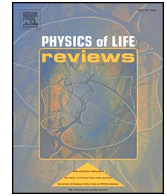




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Beyond task response—Pre-stimulus activity modulates contents of consciousness

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ABSTRACT

The current discussion on the neural correlates of the contents of consciousness (NCCc) focuses mainly on the post-stimulus period of task-related activity. This neglects the substantial impact of the spontaneous or ongoing activity of the brain as manifest in pre-stimulus activity. Does the interaction of pre- and post-stimulus activity shape the contents of consciousness? Addressing this gap in our knowledge, we review and converge two recent lines of findings, that is, pre-stimulus alpha power and pre- and post-stimulus alpha trial-to-trial variability (TTV). The data show that pre-stimulus alpha power modulates post-stimulus activity including specifically the subjective features of conscious contents like confidence and vividness. At the same time, alpha pre-stimulus variability shapes post-stimulus TTV reduction including the associated contents of consciousness. We propose that non-additive rather than merely additive interaction of the internal pre-stimulus activity with the external stimulus in the alpha band is key for contents to become conscious. This is mediated by mechanisms on different levels including neurophysiological, neurocomputational, neurodynamic, neuropsychological and neurophenomenal levels. Overall, considering the interplay of pre-stimulus intrinsic and post-stimulus extrinsic activity across wider timescales, not just evoked responses in the post-stimulus period, is critical for identifying neural correlates of consciousness. This is well in line with both processing and especially the Temporo-spatial theory of consciousness (TTC).

1. Introduction

How are conscious contents generated? The question of what has been described as the neural correlates of consciousness (NCCs) [1–3], that is, the “minimal set of neural events jointly sufficient for a specific conscious experience (given the appropriate enabling conditions)” [4]. Various neural candidate measures such as posterior or prefrontal cortex activity, complexity indexing information integration, and electrophysiological features such as N100, Visual awareness negativity (VAN), P3b, and late positive potential (and others) have been suggested as candidate NCCs [2,3,5–8]. Despite their differences, these various measures share their focus on associating the contents of consciousness with exclusively the post-stimulus period of task-related activity [3,9]. Can the NCC really be found alone and exclusively in the neural features of post-stimulus task-related activity? Or is the post-stimulus task-related activity shaped by and thus dependent on the brain’s spontaneous or ongoing activity as manifest in for instance its pre-stimulus activity?

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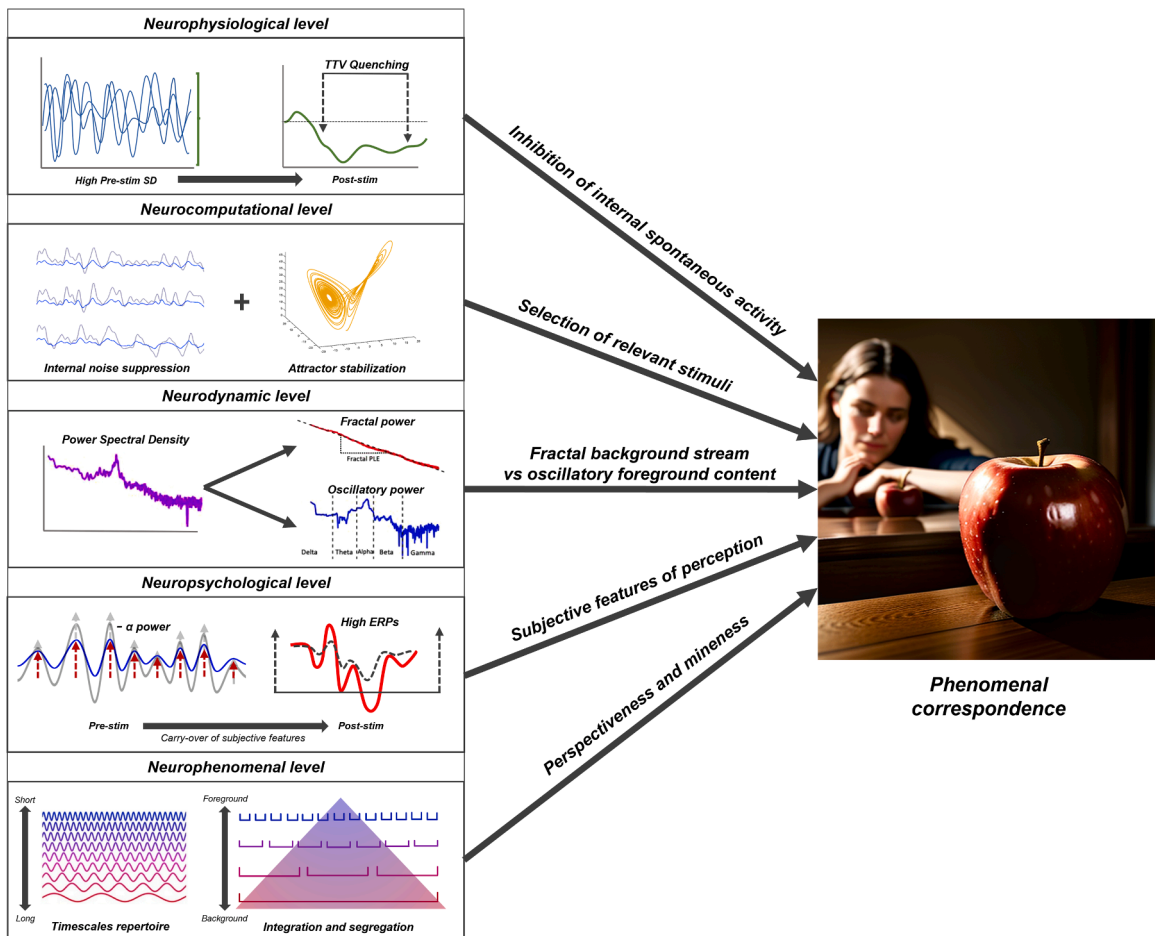


