Transient oscillations as computations for cognition: Analysis, modeling and function
Robert Schmidt¹, Jonas Rose² and Vignesh Muralidharan³

Abstract
Our view of neural oscillations is currently changing. The dominant picture of sustained oscillations is now often replaced by transient oscillations occurring in bursts. This phenomenon seems to be quite comprehensive, as it has been reported for different oscillation frequencies, including the theta, beta, and gamma bands, as well as cortical and subcortical regions in a variety of cognitive tasks and species. Here we review recent developments in their analysis, computational modeling, and functional roles. For the analysis of transient oscillations methods using lagged coherence and Hidden Markov Models have been developed and applied in recent studies to ascertain their transient nature and study their contribution to cognitive functions. Furthermore, computational models have been developed that account for their stochastic nature, which poses interesting functional constraints. Finally, as transient oscillations have been observed across many species, they are likely of functional significance and we consider challenges in characterizing their function.

Addresses
¹ Institute for Neural Computation, Faculty of Computer Science, Ruhr-University Bochum, Germany
² Neural Basis of Learning, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr University Bochum, Germany
³ Center for Brain Science and Application, School of AI and Data Science, Indian Institute of Technology Jodhpur, India

Corresponding author: Schmidt, Robert (robert.schmidt@rub.de)

Introduction
Neural oscillations play an important role in sensory, cognitive, and motor processing. The classic view is that oscillations occur over prolonged periods of time and their amplitudes are adjusted to situational, e.g. cognitive demands. However, more recently, many studies reported oscillations occurring in transient bursts, rather than being sustained, in many different brain regions, oscillations frequencies, tasks, and species. Here we review recent studies in the field that improve our understanding of the analysis, computation, and function of transient oscillations. Firstly, we consider challenges in the identification and analysis of transient oscillations. Secondly, we discuss computational models of transient oscillations and how they relate to models for sustained oscillations. Finally, we examine possible contributions and mechanisms for how transient oscillations can contribute to cognitive processing.

Identifying and analyzing transient oscillations
Different analysis methods are necessary for transient and sustained oscillations [1]. This is because they have different properties. Sustained oscillations are usually characterized by the time-course of the amplitude in the frequency band of interest. In contrast, transient oscillations are characterized as short-lived events by their rate (i.e. how frequent they occur), timing, duration, and amplitude [2–5] (or combined metrics such as their volume [6]). Therefore, the nature of the oscillation in a given data set should be considered early in the analysis, as subsequent steps depend on whether the oscillations are sustained or transient.

For the distinction of transient and sustained oscillations, the duration is obviously a main criterion. However, there is no clear duration threshold that would separate the two types. The duration of sustained oscillations usually relates to the duration of a psychological or behavioral process, so that they are present throughout. For example, sustained alpha oscillations in human EEG occur as long as the subject’s eyes remain closed [7], with some variation across individuals though [8], and sustained theta oscillations occur in the hippocampal local field potential (LFP) of rats running [9]. In contrast, transient oscillations often do not seem to cover the entire psychological or behavioral process, but only a brief part of it. For example, in a working memory task, transient beta and gamma oscillations occur in different neural circuits in the LFP of non-human primates for only a fraction of the time the item is held in working memory [10,11]. Importantly, analyzing trial averages can make transient oscillations seem persistent over time [1] and mask variations in their timing [12].
To determine the nature of the oscillation in an early analysis step, a method based on lagged coherence has been developed [13] and applied in several recent studies [14,15] (Figure 1a(i)). It estimates the duration of an oscillation by quantifying how long the phase of the oscillatory signal can be predicted by measuring the phase preservation of a time-series signal across non-overlapping time windows. Thus, lagged coherence would decrease for time-windows after the oscillation is over, and thereby provide an estimate for the duration of the oscillation.

Having established that oscillations in a given data set are indeed short-lived, the next challenge is to identify the individual transient oscillations in the data. A common, straightforward approach is to extract these

