Neuronal Oscillations in Cortical Networks

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Clocks tick, bridges and skyscrapers vibrate, neuronal networks oscillate. Are neuronal oscillations an inevitable by-product, similar to bridge vibrations, or an essential part of the brain's design? Mammalian cortical neurons form behavior-dependent oscillating networks of various sizes, which span five orders of magnitude in frequency. These oscillations are phylogenetically preserved, suggesting that they are functionally relevant. Recent findings indicate that network oscillations bias input selection, temporally link neurons into assemblies, and facilitate synaptic plasticity, mechanisms that cooperatively support temporal representation and long-term consolidation of information.

The first human electroencephalographic (EEG) pattern described was an 8 to 12 Hz rhythm, the alpha waves of Berger (*1*), followed by a barrage of intensive clinical and basic research. From scalp recordings, investigators identified various other oscillatory patterns that were particularly obvious during rest and sleep. However, the scalp EEG during conscious, waking behavior demonstrated low-amplitude, "desynchronized" patterns. This apparent inverse relation between cognitive activity and brain rhythms was further emphasized by the dominance of oscillations in anesthesia and epilepsy, states associated with loss of consciousness (*2*). Therefore, the motivation to relate these "idling" or even harmful rhythms to complex cognitive brain operations was diminished.

The recent resurgence of interest in neuronal oscillations is a result of several parallel developments. Whereas in the past we simply watched oscillations, we have recently begun creating them under controlled situations (*3–8*). Detailed biophysical studies revealed that even single neurons are endowed with complex dynamics, including their intrinsic abilities to resonate and oscillate at multiple frequencies (*9*, *10*), which suggests that precise timing of their activity within neuronal networks could represent information. At the same time, the neuronal assembly structures of the oscillatory patterns found during sleep were related to the experiences of the previous awake period (*11*, *12*). These results led to the tantalizing conjecture that perception, memory, and even consciousness could result from synchronized networks (*13–17*). The synchronous activity of oscillating networks is now viewed as the critical "middle ground" linking single-neuron activity to behavior (*2–6*, *15*). This emerging new field, "neuronal oscillations," has created an interdisciplinary platform that cuts across psychophysics, cognitive psychology, neuroscience, biophysics, computational modeling, physics, mathematics, and philosophy (*2–11*, *13–22*).

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A System of Brain Oscillators

Neuronal networks in the mammalian forebrain demonstrate several oscillatory bands covering frequencies from approximately 0.05 Hz to 500 Hz (Fig. 1). The mean frequencies of the experimentally observed oscillator categories form a linear progression on a natural logarithmic scale (*23*) with a constant ratio between neighboring frequencies, leading to the separation of frequency bands. Neighboring frequency bands within the same neuronal network are typically associated with different brain states and compete with each other (*15*, *24–26*). On the other hand, several rhythms can temporally coexist in the same or different structures and interact with each other (*2*, *25*).

The power density of EEG or local field potential is inversely proportional to frequency (f) in the mammalian cortex (*27*) (Fig. 1C). This *1/f* power relationship implies that perturbations occurring at slow frequencies can cause a cascade of energy dissipation at higher frequencies (*28*) and that widespread slow oscillations modulate faster local events (*2*, *25*, *29*). These properties of neuronal oscillators are the result of the physical architecture of neuronal networks and the limited speed of neuronal communication due to axon conduction and synaptic delays (*30*). Because most neuronal connections are local (*31*), the period of oscillation is constrained by the size of the neuronal pool engaged in a given cycle. Higher frequency oscillations are confined to a small neuronal space, whereas very large networks are recruited during slow oscillations (*2*, *25*). These relations between anatomical architecture and oscillatory patterns allow brain operations to be carried out simultaneously at multiple temporal and spatial scales (*32*).