Fig. 1. Graphical abstract. Overview of neural mechanisms at different explanatory levels. The figure shows an overview of the main hypotheses in our paper. We suppose that the interaction of pre-stimulus and post-stimulus interaction is a core mechanism of the contents of consciousness (left). The mechanisms of such pre-post-stimulus interaction can be investigated on different levels using different methodological approaches which, as we assume, capture distinct aspects of the neural correlates of the contents of consciousness. The neurophysiological level is characterized by a negative non-additive interaction of pre-stimulus and post-stimulus activity in mainly the alpha band. This is measured by decreases, e.g., “quenching”, of post-stimulus trial-to-trial variability in relation to the pre-stimulus variability. The so-called “TTV quenching” is key to suppressing the ongoing activity and its internal content relative to the stimulus-related activity featured by its external contents. The neurocomputational level is featured by attractors, with the post-stimulus trial-to-trial variability reduction being related to a transiently stable attractor reflecting the transient stabilization of a particular content in consciousness relative to others. The neurodynamic level refers to different components of the signal in neural activity. This includes periodic oscillatory activity which, due to its flexibility, regularity, and temporal precision, is supposed to be related to the processing of the contents in the foreground of consciousness. While, the fractal or aperiodic component of the signal, which exhibits higher stability, less regularity, and less temporal precision, is supposed to reflect the background of consciousness. The neuropsychological level describes the subjective features of our experience of the contents of consciousness such as confidence, discrimination, and others. These subjective features are supposed to be carried over from the pre-stimulus period to the post-stimulus interval, where they converge and are linked with the more objective features of the external stimulus itself. The subsequently experienced content of consciousness is thus an amalgam of both subjective and objective features. Finally, the neurophenomenal level refers to the structure of our experience of the contents of consciousness. Here, we point out two phenomenal features, namely mineness and perspectiveness. We hypothesize that these two phenomenal features are related to the brain’s timescales in its neural activity, the intrinsic neural timescales (INT). Through temporal integration and segregation of different stimuli the INT supposedly shape both background structure, e.g., perspectiveness, and foreground contents, e.g., mineness, of consciousness.

Addressing these questions is the goal of our paper.

Recent studies demonstrate that the post-stimulus activity is dependent upon the level of neural activity in the pre-stimulus period as it can, for instance, be measured by post-stimulus trial-to-trial variability (TTV) [10–17] (see below for details). Moreover, numerous studies observed that pre-stimulus activity, like pre-stimulus alpha power, shape the subjective features of the contents of consciousness during the post-stimulus period [18–24] (see below for details). Finally, the relevance of pre-stimulus activity is further supported by the predictive processing account [2,3,25]. Here the pre-stimulus activity is supposedly related to the empirical prior, the prediction, that shapes the subsequent prediction error during the post-stimulus period including its associated content of consciousness [2,18,19,26–28].

Together, these data suggest that pre-stimulus activity and its interaction with the external stimulus during the post-stimulus period take on a key role in shaping the contents of consciousness. Does pre-post-stimulus interaction mediate the contents of consciousness and can it serve as their candidate neural correlate? Our objective is to provide a hypothesis about the mechanism of pre-post-stimulus interaction and how they shape the neural correlate of conscious content. For that purpose, we review some (in a non-exhaustive way) of the relevant literature on pre-post-stimulus interaction for conscious contents. Specifically, we focus on the key role of the alpha frequency in mediating the impact of pre-stimulus activity as measured by both alpha power and variability on post-stimulus activity and its conscious contents. We thus converge two lines of different findings, that is, pre-stimulus alpha power and pre-post-stimulus trial-to-trial variability (TTV). This leads us to formulate specific neurophysiological, neurocomputational, neurodynamic, neuro-psychological and neurophenomenal hypotheses (Fig. 1) about the NCCs (see also Boxes 1–3 and [29]).

Finally, we briefly want to explicate what we understand by NCCs in the present context. We here focus exclusively on the NCC of the contents of consciousness while neglecting the NCC of other dimensions of consciousness like its level/state [29–33] and form or structure [29,30,34]. Moreover, we focus only on the neural correlates of the experience of the contents of consciousness, that is, their phenomenal features. In contrast, we neither take into consideration the neural consequences of the contents of consciousness like their access [35,36] and interpretation, e.g., neural correlates of the interpretation of conscious contents (IntNCC) [37]. Therefore, when we speak of NCCs in the following, we will always refer to the neural correlates of the contents of consciousness in a way similar to the notions of content-based neural correlates of consciousness, neural correlates of consciousness for content [38–40] or neural correlate of conscious content (NCCc) [41].

It shall be noted that the NCCs of the contents can be viewed in distinct ways. One may consider the “where are the NCCs” which raises the question for the spatial NCCs, that is, the regions in which they are processed. We will see later that we do not consider a specific region but rather a gradient between posterior and anterior cortical regions as spatial NCCs. While the temporal dimension is covered by “when does the NCCs occur”. Most accounts focused on a specific timepoint like 50, 100, 200 or 300 ms during the post-stimulus period [42–44]. Rather than one specific time point, we here consider a certain time period, namely from pre- to post-stimulus, as the temporal NCCs.

Moreover, one may want to ask for the “how are the NCCs mediated” which raises the question for the mechanism mediating conscious contents. While information integration, global neural workspace, prediction, and various others are considered key mechanisms in the various theories (Northoff and Lamme [3]), we here propose non-additive pre-post-stimulus interaction as key mechanism of the NCCs (see Boxes 1–3 for its relation to other theories and mechanisms). Finally, it shall be mentioned that we leave open another dimension of the NCCs like the “why are there NCCs”, that is, the question for their causes as addressed by the concept of the ‘neural predispositions of consciousness’ (NPC) [29,34,45]. Moreover, we also leave open the question for “what are the biological substrates of the NCCs” (see for instance [46,47]).

2. Part I: pre-stimulus alpha power relates to the contents of consciousness

2.1. Pre-stimulus alpha power—negative relation to the subjective features of conscious contents

Various studies demonstrate that low pre-stimulus alpha power (−300 to 0 ms) is related to the perception of conscious contents. Perception is here indexed by measures of subjective performance such as confidence, vividness, visual awareness, content detection, discrimination, and identification [23,24,48–61].

Despite their experimental differences, all these studies observe a negative relationship of alpha pre-stimulus power with the subjective features of conscious contents during the post-stimulus period, that is, lower levels of the former lead to higher degrees of the latter. Analogously, pre-stimulus alpha power is also related to the reaction times of the subjects in the same studies with lower levels of pre-stimulus alpha leading to faster post-stimulus reaction times [48]. In contrast, pre-stimulus alpha power does not relate to more cognitive features like accuracy [23,57], working memory [62], post-decision making [57] and memory [63].

Together, these findings strongly suggest that pre-stimulus alpha power shapes and interacts negatively with the subjective features of conscious contents, as distinguished from their more objective cognitive features like the specific contents. This holds for both complex (like faces) and simple (like motor cycles) stimuli or contents of consciousness [58] as well as for short (around 100 ms) [23, 24] and longer (like 1500 ms) stimuli [56]. Finally, the impact of pre-stimulus alpha power on conscious contents has been observed in various regions including lower- and higher-order cortical regions [48] and subcortical regions such as the amygdala [64].

2.2. Mechanisms of pre-stimulus alpha power—negative relation to ERP through cortical excitability indexed by high frequency broadband power

What are the neural mechanisms that mediate the impact of pre-stimulus alpha power on conscious contents? Various studies demonstrate the close relationship of alpha power with cortical excitability: a lower intrinsic pre-stimulus alpha power yields higher degrees of neural excitability (for the extrinsic stimulus) [48,57,65]. The relationship between pre-stimulus alpha power and cortical excitability is thus negative: lower levels of pre-stimulus alpha power leads to higher degrees of cortical excitability while higher alpha levels induce low excitability [48].

