Physiological and Psychological Mechanisms of Infra-slow Oscillations

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Abstract

Infra-slow oscillation (ISO) is a brain rhythm ranging between 0.01 and 0.1 Hz. ISO is widely distributed across multiple brain regions, exhibiting distinct activity patterns from high-frequency neural rhythms while interacting through cross-frequency coupling, thereby constituting an important brain functional activity. ISO may be generated by the thalamus, glial cells, and ionic dynamic activities, regulating overall brain excitability and consequently influencing the efficiency of cognitive activities. The frequency, amplitude, and phase of ISO can all modulate the overall efficiency of cognitive activities. Future research should investigate the relationship between the diverse physiological generation mechanisms of ISO and various cognitive activities, explore the principles governing the interaction between mental activity and ISO, and advance the construction of brain rhythm theory.

Full Text

Preamble

The Physiological and Psychological Mechanisms of Infra-Slow Oscillation

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Abstract

Infra-slow oscillation (ISO) is a type of brain rhythm occurring between 0.01 and 0.1 Hz. ISO is widely distributed across multiple brain regions and represents an important brain functional activity that exhibits distinct activity patterns from high-frequency neural rhythms while interacting with them through cross-frequency coupling. ISO may be generated by dynamic activities in the thalamus, glial cells, and ion dynamics, regulating overall brain excitability and thereby affecting the efficiency of cognitive activities. The frequency, amplitude, and phase of ISO can all modulate the general efficiency of cognitive activity. Future research should investigate the relationship between the diverse physiological generation mechanisms of ISO and various cognitive activities, explore the principles governing the interaction between mental activities and ISO, and advance the construction of brain rhythm theory.

Keywords: infra-slow oscillation; thalamus; glia; cognitive efficiency; ions; consciousness

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Introduction

In 1957, Aladjalova first recorded brain electrical rhythms of 0.01-0.1 Hz in rabbit brains using intracranial electrodes and named them infra-slow oscillations (ISO) [?]. However, this phenomenon did not receive sufficient attention at the time. It was not until the rise of resting-state brain network research in the early 21st century that ISO began to attract increasing attention. Resting-state brain networks are primarily measured through blood oxygen level-dependent (BOLD) signals, whose frequency range matches that of ISO with a peak around 0.02-0.03 Hz [?]. Recent studies have established a direct link between resting-state brain networks and EEG signals of ISO [?]. Further research has found that during resting states, anesthesia, sleep, and cognitive task performance, functionally connected brain regions form several independent and stable brain networks [?, ?], suggesting that ISO has specific functional distributions and performs particular psychological functions. In recent years, research on the physiological and psychological mechanisms of ISO has gradually unfolded, and the importance of ISO as a significant brain rhythm for psychological research is becoming increasingly prominent.

First, ISO is a ubiquitous physiological activity. ISO not only exists in EEG activity during resting states, task states, sleep, and anesthesia but also occurs in the cerebral cortex and extensive non-cortical regions such as the thalamus, hippocampus, basal ganglia, locus coeruleus, dorsal raphe nucleus, and olivary nucleus [?, ?]. During slow-wave sleep, ISO power in skin conductance activity is also significantly enhanced in addition to EEG activity [?]. ISO also exists in the retina and can be transmitted to the lateral geniculate nucleus; simultaneously, the same oscillatory patterns have been found in subcortical visual systems, such as the olivary pretectal nucleus responsible for pupil constriction and the suprachiasmatic nucleus involved in regulating biological clocks [?]. These evidences indicate that ISO exists in brain activities ranging from perception to movement, arousal, and higher-order cognition.

Second, ISO has close connections with higher-frequency neural activities. Almost all high-frequency neural oscillations are modulated by ISO, with the delta band (0.5-4 Hz) and sigma band (10-20 Hz) being most strongly regulated by ISO around 0.02 Hz; these two bands happen to be the two main components of non-rapid eye movement sleep, suggesting that non-REM sleep is regulated by ISO [?, ?, ?]. ISO’ s modulation of high-frequency neural oscillations is primarily achieved through cross-frequency phase-amplitude coupling, where high-frequency oscillations are enhanced at specific phases of ISO and weakened at other phases [?]. Cross-frequency coupling reflects the nested characteristic of neural rhythms, indicating that ISO is an important link between high-frequency neural oscillations and circadian rhythms.