Assembly Synchronization by Oscillation

Integration of information requires "synchrony" of the convergent inputs. Synchrony is defined

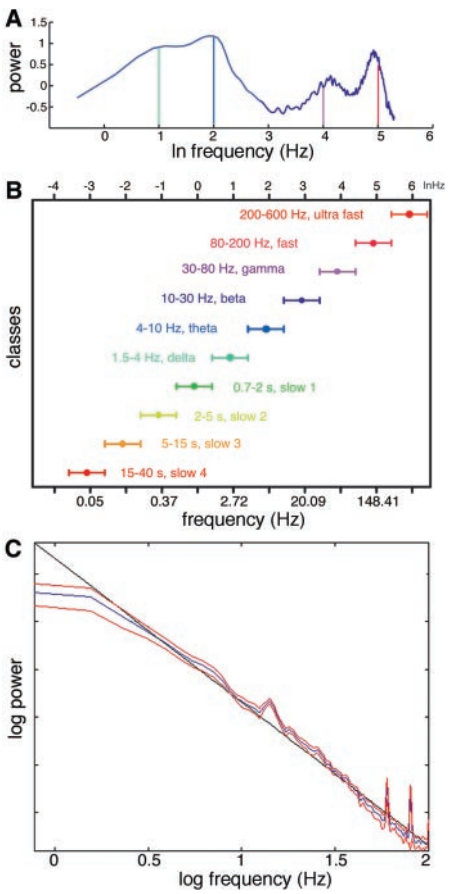

Fig. 1. An interacting system of brain oscillators. (**A**) Power spectrum of hippocampal EEG in the mouse during sleep and waking periods. The spectrum was "whitened" by removing log slope [as shown in (C)]. Note four peaks close to *ln* integers. Color-code band peaks as in (B). (**B**) Oscillatory classes in the rat cortex. Note the linear progression of the frequency classes on the *ln* scale. For each band, the range of frequencies is shown, together with its commonly used term (*23*). (**C**) Power spectrum of EEG from the right temporal lobe in a sleeping human subject. Subdural recording. Note the near-linear decrease of log power with increasing log frequency from 0.5 to 100 Hz. [Adapted with permission from *23* (A and B) and *27* (C)]

by the temporal window within which some trace of an earlier event is retained, which then alters the response to a subsequent event. In contrast, successive events that evoke identical responses are deemed nonsynchronous. Although synchronous assemblies can also be brought about by strong common inputs that occur irregularly, oscillation-based synchrony is the most energy-efficient physical mechanism for temporal coordination (*21*, *22*). Brain oscillators, like most biological rhythms, belong to limit-cycle and weakly chaotic oscillators and share features of both harmonic and relaxation oscillators (*22*, *33*). The macroscopic appearance of several brain rhythms, such as the 5- to 10-Hz theta oscillations in the hippocampus, resembles the sinusoid pattern of harmonic oscillators. A major advantage of harmonic oscillators is that their long-term behavior can be predicted from short-term observations of their phase angle (*22*, *33*). However, groups of harmonic oscillators poorly synchronize their phases (*5*). On the other hand, these macroscopic oscillations are generated by neurons, whose spiking patterns share characteristics with relaxation oscillators. Because of its phase-dependent excitability, the relaxation oscillator separates the information transfer ("duty cycle") phase from the receiving phase. Relaxation oscillators synchronize robustly and with great stability (*5*). These combined features of brain oscillators make their time course predictable and their phase easy to reset.

Scaling of Oscillatory Networks in Growing Brains

Because the different classes of oscillations (Fig. 1) and their behavioral correlates are largely preserved throughout the mammalian evolution (*7*, *13*, *14*, *17*, *20*, *34*), it is reasonable to assume that they are supported by universal mechanisms in brains of various sizes. Oscillations emerge from the dynamic interplay between intrinsic cellular and circuit properties (*2*–*5*, *7*–*10*). Whereas the spiking of single cortical principal neurons typically displays Poisson statistics (*35*), their assembly behavior is often characterized by oscillatory properties (*7*, *8*, *13*). Complex brains have developed specialized mechanisms for the grouping of principal cells into temporal coalitions: inhibitory interneuron "clocking" networks (*19*, *32*). In many systems, electrical coupling by gap junctions assists chemical synaptic signaling in oscillatory synchronization (*3*, *36*–*38*). However, local connections alone place major constraints on global synchrony in growing brains (*21*, *31*). In the cortex, the densely connected local neuron networks are supplemented by a small fraction of long-range connections (*31*), which effectively reduces the synaptic path lengths between distant cell assemblies (*32*). This architectural design, reminiscent of the mathematically defined "small-world" networks (*39*), keeps the synaptic path lengths short and maintains fundamental functions in growing brains without excessive wiring. Despite the progressively decreasing fraction of long-range connections in larger brains, synchronization of local and distant networks can be readily accomplished by oscillators because of the low energy costs involved in coupling rhythms.