Cortical excitability can be measured by the activity of broadband high frequency (70–180 Hz) activity which is well known to reflect the excitation of multi-unit activity [48]. Using mediation models, the impressive intracranial study by Jemi et al. [48] demonstrates that the effect of low pre-stimulus alpha power on increased perception of conscious contents (and their faster reaction time) is mediated by a high level of pre- and post-stimulus high frequency broadband activity measuring high degrees of cortical excitation.

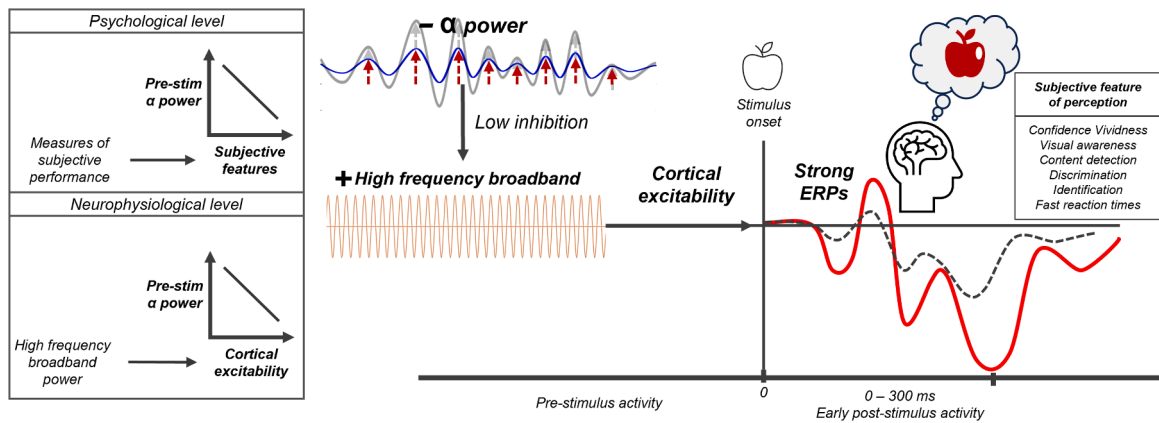


Fig. 2. Relationship between pre-stimulus alpha power and conscious contents. The figure illustrates the relationship between pre-stimulus and post-stimulus activity with regard to how the level of pre-stimulus alpha power shapes cortical excitability and subjective features of perception. Lower pre-stimulus alpha power leads to higher cortical excitability, as measured by high frequency broadband, and higher ERP amplitude associated with higher degree of subjective features in perception.

Hence, high cortical excitability as indexed by high frequency broadband is a key mediator of the effect of low pre-stimulus alpha power on conscious contents.

How does the degree of cortical excitability impact the processing of the external stimulus such that it can become a conscious content? Higher cortical excitability of the pre-stimulus activity and at stimulus onset (i.e., the time point at which the external input comes in) means that the external stimulus can induce a higher degree of task-evoked or stimulus-related activity during the post-stimulus period; this can be measured by the amplitude of event-related potentials (ERP). Various findings show that pre-stimulus alpha power shapes post-stimulus event-related potentials predominantly in their early stages (100–300 ms) and the respectively associated conscious contents in our perception [23,24,55,59,66]: lower pre-stimulus alpha power (–300 to 0 ms) is related to higher amplitude of the early post-stimulus ERP (0–300 ms). Together, pre-stimulus alpha power modulates cortical excitability (as measured by high frequency broadband activity) in a negative way (lower power leads to higher cortical excitability); this, in turn, allows to process the external stimulus in such way that it results in higher early (0–300 ms) ERP and a more conscious content (Fig. 2).

3. Part II: pre-stimulus variability shapes post-stimulus trial-to-trial variability and its conscious contents

3.1. Trial-to-trial variability in pre- and post-stimulus periods

The dynamics of the brain is manifest in the variability of its neural activity [67]. Trial-to-trial variability (TTV) can be measured by the variation of the amplitude in response (0–500 ms post-stimulus period) to the same stimulus (or task) across different trials in both EEG/MEG [11,12,14,15,68–70] and fMRI [16,17,22,71,72]. Typically, TTV is reduced in the post-stimulus interval (0–500 ms), which is often described as ‘TTV quenching’ [11,68]. TTV quenching has been observed from cellular to systemic levels of neural activity [11,14–17,22,68,69,73–75]. Finally, just as the impact of pre-stimulus alpha power on conscious contents, the TTV occurs in basically all cortical regions [16,17,22,69], and during different stimuli or tasks [11,14,15,17,22,53,68,74,75].

In addition to the impact of the external stimulus, the data suggest that pre-stimulus activity, e.g., pre-stimulus variance, also shapes post-stimulus TTV. Various studies in both animals and humans demonstrate that pre-stimulus variability, i.e., pre-stimulus TTV, does indeed strongly impact both post-stimulus activity (amplitude, variance) in alpha and associated behavioral performance, e.g., reaction time [15–17,20,71,72,76–84].

Specifically, high pre-stimulus variance in the amplitude is accompanied by a stronger TTV reduction in the alpha band during the post-stimulus period [10,11]. In contrast, lower pre-stimulus activity levels lead to lower degrees of TTV quenching. A recent study by Wolff et al. (2021) demonstrated that even the timing of post-stimulus TTV is shaped by pre-stimulus variability: the ongoing pre-stimulus variability spills over to the post-stimulus period during its early period, e.g., 0–300 ms, whereas the later post-stimulus interval (300–600 ms) is more strongly shaped by the external stimulus. This difference between early (0–300 ms) and later (300–600 ms) post-stimulus period suggests a strong role for the pre-stimulus activity in shaping especially the early post-stimulus activity (0–300 ms); this can be called pre-post-stimulus interaction (see below for details). That converges well with the findings on pre-stimulus alpha power shaping the ERP during the early post-stimulus period (0–300 ms) [12]. These findings suggest direct interaction of the pre-stimulus variability level with the external stimulus. This is also reflected in the behavior as higher degrees of non-additivity are featured by shorter reaction times and faster target detection [11,12,73]. Accordingly, direct and ultimately non-additive pre-post-stimulus interaction is relevant on both levels, neuronally and behaviorally (see below).

