neural oscillation

physiology

Also known as: brain wave, brainwave

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neural oscillation, synchronized rhythmic patterns of electrical activity produced by neurons in the brain, spinal cord, and autonomic nervous system.

Oscillations, in general, are a reflection of a balanced interaction between two or more forces. In the brain, they typically reflect competition between excitation and inhibition. Balance between the two is relative, and, within the oscillation cycle, excitation and inhibition prevail at different phases. This has two major effects. First, oscillations are energetically the most efficient way of synchronizing neurons and forming neuronal assemblies, and, thus, many excitatory neurons can be synchronized in a limited phase range, sending messages to downstream structures within the “sending” phase. Second, in its “receiving” (or perturbation) phase, the network can respond most effectively to upstream inputs.


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The first brain pattern observed by recording electrical activity from the scalp (electroencephalogram, EEG) was an oscillation (alpha rhythm), detected by German

psychiatrist Hans Berger in the 1920s. The first neuronal population pattern that emerges during development is also a rhythm, known as delta brush.

Types of brain rhythms

There are at least 10 discrete brain rhythms, covering more than four orders of magnitude in frequency, from approximately 0.02 to 600 hertz (Hz). Different brain structures and brain states have different preferred subsets of oscillations. Most oscillations are short-lived (less than a second), while others can be sustained for longer periods.

Traditionally, the frequency bands are denoted by Greek letters. They do indicate not a logical order of frequencies but roughly the order of their discoveries. Alpha oscillations (8–12 Hz) are most prominent above the occipital cortical area when the eyes are closed. Large-amplitude theta oscillations (4–10 Hz) dominate the hippocampal-entorhinal system during spatial navigation and memory processing. Delta waves (0.5–1.5 Hz), the largest-amplitude waves in the neocortex (the cerebral cortex region associated with sight and hearing), are present during non-REM sleep. Beta rhythms (13–30 Hz) are present throughout the motor system in the absence of movement, while transient beta oscillations (or sleep spindles) are present in the thalamocortical system during the early stages of sleep. Gamma oscillations (30–120 Hz) are present in nearly all structures and all brain states, although they dominate in the aroused, attentive brain. The transient ripple pattern (130–200 Hz), most prominent in the hippocampus, serves to transfer memories and action plans from the hippocampus to the neocortex. These and other rhythms can temporally coexist in the same or in different structures and interact with each other.

Hierarchy of brain rhythms

Various constellation of multiple brain oscillations, rather than particular rhythms, are associated with brain state changes, such as stages of sleep and the arousal levels of waking. The individual frequency bands, measured by EEG, form a geometric progression on a linear frequency scale or a linear progression on a natural logarithmic scale. Because the centre frequencies of the neighbouring bands have a noninteger number relationship with each other, they cannot entrain each other for a long period. Instead, the oscillatory interference between them gives rise to a

perpetual fluctuation between unstable and transiently stable states. This explains the ever-changing landscape of the EEG.

The different rhythms are bound by a hierarchical relationship and expressed by cross-frequency phase modulation between the various oscillations. The phase of a slow oscillation modulates the amplitude of a faster rhythm. In turn, the phase of the faster rhythm modulates the amplitude of an even faster one, and so on. For example, spikes of local neurons are phase-locked to the troughs of ripple oscillation. The probability of ripple occurrence is modulated by the phase of thalamocortical sleep spindles. The spindle events, in turn, are phase-modulated by cortical delta oscillations, which are nested in the brain-wide infra-slow oscillations (~0.1 Hz). Fast oscillations are local, whereas slower oscillations can recruit increasingly larger brain volume. Their interactions allow local computation to be broadcast globally and allow global brain states to control local computation in multiple brain areas.

Mechanisms of network oscillations

Two aspects of neuronal oscillations can be distinguished: the mechanism of rhythm generation and the substrate of current generation. Although individual neurons can oscillate in isolation, network rhythms typically arise from interactions of many irregularly firing neurons within and across brain structures; they are emergent patterns and their frequency is determined by the various neuronal time constants. In the case of gamma rhythm, these correspond to the time constant of the neuronal membrane and fast inhibitory and fast excitatory receptors. The phase-entrained neurons give rise to coherent fluctuation of their membrane potentials, and their summed vector in the extracellular space can be detected by electrodes and conveniently used to monitor dynamic changes of neuronal populations.