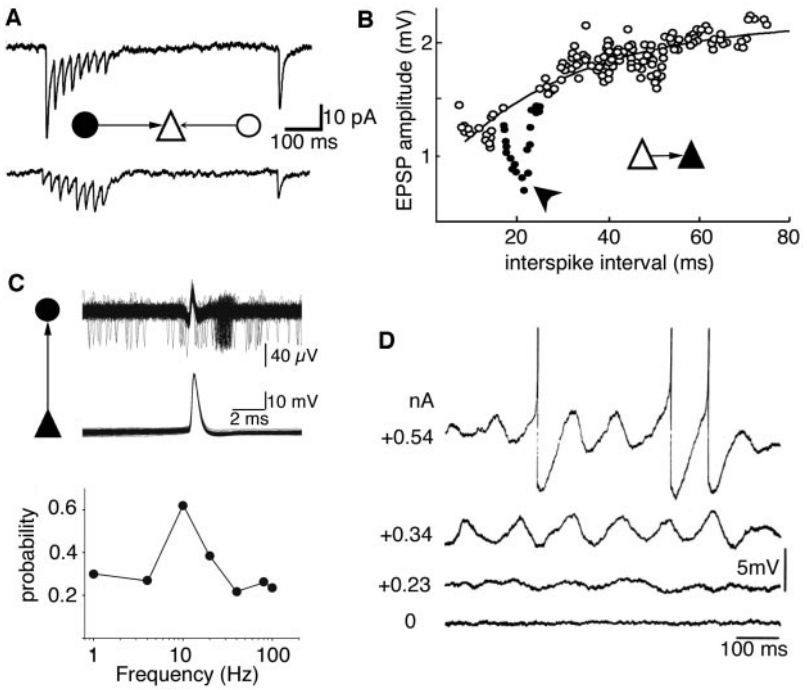

Fig. 2. Resonance and oscillation are affected by both synaptic and intrinsic mechanisms. (**A**) Depression (low-pass filtering) and facilitation (high-pass filtering) of inhibitory postsynaptic potentials by two interneurons (circles) converging onto the same neocortical pyramidal cell (triangle). (**B**) Band-stop (notch) filtering of excitatory postsynaptic potentials at gamma frequency (15 to 30 ms, arrowhead) between layer 5 pyramidal cells. (**C**) Band-pass filtering of spike transmission. (Top) Monosynaptic discharge of a CA1 interneuron by an intracellularly driven pyramidal cell. (Bottom) Spike transmission probability is frequency dependent and peaks at ~10 Hz. (**D**) Voltage-dependent, subthreshold oscillation in layer 2 entorhinal cortical neuron at ~8 Hz. [Adapted with permission from *40* (A), *43* (B), *42* (C), and *41* (D)]

Functions for Brain Oscillators

The specific benefits of a particular oscillation depend on the function of the brain system that supports it. Nevertheless, there are a few general principles, some of which are independent of physical substrate.

Input selection and plasticity. Single neurons and networks respond with transient oscillations to a strong input. The natural frequency, or eigenfrequency, of the damped oscillation is a result of two opposing effects. The leak conductance and capacitance of the neuronal membrane are mainly responsible for the low-pass filtering property of neurons. On the other hand, several voltage-gated currents, whose activation range is close to the resting membrane potential, act as high-pass filters, making the neuron responsive to fast trains of spikes (*9*, *10*). The appropriate combination of high-pass (voltage-dependent) and low-pass (time-dependent) filtering properties of neurons can be exploited for the construction of resonators (band-pass filters), "notch" or band-stop filters, and subthreshold oscillators (*40*–*43*) (Fig. 2). These resonant-oscillatory features allow neurons to select inputs based on their frequency characteristics. Input frequency preference can be dynamically tuned by biasing the membrane conductance and potential. Cortical interneuron classes have a wide range of preferred frequencies (*19*, *40*, *43*), and their diverse frequency-tuning properties are important for setting network dynamics (*3*). For example, the high-frequency discharge of a pyramidal cell in its receptive field "enslaves" its basket cells through resonance tuning (*42*), which, in turn, suppress the activity of the surrounding pyramidal neurons.