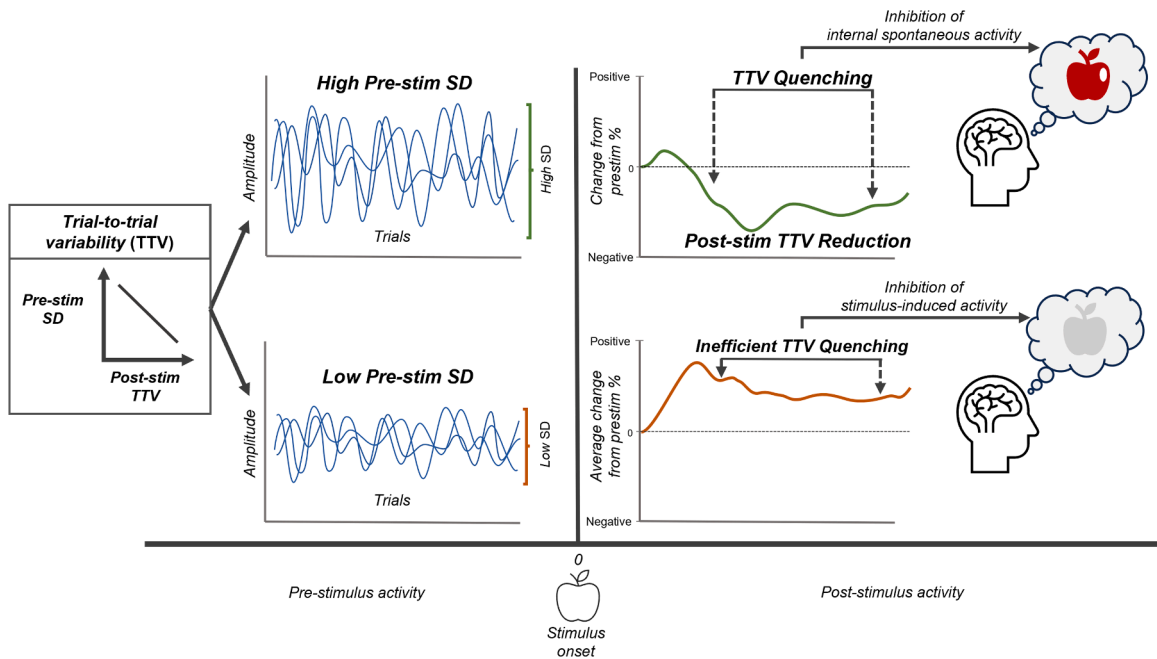


Fig. 3. Interaction between pre- and post-stimulus variability in relation to intrinsic and stimulus-induced activity. The figure shows the relation of pre-stimulus amplitude standard deviation (SD) and post-stimulus trial-to-trial variability (TTV). Upper. High pre-stimulus amplitude SD leads to high degree of post-stimulus TTV reduction, i.e., quenching indexing inhibition of internal activity with the subsequent strengthening of the external stimulus related activity and its associated perception, e.g., the red apple. Lower. Low pre-stimulus amplitude SD leads to lower, if not absent, post-stimulus TTV reduction and suppression or inhibition of stimulus related activity. This shows a negative relationship of pre-stimulus SD and post-stimulus TTV as indexed by the graph on the left.

3.2. Pre- and post-stimulus trial-to-trial variability shape conscious contents

The TTV has been related to the contents of consciousness. For instance, Arazi et al. [14] conducted an EEG study during a two-interval forced choice task in the visual domain [15]. Participants were presented two visual contrast stimuli, each presented for 100 ms and an inter-stimulus interval of 900 ms. When the fixation cross appeared afterwards, participants were asked to decide which of the two stimuli showed the highest contrast. Participants showed clear ERP responses 150 ms after stimulus onset, exhibiting a P100 in parietal electrodes. Importantly, after both the first and second stimulus, a robust post-stimulus (150–400 ms) TTV decreases or quenches in the same six parietal electrodes (P5–8, PO7 and 8) as the P100 was observed (TTV was calculated relative to pre-stimulus variance –200 to 0 ms). The area under the TTV curve correlated significantly with various subjective measures of the contents of consciousness (psychometric function of contrast detection, individual discrimination threshold). In contrast, there was no significant correlation of the mean amplitude as measured by the ERP with any of these subjective perceptual measures. Just as in the case of pre-stimulus alpha power, this suggests a specific role of TTV in mediating the subjective features of the contents of consciousness.

The association of post-stimulus TTV with the subjective features of content of consciousness is further supported by other studies. Several studies in healthy participants demonstrated that strong TTV suppression, e.g., quenching, in the post-stimulus period goes along with consciousness of the contents [15,20,69,70,85–88]. A recent study combined EEG and computational modeling to demonstrate that the TTV quenching around 300–400 ms is well compatible with the ignition of the global workspace during conscious contents [13]. In contrast, unconscious states as in sedation, anesthesia, or unresponsive wakefulness are featured by the disappearance of TTV quenching in the post-stimulus period [13,22,69,89].

These findings suggest that post-stimulus TTV reduction is related to the contents of consciousness including their subjective features (Fig. 3). Given that pre-stimulus alpha power modulates conscious contents, one would expect that the variability during the pre-stimulus period also exerts an impact on conscious contents. That is indeed the case. Several studies in both fMRI [26–28,90] and EEG/intra-cranial recording [20,23,89,91,92] demonstrate that pre-stimulus activity levels including their variance can predict which content is subsequently perceived by the participants. For instance, employing bistable stimuli, high pre-stimulus activity levels in the fusiform face area (FFA) predicts that the subsequently presented face will be consciously perceived (rather than remaining unconscious and thus not perceived as in the case of low pre-stimulus activity in FFA) [26].

Together, this further converges TTV with pre-stimulus alpha power as in both instances, pre-stimulus activity levels, that is, alpha power and variability, exert an impact on the contents of consciousness. In contrast, it leaves open (i) the exact mechanisms how pre-stimulus power and variability interact with the external stimulus and (ii) how such pre-post-stimulus interaction renders conscious the external input. Addressing these open issues in the following, we develop specific neurophysiological, neurocomputational, neurodynamic, neuropsychological and neurophenomenal mechanisms of pre-post-stimulus interaction including how it yields