Third, ISO has unique activity patterns distinct from high-frequency neural activities. Early views suggested that BOLD signals represent a low-pass filter of high-frequency neural activity, thus considering ISO as the summation of rapid local neural activities [?]. However, this view is inconsistent with evidence showing that BOLD signals directly correlate with gamma-band local field potentials and is not supported by simulation studies [?]. Recent research tends to consider ISO as a unique neurophysiological activity [?]. Li et al. [?] found that the frequency characteristics of functional connectivity between brain regions cannot be explained by the transmission of local neural activity between brain regions but rather reflect the propagation of rhythmic or oscillatory activity between brain regions, meaning that functional connectivity itself has oscillatory characteristics. Keinänen et al. [?] found that the correlation strength between scalp potential ISO and BOLD signals changes over time, with this dynamic change depending on the connection strength of resting-state brain networks rather than average signal level or activity intensity, further supporting the notion that ISO governs the essential nature of inter-regional information exchange. Mitra et al. [?] further discovered evidence of opposite propagation directions between ISO and delta waves in the neocortex. Thus, ISO possesses unique generation mechanisms and activity patterns distinct from high-frequency neural oscillations.

These studies demonstrate that ISO, as an important brain rhythm, has both independent generation mechanisms and effectively connects extremely low-frequency circadian rhythms with high-frequency neural oscillations. Characteristics such as universality, nestedness, and independence make ISO an important medium linking behavior, psychology, and brain activity. ISO is bound to become a new window for studying the brain mechanisms of mental activities.

2 Physiological Origins of ISO

Current research has extensively investigated the physiological origins of ISO. Converging evidence suggests that ISO may not originate from neural activity per se but rather from dynamic changes in intra- and extracellular ion concentrations, primarily acting on glial cells.

2.1 Thalamic Origin

Early views held that ISO originates in the thalamus and acts on the entire cerebral cortex through thalamocortical circuits. Regarding the thalamic driving mechanism, first, intracellular potentials, action potentials, and local field potentials recorded in the thalamus and thalamic slices of anesthetized animals all exhibit ISO [?]. Second, sigma waves and sleep spindles during natural sleep in animals are both modulated by thalamic ISO; local heating of the thalamus only changes spindles in the heated region, indicating that ISO' s modulation of spindles depends on thalamic networks [?, ?]. Third, the ability of optogenetic methods to evoke spindles in the thalamus of anesthetized animals fluctuates in an ISO pattern [?]. Finally, ISO recorded in the thalamus of freely moving cats directly modulates the amplitude of 9-13 Hz oscillations [?]. These evidences suggest that the thalamus is key to ISO generation across wakefulness, sleep, and anesthesia states. However, hyperpolarization between neurons has delays of seconds rather than milliseconds, differing from the timescale of neural information exchange; moreover, hyperpolarization correlates with downward rather than upward local field potentials, suggesting that ISO is not driven by thalamic neurons [?].

2.2 Glial Cell Origin

Another perspective holds that ISO originates from glial cell activity. Early studies using brain slices observed that calcium ion activity in thalamic glial cells fluctuates around 0.01 Hz and further modulates neuronal activity through ATP release [?]. Subsequent in vivo detection found that glial cells in the hippocampus also fluctuate on the timescale of minutes and affect subsequent local field potential amplitudes [?]. During natural sleep, disruptions in local field potential power spectra coincide with enhanced cortical glial cell activity; conversely, activating astrocytes also changes delta oscillation amplitudes [?]. Taken together, both spontaneous and evoked astrocyte activity alter local field potentials. Although glial cell ISO exists in the hippocampus and cortex, thalamic glial cell ISO is independent and can drive cortical activity through different nuclei [?]. These evidences suggest that thalamic astrocytes may be the main drivers of ISO. ISO may reflect bottom-up oscillatory regulation from thalamus to cortex, switching cortical excitability between offline and online states [?].

2.3 Ionic Origin

Recent research has revealed at the molecular level how various macromolecular and small-molecule activities regulate ISO. Zylbertal et al. [?] found that ISO synchronous activity in mitral cells of the mouse accessory olfactory bulb originates from intracellular Na+ dynamics and network connectivity interactions. Slow intracellular Na+ dynamics endow mitral cells with weak firing tendencies that are further strengthened by chemical and electrical synapses between cells. Krishnan et al. [?] observed in a brain network model simulating awake resting states that extracellular K+ concentration, Na+/K+ pump activity, neuronal firing rates, and local field potentials all exhibit ISO; maintaining constant K+ concentration abolishes ISO. ISO amplitude and peak frequency are regulated by Na+/K+ pumps, GABA, synaptic currents, and glial cell properties. Dynamic changes in ion concentrations regulate glial and neuronal activity, further forming ISO of large-scale brain activity [?]. Additionally, molecular activities such as dopamine, adenosine A1 receptors, and intracellular calcium ions can all modulate glial and neuronal ISO [?, ?, ?]. More studies have found that factors including hormones, metabolism, activity of neuromodulatory hubs like the locus coeruleus and raphe nuclei, and neurovascular coupling may all influence ISO [?, ?].