Subthreshold oscillations in single neurons can occur at a different frequency from that of the network. The augmenting properties of resonators-oscillators are also at work at the network level, and coherent summation of oscillators is an effective mechanism for the detection and amplification of weak signals (*44*, *45*). For example, rhythmic cortical feedback to the thalamus is a major factor in the amplification of thalamocortical oscillations (*2*, *7*, *45*). With their increasing commitment to an oscillatory network, the responsiveness of neurons to external inputs progressively decreases. As a result, thalamocortical spindle oscillations effectively reduce environmental influences on neocortical activity, thereby actively shifting sleep into deeper stages (*46*).

A further refinement of input selection can be achieved by phase biasing. The ongoing phase of a centrally organized oscillatory network is independent of the temporal fluctuation of sensory signals. The oscillation-related fluctuation of the membrane potentials in the participating neurons continuously and predictably biases the open-time probability of a multitude of voltage-gated channels (*9*). This design is an energy-efficient solution for periodically elevating the membrane potential close to threshold, providing discrete windows of opportunities for the neuron to respond. If the input is not appropriately timed, however, it is ignored altogether or the response is delayed (*10*). For example, proper coordination of afferent activity with the phase of an intrinsic oscillation can amplify the somadendritic backpropagation of the action potential (*47*) and bias the magnitude and direction of spike-timing–dependent plasticity (*48*). In the hippocampus, brief pulse trains delivered at the peak of the theta oscillation result in long-term potentiation, whereas the same trains applied out-of-phase weaken the previously strengthened inputs (*49*). Conversely, rhythmic but out-of-phase influences can selectively suppress oscillations in the target network, as exemplified by the suppression of gamma-frequency rhythm in the hippocampus by the dentate gyrus input (*25*). The systems level implication of these oscillation-gating functions is that perception is not a continuous event but is subject to the cyclic changes of the networks processing the input (*15*–*16*).

Binding cell assemblies. Information in the brain has been hypothesized to be processed, transferred, and stored by flexible cell assemblies, defined as distributed networks of neuronal groups that are transiently synchronized by dynamic connections (*15*, *16*). The mechanisms by which such ephemeral neuronal coalitions are brought about are not known. One possible mechanism supporting synchrony is a dynamic change in synaptic strengths across the assemblies, a process that would require energy-demanding biochemical steps. An alternative mechanism is oscillatory synchrony (*13*, *15*). Transient assembly synchronization by oscillation is cost effective. The ability of neuronal assemblies to synchronize depends on the coupling strength and the distribution of natural frequencies (*21*, *22*). As long as the frequencies of the coupled oscillators remain similar, synchrony can be sustained even with very weak synaptic links (*21*, *32*). This inherent feature of oscillations allows activated neuronal groups in distant cortical regions with sparse interconnections to become temporally linked and then activate unique sets of downstream assemblies. For example, the various attributes of a visual image might be processed separately in distributed neuronal assemblies across widespread cortical regions and linked by a common gamma-frequency oscillation. In turn, the phase-locked discharges of these distributed groups may be responsible for the "binding" of the various features into a coherent cognitive percept (*13*). Numerous experiments support and expand the "binding-by-gamma" hypothesis (*15*) (but see *50*, *51*). The time span required for bringing together transient cell assemblies (*52*) closely fits the gamma cycle, and the induced oscillation is long enough to establish an elementary cognitive act (*14*–*17*).