Figure 1

Analysis, generation, and functions of transient oscillations. (a). (i) Transient oscillations can be identified by estimating the rhythmicity of time-series signals using lagged coherence. Non-overlapping time-windows matched to the oscillation frequency can be used to estimate lagged coherence. The arrows below denote the phase across different time-windows and in case of transient bursts, one can see that it is different across the time-windows leading to lower lagged coherence values. (ii) Amplitude-based thresholding methods to extract transient oscillations can be augmented using data-driven Hidden Markov Models (HMM) that estimate the probability of a particular non-oscillatory (State 0) or oscillatory state (lower frequency State1, higher frequency State 2 as seen in the power spectrum). (b). (i) Sustained oscillations can be generated e.g. as a result of excitatory-inhibitory feedback in microcircuits or networks. Excitatory and Inhibitory neuronal subpopulations are shown as blue and red circles respectively. (ii) In both, transient oscillations can be elicited at a specific time using a strong but brief input. (iii) Alternatively, the network dynamics can be shifted into a regime capable of producing stochastic, transient oscillations, with e.g. inputs modulating the probability distributions compared to baseline ("endogeneous") uniform probabilities. (c). (i) The presence of transient oscillations across species despite structural differences between layered mammalian cortex and unlayered avian pallium indicates a high functional significance of networks generating and utilizing transient oscillations. (ii) Contributions of transient oscillations to cognitive functions include spontaneously emerging oscillations, increasing synchrony among regions, e.g. in working memory. (iii) In addition, transient oscillations can be triggered at the right time by salient stimuli ("bottom-up") and higher areas can tune-in to promote spike propagation ("top-down").
periods by thresholding the amplitude or power of the relevant frequency band, e.g. based on the median amplitude and standard deviation [16–18] or percentile [19] (Figure 1a(ii)). It should be noted that such methods by themselves could misinterpret amplitude-modulated sustained oscillations to be transient. The thresholding of the analysis could make a sustained oscillation seem like a transient event and the choice of the threshold directly affects the duration of the oscillation. Therefore, it is important to verify the nature and duration of the oscillation with another method, such as lagged coherence.

An alternative to using amplitude-based thresholds are data-driven Hidden Markov Models (HMM; Figure 1a(ii)) [20]. These models identify different states in the data, such as oscillatory and non-oscillatory states. In some model variants, the states are identified with respect to a pre-defined frequency band (amplitude envelope HMM), so that pre-knowledge about a given oscillation frequency of interest can be integrated. In other variants (time-delay embedded HMM) the states are identified based on the distinctness of the power spectrum, without restricting oscillatory states to a specific frequency band. This helps to overcome issues arising due to domain reduction in the spectral and spatial domain [21]. As these methods also provide the duration of the oscillatory states, they can also be used to identify the nature of oscillation as well as the individual oscillatory events. One main advantage of HMM approaches is that they are less susceptible to arbitrary amplitude thresholds, as the thresholding is instead done on the typically bimodal state probability distributions. An additional challenge for identifying transient oscillations is to distinguish them from background $1/f$ noise, which may contain brief, spurious oscillations [22]. The inherent autocovariance structure in time-delay embedded HMMs can be exploited to reduce the risk of false positive transient oscillations [20].

Having established the transient nature of oscillations and identifying the individual events in a data set opens the door to several interesting analyses that would not be possible or appropriate for sustained oscillations. For example, transient oscillations can be treated as point processes [2], so that similar analysis methods as for spike trains are available. This allows us to closely relate them to cognition, with respect to their rate, timing, duration, amplitude, or volume [6]. For example, in the domain of sensory and motor control, the rate, amplitude, and timing of pre-movement transient beta oscillations have recently been linked to behavioral metrics [15–18,23–25]. Furthermore, time-warping methods to compensate for variations across trials are well-suited for single-trial analyses of transient oscillations and might provide a means to connect transient LFP oscillations to the spiking level [12]. Analyzing the characteristics of transient oscillations points to the importance of the mechanisms by which transient oscillations are generated and how they could potentially aid communication between regions involved in a particular cognitive function.

**Computational mechanisms generating transient oscillations**

Sustained oscillations in neural activity can be generated by a variety of mechanisms, such as cortical microcircuits involving excitatory pyramidal and inhibitory interneurons (PING) or only inhibitory neurons (ING) [26,27], or also by interacting subcortical excitatory and inhibitory networks as in the basal ganglia [28]. In those models, oscillations can be triggered by a sufficiently strong drive so that, e.g., sustained excitatory inputs lead to a cascade of events that manifest as oscillatory activity (Figure 1b(i)). How do the mechanisms of sustained oscillations relate to possible mechanisms underlying transient oscillations?