To date, no study has proven that ISO has a single physiological origin. This unique oscillatory phenomenon may result from the combined action of multiple systems, and thus its impact on cognitive activity may be complex and diverse.

3 Psychological Significance of ISO

A widely accepted current view is that neural oscillations constitute the fundamental working mode of the brain and the basis of cognitive activity [?, ?]. The psychological functions of neural oscillations in theta, alpha, and gamma bands are relatively well established, such as attentional oscillations in the theta band and cognitive control in the alpha band [?, ?], but the psychological functions of ISO remain far from clear. Below, we introduce research on the psychological functions of ISO from the perspectives of frequency, amplitude, and phase.

3.1 Relationship Between ISO Frequency and Mental Activity

Like high-frequency neural oscillations, infra-slow waves can be subdivided into multiple sub-bands. Electrophysiological studies have found that ISO can be divided into at least three frequency bands: zeta (period 2-12 seconds), tau (period 12-60 seconds), and epsilon (period greater than 60 seconds) [?], as well as non-periodic omega potentials [?]. Although BOLD signal-based research lacks unified frequency division standards, multiple metrics including functional connectivity [?], regional homogeneity [?], and low-frequency amplitude [?] have shown different characteristics across subdivided frequency bands. Different frequency bands exhibit distinct patterns of local activity and inter-regional information exchange, which must influence psychological functions, but current research linking specific ISO frequency bands to psychological functions remains scarce. Some studies have found that the brain’ s small-world properties (high clustering coefficient and low characteristic path length) are strongest at 0.03-0.06 Hz, and abnormalities in small-world properties in major depressive patients also occur primarily in this band [?, ?]. BOLD signals in the pregenual anterior cingulate cortex 13-20 seconds before stimulus presentation, oscillating at 0.01-0.027 Hz, can predict whether faces near perceptual threshold can be consciously perceived [?]. Zhang et al. found that ultra-low frequency (0-0.01 Hz) oscillation amplitude in the basal ganglia can distinguish true from false feedback and correlates with participants’ behavioral responses [?]. These studies indicate that different ISO sub-bands are associated with different brain functional activities, but systematic research on the relationship between different frequency bands and different cognitive functions is still lacking.

3.2 Relationship Between ISO Amplitude and Mental Activity

ISO amplitude is typically measured using amplitude of low-frequency fluctuation (ALFF) or brain signal variability (BSV). Our research has found that ALFF and BSV reflect the same brain activity patterns [?]. Based on the frequency tagging experimental paradigm, we found that ISO amplitude at task frequency increases, while amplitude below task frequency decreases, and amplitude above task frequency remains unaffected; suppression of low-frequency amplitude is influenced by hemodynamic responses, thus it may reflect inhibition of hemodynamic rather than neural activity [?, ?]. Garrett' s research group has shown that higher cognitive efficiency corresponds to stronger BSV; compared to BOLD signal mean, BSV better predicts cognitive efficiency and brain aging [?, ?]. Generally, higher BSV represents more stable information processing capacity, stronger encoding ability, and stronger adaptability [?]. Additionally, EEG studies have shown that ISO power (amplitude squared) decreases by about 20% during reaction time tasks compared to resting state [?]. Source localization analysis revealed that ISO power reduction primarily occurs in the default mode network [?]. Although deactivation of the default mode network during task states is well established, ISO suppression by tasks has not been widely reported, and the above research establishes a direct relationship between default mode network ISO amplitude and cognitive activity. In summary, ISO amplitude is modulated by various cognitive activities but has not established a one-to-one correspondence with specific cognitive activities, thus ISO amplitude reflects general cognitive activity efficiency.

3.3 Relationship Between ISO Phase and Mental Activity

Phase synchronization of neural oscillations is an important mechanism for inter-regional information exchange [?]. Omidvarnia et al. used dynamic phase synchronization methods to detect that the dynamic changes in connection strength between brain regions during resting state peak at 0.002-0.02 Hz, indicating that dynamic changes in phase synchronization oscillate regularly at extremely low frequencies [?]. These changes reflect the continuous formation and dissolution of different functional modules [?], thereby creating dynamically changing brain states [?]. The infra-slow frequency band constitutes a network framework for cognitive activity through phase-locked brain regions, with regions of opposite phase potentially producing antagonistic effects [?]. For example, the antagonism between task-positive and task-negative networks in the infra-slow band correlates with behavioral responses in the Eriksen flanker task [?]. Widely distributed brain networks provide a basic skeleton for inter-regional information exchange, while ISO provides a temporal framework for dynamic coupling of inter-regional information flow, together determining cognitive activity efficiency.