Oscillations in the same frequency band can be generated by different mechanisms in different structures (e.g., hippocampal and midline theta oscillations). Oscillations per se do not serve special cognitive or motor functions. Instead, the benefits of a particular oscillation depend on the brain system by which it is supported. For example, the meaning of gamma oscillations in the sensory olfactory bulb is different from those in prefrontal circuits serving cognitive functions.

Preservation across species

A remarkable aspect of brain rhythms is their evolutionarily conserved nature. Every known oscillation in one species is also found in virtually all other mammals. The frequency bands, the temporal aspects of oscillatory activity (e.g., duration and temporal evolution), and their behavioral correlations are conserved, despite a 17,000-fold increase in brain volume from the small tree shrew to large-brain cetaceans. The preservation of brain oscillations and their cross-frequency coupling effects across species suggest a fundamental role for temporal coordination of neuronal activity.

Role in neural syntax

Brain oscillations can segregate and group neuronal activity to decompose and package neuronal information for communication between brain areas. Because all neuronal oscillations are based on inhibition, they can parse and concatenate neuronal messages, a prerequisite for any coding mechanism. Gamma waves combine neurons into assemblies, which can be conceived as a neuronal “letter.” The hierarchical nature of cross-frequency-coupled rhythms can serve as a mechanism for combining neuronal letters into neuronal words and words into sentences, so that unbounded combinatorial information can be generated from spike patterns. Neuronal oscillators are pulsatile and can readily entrain one another, facilitating the effectiveness of message exchange between brain areas.

Neural oscillations in disease

Every mental disorder is associated with some kind of rhythm alteration. Fast ripples and hypersynchrony are indicative of epilepsy, gamma oscillations are diminished in schizophrenia, depression is characterized by changes in sleep spindles, and enhanced beta oscillations in motor areas are diagnostic in Parkinson disease.

However, the relationship between disease and oscillations is complex. Altered coupling between different oscillatory patterns and changes across different structures are more important than increased or decreased amplitude in a particular frequency band.

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sensory neuron

anatomy

Also known as: sensory cell, sensory nerve-cell

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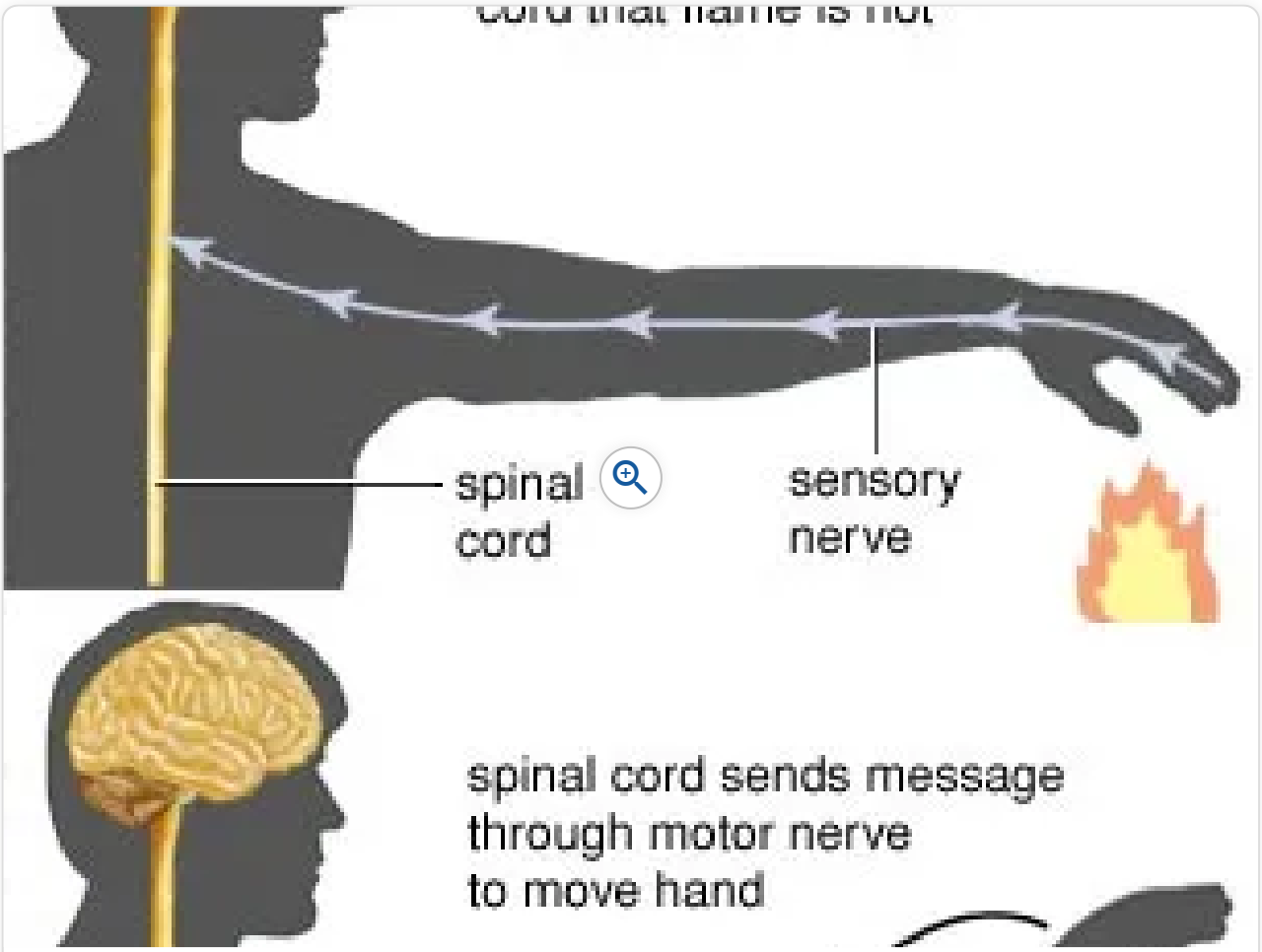