Consolidation and combination of learned information. Global oscillation is an inherent behavior of balanced systems, and the frequency is determined by the time constants of its constituents (*8*, *53*). Networks built from nonoscillating pyramidal neurons of similar types inevitably gave rise to a self-sustained oscillation (*54*). The pattern of neuronal activity depends not only on the precise neuronal architecture but also, importantly, on its initial conditions (*22*, *33*, *53*). Unless the oscillator is perturbed, the sequences of neuronal activity will repeat infinitely in a noise-free system (*53*, *55*). In other words, the conditions that gave rise to a rhythm are "frozen" into the deterministic nature of the oscillatory dynamics.

The "default" state of the unperturbed, sleeping brain is a complex system of numerous self-governed oscillations, particularly in the thalamocortical system (*2*, *45*, *46*). The content of these oscillations reflects spike sequence patterns created by prior waking experience (*2*, *7*, *11*, *12*). Synaptic modifications brought about by learning are thus frozen into the various time windows of self-organized oscillatory networks of sleep to be turned ultimately into long-term memory by means of functional and structural synaptic modifications (*11*, *12*). This self-sustained replay of learned information allows for the dissemination and combination of temporally discontiguous patterns of activity acquired during previous waking behaviors. This "off line," assembly-

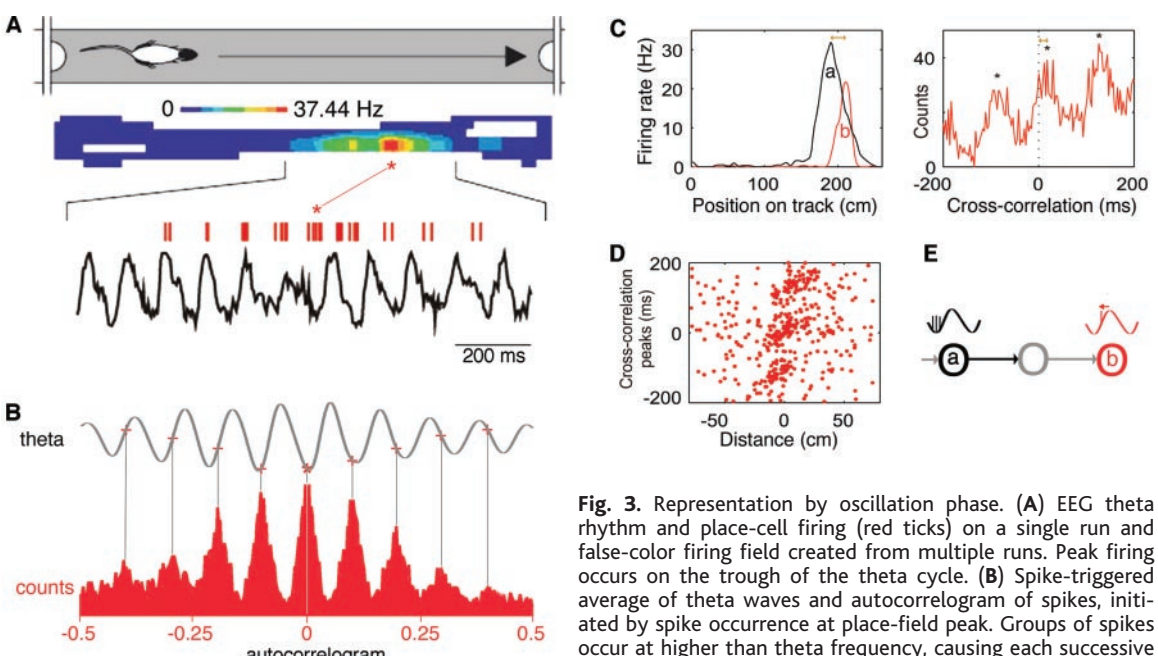

Fig. 3. Representation by oscillation phase. (**A**) EEG theta rhythm and place-cell firing (red ticks) on a single run and false-color firing field created from multiple runs. Peak firing occurs on the trough of the theta cycle. (**B**) Spike-triggered average of theta waves and autocorrelogram of spikes, initiated by spike occurrence at place-field peak. Groups of spikes occur at higher than theta frequency, causing each successive burst to move to an earlier phase of the theta cycle. Note the progressive forward shift of the preferred phase. (**C**) Place fields for two neurons (a and b) with overlapping place fields and time cross-correlation between them. Note the theta-frequency modulation of the cross-correlogram. (**D**) Relation between distance of place-field peaks and temporal peaks of cross-correlograms [stars in (C)] for a population of neurons. Dot clouds correspond to three theta cycles and reflect ~30-cm distance representation by the cell assembly in each theta cycle. During subsequent cycles, representation shifts by ~6 cm, so that overlapping portions of the environment are scanned repeatedly. (**E**) The current position of the rat is identified by the most strongly discharging neuronal assembly (a) at the trough of the theta cycle that forces the trailing oscillator(s) (e.g., b) to advance its phase (*21*, *58*). [Adapted with permission from *58* (A) and *60* (C and D)]

grouping mechanism may be the physiological basis for the creativity and insight-promoting nature of sleep (*56*).

Representation by phase information. The timing of neuronal spikes in oscillatory networks is under the combined influence of external inputs and the internal dynamics of the network (*52*). This is the basis for information representation by phase. Consider the consequences of phase-coupled rhythmic somatic inhibition and dendritic depolarization in a single pyramidal neuron, a typical scenario during sustained oscillations (*7*, *19*). If the somatic inhibitory oscillation remains unchanged but dendritic depolarization increases, spike threshold will be reached at progressively earlier phases of the inhibitory cycles (*19*). Generalizing this scenario to a network of cells, neurons with stronger dendritic inputs will discharge earlier in the cycle than neurons with weak dendritic excitation. This property is universal for oscillators: The coupling strength is proportional to the magnitude of phase advancement (*21*, *57*). Thus, the input magnitude–dependent forward phase shift of action potentials (*19*) may be exploited for short-term storage of information (*55*).