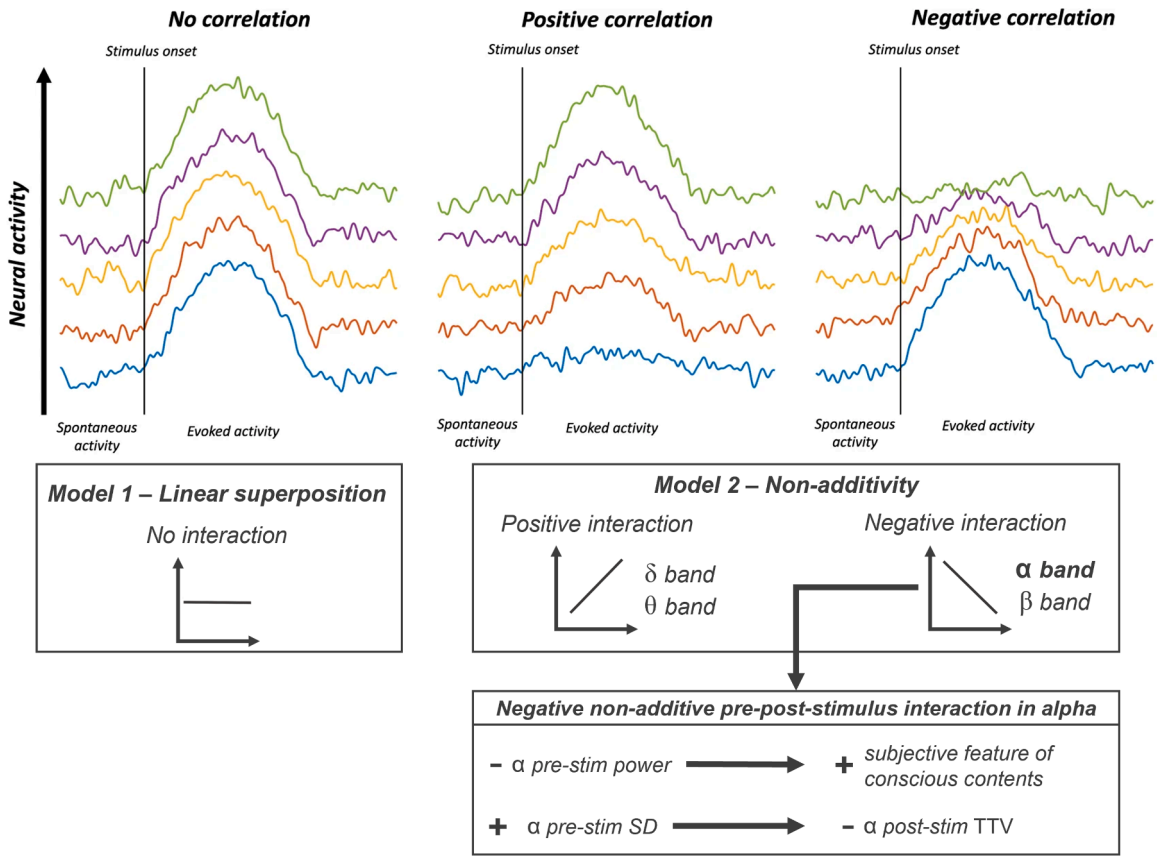


Fig. 4. Additive (linear superposition) vs non-additive (positive and negative) interaction between pre-stimulus and stimulus-induced activity. The figure illustrates distinct models of the relationship between or pre-stimulus and post-stimulus activity. Left part. There is no significant correlation and hence no interaction between pre- and post-stimulus activity entailing that the post-stimulus activity is simply added or linearly superimposed upon the pre-stimulus activity level without any interaction between them. Middle and right part. Pre-stimulus and post-stimulus activity can correlate either positively or negatively with each other indicating their interaction. This amounts to non-additive interaction or relationship of pre- and post-stimulus activity which is positive in delta and negative in alpha (Box in middle level). Moreover, such negative non-additivity converges the lower pre-stimulus alpha power findings with the elevated pre-stimulus SD findings about the subjective features of consciousness and the post-stimulus TTV reduction (Box in lower level). Adapted from [10].

conscious contents.

4. Part III: neural correlates of the contents of consciousness (NCCc)—neurophysiological, neuro-computational, neurodynamic, neuropsychological, and neurophenomenal mechanisms and hypotheses

We showed that both pre-stimulus alpha power and pre-post-stimulus alpha TTV relate to the subjective features of the contents of consciousness. While these are different lines of research and have rarely been considered together, we here aim to converge them in order to better understand the mechanisms of the contents of consciousness. The two lines of findings show that pre-stimulus alpha activity, e.g., power and variance, modulates both post-stimulus activity and its associated contents of consciousness. Moreover, they show that there seems to be negative relationship of the pre-stimulus activity with post-stimulus features like TTV and conscious contents. Finally, given that the alpha power findings show high levels of excitation relative to inhibition in the post-stimulus period (see above), we assume that conscious contents during the post-stimulus period are related to a shift in the excitation inhibition balance towards excitation. This remains to be shown in the future, though.

Together, these findings strongly suggest that the interaction of the pre-stimulus alpha activity with the external stimulus is key for rendering the latter conscious. The two lines of research converge on alpha by pointing out different features of alpha. The findings on the alpha power focus on a more static event related analysis of alpha indexing its more cognitive features. While the findings on TTV highlight the dynamic nature of alpha, that is, its changes over the various time points from pre- to post-stimulus activity periods. We now converge both cognitive and dynamic features of alpha in one coherent model, that is, non-additive pre-post-stimulus interaction as a proposal for the NCCc.

We consider our candidate NCCc on different levels including neurophysiological, neurocomputational, neurodynamic, neuropsychological and neurophenomenal. We hypothesize that the mechanisms of non-additive interaction of the pre-stimulus activity

with the external stimulus, e.g., pre-post-stimulus interaction are manifest on these different levels in slightly distinct ways. We understand that one and the same mechanism, e.g., non-additive pre-post-stimulus interaction can be viewed and investigated on different levels. These different levels are featured by different methods of investigation, e.g., physiological, computational, dynamical, psychological and phenomenological. While, at the same time, the different levels ultimately target one and the same mechanism, e.g., pre-post-stimulus interaction, and how that is relevant for yielding conscious contents.

4.1. Neurophysiological hypothesis Ia—non-additive pre-post-stimulus interaction

Two main models of pre-post-stimulus interaction have been conceived [16,17,71]. First, there could be linear superposition of the activity evoked by the external stimulus in the post-stimulus period added on top of the ongoing activity without directly interacting with the latter. This model presupposes that the external stimulus shapes evoked activity parallel to and independent of the ongoing activity as carried over from the pre-stimulus period without any changes. One would consequently expect TTV increase in the post-stimulus period: the amplitude variance changes evoked by the external stimulus should be simply added to the unchanged variability level carried over from the pre-stimulus period [16,17]. This is not in accordance with the data, though. Instead of TTV increase, one can observe TTV decrease during the post-stimulus period as described above [10,12,16,17,68,73,93,94]. This suggests the need for an alternative model of pre-post-stimulus interaction beyond the additive (linear) view (Fig. 4).

Where and how is the TTV reduction in the post-stimulus period coming from? He (2013) assumes direct interaction of the external stimulus with the ongoing variability of the pre-stimulus activity. The post-stimulus TTV reduction suggests that the external stimulus must somehow suppress post-stimulus TTV below the level of its mere superposition or addition of the variability changes of both pre-stimulus activity and the ones evoked by the external stimulus. This suggests negative non-additive pre-post-stimulus interaction: the post-stimulus TTV is either lower compared to the addition or sum of pre-stimulus and stimulus-evoked variability. If, in contrast, the post-stimulus TTV is higher than the addition or sum of pre-stimulus and stimulus-evoked variability, one would speak of positive pre-post-stimulus interaction [16].

