The following review will include studies from animals and humans showing rhythmic neural activity. The review of the animal literature includes studies using single or multi-unit recording and local field potentials (LFPs). The review of the human literature includes studies using intracranial electroencephalography (iEEG) in patients

with epilepsy and scalp electroencephalography (EEG) and magnetoencephalography (MEG) in normal subjects. Single and multi-unit recording intracellularly

Neural mechanism of rhythmic activity

To understand how gamma and theta oscillations contribute to episodic memory, it is essential to first consider their basic underlying neural mechanisms of rhythmic activity. Studies using single unit and multi-unit recording show that rhythmic firing can occur because of intrinsic firing patterns of excitatory principle cells or common input from a pacemaker like the thalamus. More commonly in the cortex and the hippocampus, rhythmic firing is an emergent property of interactions between

Unified model of gamma and theta oscillations in episodic memory

Neural oscillations in the gamma and theta frequencies have been found in cognitive tasks such as those used to investigate episodic memory (reviewed in Başar et al., 1999, Bastiaansen and Hagoort, 2003, Herrmann et al., 2004b, Jensen et al., 2007, Kahana, 2006, Kahana et al., 2001, Klimesch, 1996, Klimesch, 1999, Klimesch et al., 2010, Klimesch et al., 2008, Sauseng et al., 2010). The following section will provide a comprehensive review of studies measuring gamma and theta oscillations using

Conclusions

Many current models of brain function involve the interaction of different brain systems, but little research has addressed how the functionally specialized areas of the brain interact to perform cognitive tasks. The brain is made up of neural assemblies with reciprocal connections that connect local populations to combine multiple processes that are important for higher-level cognitive tasks. Since cognitive demands change over time there must be transient interactions between neurons to

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Review

Neural Cross-Frequency Coupling: Connecting Architectures, Mechanisms, and Functions

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Trends

Cross-frequency coupling (CFC), in other words the association of multiple frequency neural oscillations, is present across different frequency bands and neural systems.

Circuit mechanisms determine CFC characteristics: oscillations generated in distinct versus overlapping circuits, and continuously active versus intermittent fast oscillation (FO).

Dynamic network properties determine CFC signatures: phase–phase coupling occur under weakly coupling and do not co-occur with phase–frequency coupling; phase–amplitude coupling is present when the FO is intermittent or sparse spiking; amplitude–amplitude coupling requires asymmetrical slow oscillations.

CFC is mechanistically implicated in three cognitive operations: multi-item representation, long-distance communication, and stimulus parsing.

Modeling shows that theta–gamma CFC is an intracortical mechanism for parsing speech.

Neural oscillations are ubiquitously observed in the mammalian brain, but it has proven difficult to tie oscillatory patterns to specific cognitive operations. Notably, the coupling between neural oscillations at different timescales has recently received much attention, both from experimentalists and theoreticians. We review the mechanisms underlying various forms of this cross-frequency coupling. We show that different types of neural oscillators and cross-frequency interactions yield distinct signatures in neural dynamics. Finally, we associate these mechanisms with several putative functions of cross-frequency coupling, including neural representations of multiple environmental items, communication over distant areas, internal clocking of neural processes, and modulation of neural processing based on temporal predictions.

Section snippets

Mechanistic and Functional Characteristics of Cross-Frequency Coupling

Brain oscillations are observed *in vivo* and *in vitro* in almost any neuronal population of the neo- and paleocortex. While it is relatively easy to measure oscillations and observe their modulations in various sensory states and cognitive operations, it remains largely unclear what role, if any, they play in neural information processing or, more generally, in cognition 1, 2. An intriguing feature of neural oscillations is that rhythms of distinct frequencies show specific coupling properties 3,

Multi-Item or Sequence Encoding

Many neural systems need to concurrently maintain active representations of distinct items, while avoiding interferences: these can be objects in the visual field, items in working memory, or sequences of motor commands in a complex movement [4]. Neural oscillations offer a potentially efficient tool for multi-item representation by temporally clustering spikes pertaining to each item within distinct oscillations phases. This principle allows downstream neural systems to read-out a given item

Synchronization of Fast Oscillations for Long-Distance Communication

One of the most prominent roles assigned to neural oscillations is to mediate selective neural communication between areas, with in-phase regions communicating more efficiently than out-of-phase ones [73]. Gamma rhythms have predominantly been implicated in this so-called ‘communication through coherence’ mechanism, especially for bottom-up processes [74]. However, fast oscillations only synchronize at a local scale. By contrast, slower rhythms (<10 Hz) may synchronize between distant areas 75,