Firstly, transient oscillations might simply be generated by the same mechanisms that have been proposed for sustained oscillations, but are just triggered for a shorter period by a short, but strong input (Figure 1b(ii)). For example, in the context of the basal ganglia, pathological beta oscillations in Parkinson’s disease can be explained by push–pull interactions between the excitatory subthalamic nucleus and the inhibitory globus pallidus networks [28]. In healthy animals, the same networks also seem to generate transient beta oscillations [29], which are pathologically exaggerated and prolonged in Parkinson’s disease, even though they can still be characterized as transient bursts in EEG and LFP signals in humans and rodents [30,31]. In a computational model utilizing striatal input patterns from rats during movement initiation, movement-related firing rate increases lead to transient beta oscillations in the subthalamic-pallidal networks that closely resembled the transient basal ganglia LFP beta oscillations in those animals [29]. This demonstrates that transient oscillations can be explained by the same mechanisms as sustained oscillations operating in a different input regime, and that their timing can be controlled by input signals. Similarly, cortical PING or ING mechanisms could generate transient oscillations as the result of a brief input triggering only a few oscillation cycles. Another approach focused on inputs to cortical layers that can account for the specific waveform of single cortical beta oscillation cycles in human magnetoencephalography (MEG) measurements and monkey and mice LFPs [4]. In this model the beta waveform resulted from the interaction of proximal and distal inputs to pyramidal neurons, so that the transient oscillation can be reliably triggered and precisely timed by the inputs. Transient oscillations triggered by inputs are useable for cognitive functions, as they can be generated quickly based on the current cognitive demands. This is important because it distinguishes them from other potential mechanisms that
would generate transient oscillations spontaneously in a stochastic manner.

Secondly, a recent modeling study demonstrated the intriguing possibility that transient oscillations might be generated by networks operating in an activity regime slightly below an oscillatory state, where transient oscillations occur stochastically [32] (Figure 1b (iii)). In this regime, oscillations are spontaneously generated by recurrently connected inhibitory and excitatory sub-populations. The occurrence of these oscillations depends on the connection probability within the inhibitory subpopulation and the firing rate of the background Poisson inputs. Interestingly, when several such networks are coupled via long-range excitatory connections, they spontaneously synchronize, enabling directed information transfer between them [32]. As in some empirical studies it was noted that transient oscillations seemed to occur, at least partly, at random [33,10,23,3,31], this could be well explained by the network model operating in a transient-oscillation regime. Possibly though, despite their partly stochastic appearance, transient oscillations in the brain might be predictable by certain neural signatures, such as upstream inputs from other regions that currently have not been identified. However, if the timing of a transient oscillation is not controlled by an internal process, this constrains their potential functions in cognitive processing as it seems at odds with executing a process when it is needed.

Finally, one can imagine that the underlying stochasticity in the transient activity regime [32] could still be modulated, so that it leads to a precisely timed synchronization of regions. A potentially profound way of achieving this could be that inputs from upstream areas modulate a network operating in this regime, such that the probability of transient oscillations increase at specific time periods (Figure 1b(iii)), leading to interareal synchronization at those times. Under baseline conditions, a network in the transient regime could exhibit transient oscillations distributed uniformly over a period of time (Figure 1b(iii)). However, based on the situational demands the network inputs could increase so that the network’s activity regime shifts, and as a result, the probability of transient oscillations is increased for a relevant time period. This would reduce the problems associated with purely stochastically occurring oscillations, and enable them to support cognitive functions at the right time.

In conclusion, a key aspect of the mechanisms underlying transient oscillations relates to the stochasticity of their occurrence. While strong, brief inputs could enable a directed, precisely timed transient oscillation, networks operating in a transient regime would account for a stochastic nature of transient oscillations. As these options are not exclusive, we consider below the possibility that a combination of these two mechanisms can explain both the stochastic and directed nature of experimental transient oscillations observed in a variety of species.

**Functions of transient oscillations**

The last decades have seen a vivid discussion on how far oscillations reflect a causal mechanism, or merely an epiphenomenon of neural processing. Likewise, one may wonder if transient oscillations reflect general neurobiological principles. The mammalian cortex offers an ideal structure to generate specific oscillations, layer-specific frequencies and even reversals of polarity between deep and superficial layers [11,34]. If transient oscillations are present during similar computations in unlayered, evolutionarily distant brains, this would support the notion of a functional principle in neural processing (Figure 1c(i)). Comparative approaches in birds offer this unique perspective since cognitive abilities of birds are on par with those of mammals (except humans) and both species evolved higher cognition independently [35,36]. The result is a substantially different neural organization, most prominently the absence of cortical layers and columns in the avian endbrain (sensory, but not high associative structures share some aspects of cortical circuitry) [37,38]. A recent study investigated oscillations in the LFP of the avian endbrain during working memory, demonstrating that these occur in similar frequency ranges as in mammals and importantly, in bursts, rather than as sustained activation [39].

A common view is that transient oscillations open communication channels between different circuits of a network or even between different brain regions [40]. How can this be compatible with the apparent stochasticity of transient oscillations? Even if the rate of transient oscillations would be relatively high, it seems counter-intuitive to restrict important cognitive processing to randomly selected, brief time periods. For working memory, this might not be a problem as long as the whole delay period is covered by transient oscillations in different microcircuits [10,11]. In contrast, inhibitory control often requires fast action, which would render transient oscillations as a flawed, unreliable mechanism. However, there are two arguments to consider against this extreme view.