The first experimental support for representation by phase came from work on the hippocampus (*18*). When the rat walks through the receptive field of a recorded pyramidal cell, the phase assignment of spikes progressively advances from the peak to the trough of theta while the rat enters into the place field and reaches its center (Fig. 3, A and B), independent of the size or shape of the field or the speed of the rat (*18*, *58, 59*). A consequence of this relation is that the future positions of place fields can be predicted from the phase sequence of spikes of neuronal assemblies in a single theta cycle (Fig. 3, C and D) (*57*, *60*). At least part of the spike phase precession effect is accounted for by the mathematical rules of relaxation oscillators (*57*) (Fig. 3E). On the other hand, prediction of long-term behavior from phase information is a characteristic feature of harmonic oscillators. The within-cycle phase sequences of assemblies are discrete quanta of information, the beginning and end of which are marked by an oscillatory cycle. The repeating temporal sequences of spikes over several cycles can exploit spike-timing–dependent plasticity (*48*) for consolidating representations (*61*). Without oscillations, such packaging is not possible, as evidenced by the impairment of learned spatial behavior after interfering with theta oscillation (*62*).

Unexplored Benefits of Brain Oscillations

Oscillatory coupling of neuronal assemblies is usually examined within single frequency bands. However, different oscillatory classes might carry different dimensions of brain integration, and the coupling of two or more oscillators could provide enhanced combinatorial opportunities for storing complex temporal patterns and optimizing synaptic weights when used in conjunction with appropriate algorithms. The nature of these algorithms in the brain remains to be discovered. Slow rhythms synchronize large spatial domains and can bind together specific assemblies by the appropriate timing of higher frequency localized oscillations (*15*, *16*, *29*, *45*). The sleeping brain is a rich source of self-organized multiple oscillators, but the content of these rhythms is poorly understood (*7*, *45*). Large-scale, simultaneous recording of multiple neuron activity across interacting brain systems will be required to reveal how neuronal assemblies are specifically organized by sleep rhythms. The study of oscillations has always been entwined with the study of self-organization. Understanding the physiological mechanisms of self-emerging oscillations not only will provide insight into their functions but also may assist in the diagnosis and treatment of brain disorders (*63*, *64*). Uncovering the relation between neuronal oscillators and the much slower biochemical-molecular oscillators, including ultradian and circadian rhythms (*33*), is yet another daunting challenge. An important function of the brain is the prediction of future probabilities. Feed-forward and feedback networks predict well what happens next. Oscillators are very good at predicting when.

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