The existence of especially negative non-additive pre-post-stimulus interaction in the alpha band is indeed supported on independent grounds. Various studies demonstrated negative non-additive pre-post-stimulus interaction in different modalities including EEG [10,11], intracranial recording [12], MEG [10], cellular recording [73], and fMRI [13,17]. Specifically, negative non-additive pre-post-stimulus interaction can be observed in the alpha band while other bands such as delta and theta exhibit rather positive non-additive interaction [10–12]. Accordingly, TTV in alpha is suppressed during the post-stimulus period indexing negative non-additive pre-post-stimulus interaction while TTV in delta is increased indexing positive non-additivity.

4.2. Neurophysiological hypothesis Ib—non-additive pre-post-stimulus interaction mediates the contents of consciousness

We now suppose that the negative non-additive pre-post-stimulus interaction in alpha converges both lines of findings, that is, pre-stimulus alpha power and pre-post-stimulus TTV. Primarily, both occur in the alpha band across the divide of pre- and post-stimulus periods. Second, both indicate negative interaction of pre- and post-stimulus measures like between pre-stimulus alpha and cortical excitability/ERP as well as between pre-stimulus and post-stimulus variance. Third, both relate pre-stimulus and post-stimulus activity in a non-additive rather than additive way. Fourth, both occur in various regions/networks across the whole brain [16,17] and remain task-unspecific as both occur across different stimuli or tasks [10–12,17,73].

Together, this suggests that, neurophysiologically, negative non-additive pre-post-stimulus interaction in alpha is key in modulating both conscious contents and their subjective features. Lower pre-stimulus alpha power and higher pre-stimulus alpha variability lead to lower post-stimulus TTV and higher degrees in the subjective features of conscious contents [10–12,14,22,69]. This attributes a major role to the amplitude and its variance in mediating non-additive interaction. That leaves open the role of phase related processes which, as distinguished from the amplitude, have been shown to mediate non-additive interaction in the infraslow frequency range of fMRI [17]. In contrast, this does not seem to be the case in EEG and MEG where non-additivity is related to the amplitude rather than the phase [10–12]. Future studies are thus warranted to reconcile these findings.

In addition to the temporal features, non-additive pre-post-stimulus interaction can also be characterized in spatial terms. Applying fMRI, Huang et al. [17] observed higher degrees of both TTV quenching and non-additivity in higher order regions like the default mode network while lower order regions like sensory and motor cortex exhibited lower degrees in both measures (see also [16]). Interestingly, higher and lower order regions also differ in their timescales. Higher order regions show longer timescales as measured by the autocorrelation window (ACW while the lower order regions' timescales are shorter [94–98]. Correspondingly, Huang et al. [17] observed that regions with longer timescales during the spontaneous activity's relate positively to both the degrees of both task related TTV quenching and non-additivity. Hence, the longer timescales of higher order regions seem to better facilitate stronger TTV quenching and higher degrees of non-additivity than the shorter timescales of lower order regions.

This is relevant for the contents of consciousness and the current debate about the anterior vs posterior cortical origins. Following these findings, we suggest that there is no principal difference albeit a difference in degree between posterior and anterior cortical regions with respect to the contents of consciousness [3,99]. As described above, the findings show higher degrees of both TTV quenching and non-additivity in the anterior more higher order regions featured by their longer timescales than in the posterior more lower order regions [17]. This makes it more likely that the contents processed in the anterior higher order regions' longer timescales have a higher likelihood of becoming conscious compared to those processed in the posterior more lower order regions' shorter timescales.

Taken together, we propose that the difference of anterior and posterior regions with respect to the contents of consciousness is not

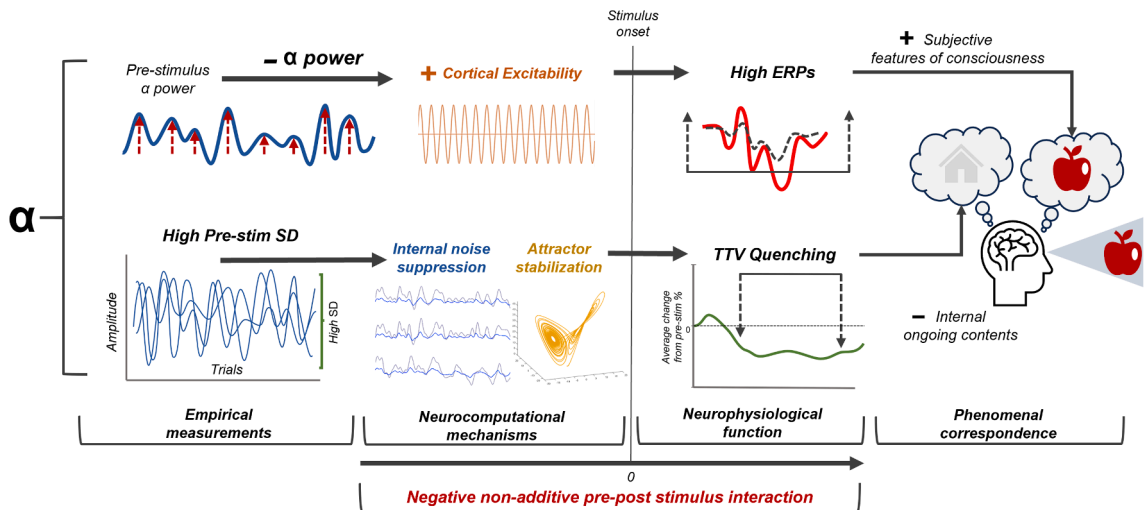


Fig. 5. Neurophysiological and neurocomputational hypothesis about the relationship between non-additive pre-post-stimulus interaction and contents of consciousness. The figure illustrates the convergence of alpha power and SD in the pre-stimulus period (left) with respect to their non-additive interaction with the neural measures of the post-stimulus period (right), i.e., event-related potentials and TTV reduction that results in the concurrent suppression of internal contents (the gray house in the cloud), and the highlighting of the external contents (the red apple in the cloud), with the latter subsequently becoming the content of consciousness (the red apple in the visual triangle indexing what the subject perceives).

a principal difference but rather a gradual one as manifest in different likelihoods of contents becoming conscious. This, as we hypothesize, may ultimately be related to the difference in the length of timescales subsequently different degrees of TTV quenching and non-additivity in anterior and posterior regions. This, albeit tentatively, reconciles the often states opposition of anterior and posterior regions in the current debate about neural correlates of consciousness [2,3,99].