Firstly, even though transient oscillations might improve cognitive performance in many situations, they might not be an absolute prerequisite for cognitive processing and could just aid processing during their presence. This would explain why in many cognitive tasks where transient oscillations have been observed, there is not a simple distinction so that e.g. error trials would just lack any transient oscillations. Instead, cross-region communication might still work fine without an additional enhancement of the relevant communication.
Transient oscillations for cognition

channels provided by transient oscillations (Figure 1c(ii)). Therefore, the stochastic nature of transient oscillations would not be a major problem, but rather limit the possible improvement it provides.

Secondly, transient oscillations do not seem to be entirely stochastic. They might be mostly stochastic in resting state situations, but as soon as cognitive demands arise from the environment or internal processing, their rate could be increased or they could even be evoked, e.g. by salient external stimuli. There are several studies supporting this by having found an increase in the rate of transient oscillations following important task cues, so that the transient oscillations appear close, but not necessarily time-locked, to the stimulus, or depend on other task conditions [10,14,29,33,41,42]. Mechanistically, relevant sensory inputs would thereby provide the required strong, but brief inputs that could evoke a transient oscillation (Figure 1b), as a bottom-up cognitive process. A requirement would then be for other brain regions to quickly tune into the appropriate frequency so that the corresponding stimulus can be further processed (Figure 1c(iii)). Speculatively, this could be one reason why neural responses to sensory stimuli are so abundant in the brain and can even be found in deeper/higher brain regions that are usually considered not to be part of conventional sensory processing (motor cortex, basal ganglia, prefrontal cortex). Allowing potentially relevant salient stimuli some access to these regions might be a means to support the quick development of a transient oscillation.

To gain further insights into these non-exclusive possibilities, the stochasticity of transient oscillations needs to be clearly quantified in different behavioral states using reliable measures to identify transient oscillations (see above). This would also be necessary to determine whether the timing of the transient oscillations can actually be predicted by other neural signals. Current evidence suggests that transient oscillations are stochastic but can also be evoked by certain salient stimuli [3,10,14,23,29,31,33]. If that is the case, one important question is whether stochastic, baseline transient oscillations and evoked, bottom-up transient oscillations can be distinguished based on the involved networks or the underlying, generating mechanisms. This might be accessible in measured signals so that e.g. the volume of transient oscillations [6] might differ between evoked and stochastic transient oscillations.

Finally, even though transient oscillations are regarded as a means to provide communication channels, it is less clear what this precisely means for cognitive processing on a neural level (Figure 1c). One possibility has been demonstrated by Akam and Kullmann [43] with a model that allows the flexible routing of signals via oscillations. For cognitive functions, this could also be applied so that e.g. for inhibitory control a transient oscillation supports the propagation of a neural response to the stop-signal from sensory to motor circuits [44,45], similar to what has recently been described for attention during decision-making [46,47] and working-memory [48]. However, it is not clear whether the function of transient oscillations can be reduced to a simple gating or selection of inputs in the context of cognitive processing, or whether a more complex interplay of different regions is employed [49]. Thus, a key challenge for future studies is to identify neural signals predicting transient oscillations and to determine their causal effects on spiking activity and cognitive functions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in this article.

Acknowledgements

J.R. is supported by Volkswagen Foundation Freigeist Fellowship (Nr: 93299); Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) SFB 1280, A19 (Nr: 316803389) and SPP 2205 (Nr: 430157321).

References

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

oscillations are transient or sustained.

**Development and application of a key method to determine whether oscillations are transient or sustained.**

**Key perspective on a new theory of working memory grounded in neurophysiology and transient oscillations.**

**Muralidharan V, Aron AR, Cohen MX, Schmidt R: Two modes of mid-frontal theta suggest a role in conflict and error processing.** *Neuroimage* 2023, 273, 120107, https://doi.org/10.1016/j.neuroimage.2022.03.25.485421.

Recent study in which the lagged coherence measure is applied to theta oscillations in humans and compared to synthetic data. The study supports a role of transient theta oscillations in error processing, including potentially error correction.


**Unpacking transient event dynamics in electrophysiological power spectra.** *Brain Topogr* 2019, 32: 1020–1034.


**Muralidharan V, Aron AR, Schmidt R: Transient beta modulates decision thresholds during human action-stopping.** *Neuroimage* 2022, 254, 119145.


Key modeling study that demonstrates how oscillations can play a causal role in neural processing by modulating the effect of inputs on different target regions.