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sensory neuron, nerve cell that carries information about changes in external and internal environments to the central nervous system (CNS). Such neurons are part of the peripheral nervous system, which lies outside the brain and spinal cord. They collect information from so-called sensory receptors, which are located in specialized tissues of the ears, eyes, mouth, nose, skin, and internal organs. In general, sensory neurons are described as afferent (carrying information to the CNS), whereas motor neurons are described as efferent (carrying information away from the CNS).

Information from a sensory neuron is transmitted to the CNS in the form of an action potential, a brief reversal of electric polarization of the membrane of a neuron or a muscle cell. The information flows across a synapse, or junction between neurons. In

a few cases, sensory neurons communicate directly with motor neurons via synapses, allowing for a very fast reflex response. In most cases, however, sensory neurons communicate with interneurons in the CNS before a response is sent back to the body.

Sensory neurons may be categorized as peripheral or visceral. Peripheral sensory neurons are activated by stimuli external to the body, such as light, touch, sound, scent, or taste. Visceral sensory neurons respond to stimuli that originate within the body, such as pain, blood pressure, hunger, or inflammation. The body's response to visceral sensory information allows it to maintain homeostasis (the self-regulation of physical systems that are necessary for survival).

Like other types of neurons, each sensory neuron has a cell body and projections (dendrites and axons) that gather and transmit information. The cell bodies of sensory neurons are often clustered into ganglia, which are located outside the CNS. The specific shapes and sizes of sensory neurons vary according to their function. Many sensory neurons are pseudounipolar; that is, each has one projection from the cell body that branches into two axons—one axon projecting to the periphery of the body and the other toward the CNS. Other sensory neurons are bipolar, each having two projections departing the cell body—one gathering information and the other passing information to other cells. In addition, many sensory neurons are enclosed in myelin, a coating consisting primarily of fatty materials that increases the speed of signaling along the axon. The layer of myelin varies in thickness, and it may be absent altogether.

Sensory neurons can be affected by diseases and disorders, such that affected individuals lose access to information about their external or internal environment. For example, humans rely on three types of cones (the light-sensitive cells in the retina of the eye that function in the perception of colour) to sense the full range of colours. In certain forms of colour blindness, however, only one or two types of cones are functional, resulting in a reduction of sensory information about colour in affected individuals' environment. Another example of sensory impairment is hearing loss caused by repeated exposure to extremely loud noise that damages sensory receptors in the inner ear. Damage to auditory sensory neurons or to the temporal lobes of the brain, which normally process auditory information, can also result in hearing loss.

When sensory neurons become nonfunctional, the brain may adapt through a process known as neuroplasticity. For example, individuals who are blind from an early age can learn to use biosonar, or echolocation, to sense objects (similarly to bats). In this case, echoes are detected by auditory receptors and sensory neurons, but they are processed in the occipital lobe of the brain, which normally integrates visual, rather than auditory, information. Thus, individuals who are blind but who learn to employ biosonar can use auditory information to create mental images of their surroundings.

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