On the other hand, different phases of ISO carry different information and contain different brain network computational strategies [?]. Some studies have shown that BOLD signals during cognitive activity and resting state are not linearly superimposed but exhibit negative interactions [?], with this interaction influenced by BOLD phase at cognitive activity onset [?]. ISO phase contains different levels of instantaneous excitability. When cortical excitability is low, responses to stimuli are also reduced, and vice versa. In other words, the phase of spontaneous cortical activity modulates the efficiency of stimulus or task processing, thereby producing different levels of activation and behavioral responses [?]. fMRI studies have found that functional connectivity in core face-processing brain regions is enhanced during both the rising and falling phases of ISO [?, ?]. An EEG study found that the rising and falling phases of EEG ISO modulate hit rates and miss rates for weak signals [?]. Additionally, ISO plays an important role in sleep learning and memory consolidation by modulating delta waves and spindles through phase regulation [?]. Recent research further demonstrates that different phases of global signals correspond to different brain network connectivity patterns, forming different brain states [?]. Therefore, different ISO phases may correspond to different inter-regional information exchange patterns and further influence cognitive activity efficiency.

In summary, different ISO phases correspond to different patterns of synchronized activity between brain regions, with the rising and falling phases in particular containing brain connectivity patterns closely related to cognitive activity efficiency. ISO’ s temporal extension allows the brain to dynamically change between different states, becoming the background for adaptive evolution of brain networks.

4 Summary and Outlook

Current ISO research has yielded fruitful results, but systematic investigation of ISO’ s psychological significance remains lacking. ISO ubiquitously exists across multiple levels from neural firing to behavioral operations and in various states from wakefulness to sleep to disease, suggesting that ISO is a constant temporal framework that must have special physiological and psychological significance [?].

First, ISO has multiple origins. On one hand, different brain activities such as local activity and inter-regional functional connectivity have different frequency characteristics, indicating independent ISO patterns for different activities. On the other hand, whether thalamic glial cells dominate or cortical spontaneous ISO exists, and whether ionic dynamic changes or brain network coupling occurs, there is no exclusive evidence that ISO has a single origin. To date, whether ISO has a single origin remains undetermined, and its physiological generation mechanisms require further investigation. The multiple origins of ISO complicate psychological research by necessitating consideration of complex interactions among multiple systems, which is also an important reason why current research on ISO’ s psychological mechanisms is difficult to deepen.

Second, research on ISO frequency, amplitude, and phase all indicates that ISO modulates general cognitive activity efficiency rather than being related to specific cognitive activities. Different spatiotemporal scales must carry different mental activities. ISO' s extremely low periodicity makes it impossible to directly relate to brief (tens to hundreds of milliseconds) cognitive activities. The psychological mechanisms of ISO revealed by DC-EEG and fMRI research must differ from those involved in traditional electrophysiological studies. ISO reflects slow periodic modulation of overall cortical excitability [?] and modulates brain responses to stimuli by changing neuronal excitability [?], which provides both a temporal scale for sensitivity changes to internal and external environments and a background for fluctuations in cognitive activity efficiency. In other words, ISO' s influence on cognitive activity is global.

Third, ISO may be related to complex thought processes and even consciousness generation. Different brain network patterns correspond to different thinking styles [?], and ISO' s close association with large-scale brain networks means it can play an important role in complex thought processes. For example, mood changes occur on the timescale of minutes [?]. Research has shown that spontaneous brain activity ISO is related to behavioral and cognitive flexibility, can coordinate brain activities across different spatiotemporal scales, and may even be a necessary condition for consciousness generation [?, ?, ?]. Therefore, consciousness generation, complex thought activities, and mood disorders may all be regulated by ISO.

Finally, the connection between ISO' s physiological and psychological mechanisms remains unclear. On one hand, ISO's physiological generation mechanisms involve different levels from molecules to cells to tissues to systems, making it a complex and arduous task to examine the relationship between these physiological activities and mental activities. On the other hand, brain activity ISO revealed by different metrics (such as local activity, network connectivity, network topological properties, etc.) has different frequency characteristics, and these different frequency patterns have not yet been linked to specific mental activities. Additionally, current research has only examined the relationship between ISO and a few types of mental activities, particularly lacking studies on higher-order thought processes. Research on ISO' s physiological and psychological mechanisms requires multidisciplinary collaboration among psychologists, physiologists, neuroscientists, and others. It is foreseeable that research on ISO' s physiological and psychological mechanisms will become a new frontier in brain science.

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Note: Figure translations are in progress. See original paper for figures.

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