Temporal Parsing of Continuous Stimuli

Many biological stimuli are characterized by an intrinsic quasi-rhythmic temporal structure, or are processed in a rhythmic mode. Speech is marked with syllabic contours, odors are sniffed at the respiratory rhythm, visual scenes are explored at the pace of saccades, etc. 81, 82. While slow oscillations in sensory areas reflect the rhythm of the sensory signal or of sensory sampling, fast gamma oscillations underpin fine-grained sensory processing in a bottom-up fashion 28, 39, 74, 83. The

Concluding Remarks

The coupling between neural oscillations may take a variety of forms, emerge from different architectures, and underpin distinct functions. However, causal relationships between neural CFC and cognitive functions are yet to be demonstrated. We hope that, by clarifying the concepts and the relationships between mechanisms and function, the framework we outlined here will stimulate original research and hence contribute to filling conceptual and empirical gaps. Essential future developments in

The roles of cortical oscillations in sustained attention

Authors, Michael S. Clayton, Nick Yeung, Roi Cohen Kadosh

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Highlights

We present a model of the roles of cortical oscillations in sustained attention.

Cortical oscillations support specific cognitive functions.

These oscillations interact with one another across attention-related brain networks.

The roles of cortical oscillations in sustained attention

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).

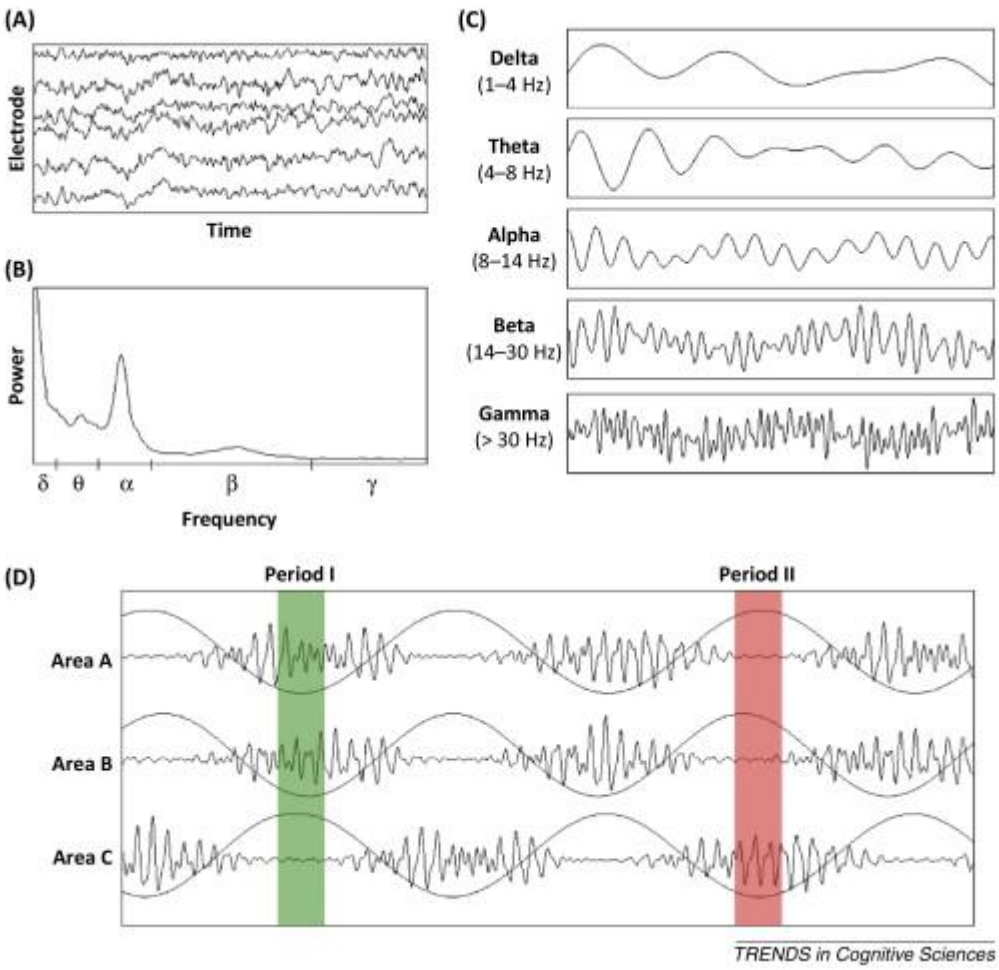

Figure I. Illustration of what cortical oscillations are, how they are analysed, and how they interact with each other. **(A)**_EEG data recorded from six electrodes positioned on the scalp. **(B)**_A plot of the power of specific oscillatory frequencies in a sample of eyes-closed, resting state EEG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

Rhythmic brain stimulation can facilitate testing of this model.

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, inter-areal 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.

Section snippets

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

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

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

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

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