4.3. Neuro-computational hypothesis—balance of noise suppression and attractor stabilization constitutes the balance of internal and external contents in consciousness

In order to understand how that constitutes conscious contents, we will now suggest specific neurocomputational, neurodynamic, neuropsychological and neurophenomenal hypotheses. We thus start with the neurocomputational mechanisms of non-additivity.

On a computational level, the TTV can be conceived as a transient short-term noise suppression [100,101]. Transiently suppressing the intrinsic noise from the brain's ongoing activity during the post-stimulus period, the external stimulus will stabilize and favor one particular attractor during the post-stimulus period while suppressing others, e.g., the meta-stable ones related to the intrinsic ongoing dynamics in the pre-stimulus period [16,100,101]. This will lead to one more stable transiently dominating attractor during the early post-stimulus period while other competing more metastable attractor will be transiently suppressed as manifest in noise suppression. Hence, attractor stabilization goes hand in hand with noise suppression.

The transient stabilization of one attractor and concurrent suppression of other more meta-stable attractors [69,102] may be reflected in the post-stimulus TTV reduction [101–103]. The transient noise suppression may be mediated by recurrent connections. A recent modeling study of a deterministic self-organizing recurrent neural network model (SORN) demonstrated that TTV suppression is mediated by recurrent processing through re-entrant (or feedback) connections [13,104]. One may thus want to computationally characterize the TTV and non-additive pre-post-stimulus interaction by the relationship of noise suppression, attractors, and recurrent processing (Fig. 5).

How is such transient noise suppression with the transient stabilization of one particular attractor related to the content of consciousness? Although tentative, one may suppose that the balance of noise suppression and attractor stabilization is related to the balance of internal and external contents [105]. Internal contents emerging from the ongoing conscious thoughts may be traced to the brain's intrinsic activity, that is, its ongoing spontaneous activity as during the pre-stimulus period while external contents may be rather related to external stimuli [106]. Accordingly, we suppose that the balance of internal and external contents in consciousness is related to the balance of the degree of carry-over of pre- to post-stimulus activity with the impact of the external stimulus on the latter (see also [105]).

The characterization of pre- and post-stimulus activity by internal and external contents respectively carries major implications for the contents of consciousness. By suppressing the neural activity of the pre-stimulus period, e.g., noise suppression, one may assume that its associated internal contents are also suppressed. In contrast, the transient attractor stabilization during the post-stimulus period may be related to a prolonged representation of the external stimulus which thereby has a higher likelihood to become a conscious content (see also [13]). Accordingly, we tentatively hypothesize that the balance of pre-stimulus noise suppression and post-stimulus attractor stabilization is related to the balance of internal and external contents in consciousness (Fig. 5).

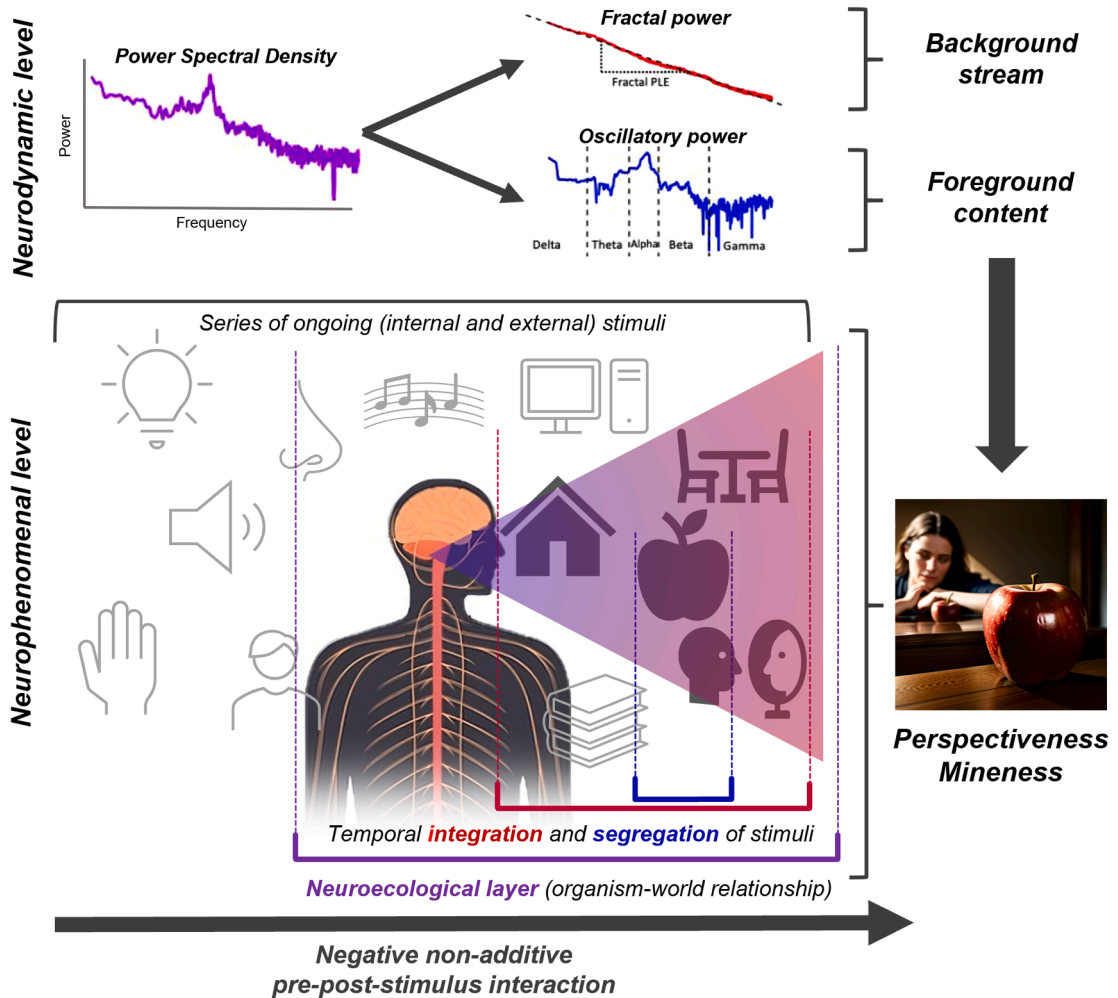


Fig. 6. Neurodynamic hypothesis on the distinction between background fractal aperiodic background activity and oscillatory periodic foreground activity, and neurophenomenal hypothesis on analogous background structure and foreground contents in consciousness temporal integration and segregation of stimuli. The figure illustrates the integration of an external stimulus, exemplified by an apple on a table (right), into the continuous neural spontaneous activity. On the neurodynamic level (top), the distinction between aperiodic fractal background activity and more periodic oscillatory foreground activity contributes to discerning the background structure like the stream elements (in this case, the room, mirror, reflection, and table) and the more foreground content of consciousness (the apple). On the neurophenomenal level, the repertoire of neural timescales allows the temporal integration and segregation of stimuli, with longer timescales capturing broader aspects (e.g., the room) and shorter timescales focusing on specific details (e.g., the apple). Together, the relationship between fractal-aperiodic and oscillatory-periodic activity, as well as the dynamics of temporal integration and segregation through longer and shorter timescales, becomes manifest in our subjective experience of the phenomenal features of our conscious contents, e.g., mineness and perspectiveness as based on the subject’s neuroecological point of view. Adapted from [93].

4.4. Neurodynamic hypothesis—‘fractal background stream’ and ‘oscillatory foreground content’

What are the neurodynamic mechanisms of such negative non-additive pre-post-stimulus interaction? Roughly, dynamics concerns the change of neural activity over time. One key dynamic feature we focused on so far is oscillatory activity in specifically the alpha band which is supposed to drive non-additive interaction of pre- and post-stimulus activity (see [10–12]) including its association with the content of consciousness). The alpha oscillation does not act in isolation, though. It is closely linked with the oscillations in other frequencies like delta and gamma [107]. Even more important, these highly regular periodic oscillations are embedded or nested within more irregular aperiodic fluctuations that, following scale free dynamics [108–111] designate the fractal-aperiodic component of the signal [10,93].

Recent comparison of oscillatory and fractal components observed much stronger pre-post-stimulus correlation for the oscillatory components in especially alpha and delta when compared to the fractal component in the same frequency band [10]. This does not mean that the fractal component has no impact at all on pre-post-stimulus interaction. Both measures of the fractal broadband signal by

itself, e.g., the scaling exponent reflecting the fractal-aperiodic slope of the curve of the broadband power spectrum, and the pure fractal power as measured by the fractal intercept, showed positive rather than negative correlation among their pre- and post-stimulus activities (see [10] Fig. 5). Together, these findings suggest differential roles of fractal, e.g., scale-free aperiodic, and oscillatory more periodic, e.g., alpha, activities during pre- and post-stimulus interaction.

In a separate study, Wainio Theberge et al. [93] demonstrate higher intra and intersubject variability of oscillatory than fractal activity during both rest and various task states with the variability being the strongest by far in specifically the alpha band. Further analysis revealed that such differential variability pattern conforms well to the distinction of background and foreground (rather than trait and state). Oscillatory measures with especially alpha exhibit high variability in a highly subject and context dependent manner, they are thus highly flexible operating in the foreground. While fractal-aperiodic measures show lower variability and remain more stable across both intra and intersubjective states and distinct task contexts, they thus display stability operating more in the background.

We now raise the question how the distinction of a more stable fractal background and the more flexible oscillatory foreground relates to the contents of consciousness. Timescales may be of key importance here. Oscillatory activity operates on specific timescales like alpha being restricted to the shorter timescale of 8 to 13 Hz. Each oscillatory band can thus be featured by a specific highly circumscribed and therefore rather short timescale. This is different in the case of the fractal component. By definition, the irregular aperiodic fluctuations of the fractal component operate across different timescales and thereby includes a wider array of both shorter and longer timescales [97,98,109–112]. Together, the more stable fractal background reflects neural activity across a broader array of different timescales including longer and shorter ones. While the more flexible oscillatory foreground singles out specific timescales.

We hypothesize that this difference in their range of timescales is highly relevant for their association with distinct features of consciousness, e.g., ‘background stream’ and ‘foreground content’. The specific and rather short timescales in the neuro-oscillatory more periodic foreground may be related to specific short-lasting contents in the post-stimulus period which, correspondingly, characterize the psychological foreground contents of consciousness at that particular short timescale in the millisecond range. While the combination of longer and shorter timescales in the neural fractal aperiodic background structure may index the deeper underlying temporal continuity across the distinction of pre- to post-stimulus activity. This temporal continuity in the fractal-aperiodic component of the neural activity may allow for embedding the shorter timescales of the short lasting often fleeting contents of consciousness within the much longer timescales of the ongoing stream of consciousness [113]. That is empirically supported by the various findings of the key relevance of fractal aperiodic activity for consciousness as that is lost during for instance anesthesia [109,114].

Together, we assume that, through their distinct timescales, the more stable fractal background activity shapes the longer lasting and more temporally continuous psychological background stream and structure of consciousness. While the more flexible, short lasting and more temporally discontinuous oscillatory foreground activity may be key for the psychological foreground contents of consciousness (Fig. 6). This carries major implications for the phenomenal features of consciousness as we will discuss them below.

4.5. *Neuro-psychological hypothesis—carry over of the subjective features of conscious contents from pre- to post-stimulus activity*

We addressed the neurophysiological and neurocomputational mechanisms of pre- and post-stimulus interaction with negative non-additivity and transiently stable attractors as features of conscious contents. This leaves open why specifically the subjective features of conscious contents are related to such pre-post-stimulus interaction. That touches upon the neuropsychological hypothesis of our model of conscious contents.

The subjective features of conscious contents concern vividness, confidence, visual awareness, and content detection, discrimination, and identification (see above). Where and how do the subjective features of the contents of consciousness come from? They cannot come from or with the external stimulus itself as that contains only extrinsic features. In contrast, the subjective features can only come from the subject itself and, more specifically, its own intrinsic spontaneous neural activity as for instance manifest in its pre-stimulus activity and reaction with stimulus-induced activity (pre-post-stimulus interaction).

Recent studies show that pre-stimulus activity is indeed associated with various subjective features like alertness [21], pupil linked arousal [19,115] and self relatedness [116–118]. One may consequently assume that these subjective features concerning both internal bodily and psychological manifestations are associated with and connected to the external stimulus. We hypothesize that such connection is possible by the direct non-additive interaction of pre-stimulus activity with the external stimulus. This allows for the neuronal carry over of the subjective features associated with the pre-stimulus activity to the post-stimulus period where they can be connected to and associated with the external stimulus. If, in contrast, the intrinsic pre-stimulus activity and external stimulus were processed merely in parallel, e.g., additive interaction, no such direct connection and association of the former’s subjective features with the external stimulus would be possible. Albeit tentatively, we hypothesize that in such case of purely additive pre-post-stimulus interaction neither the subjective features nor consciousness altogether would be possible.

Together, we suppose that the direct non-additive interaction of the intrinsic pre-stimulus activity with the external stimulus is key for associating the latter with subjective features and ultimately with consciousness. This is well in line with the findings that both alpha pre-stimulus power and TTV are related to the subjective features of conscious contents. Accordingly, it is not sufficient to just consider pre-stimulus activity in addition to post-stimulus activity in shaping the contents of consciousness. We need to go even further by also showing the mechanisms of how the intrinsic pre-stimulus activity directly interacts and integrates with the external stimulus on neuronal, e.g., non-additive rather than additive, neurocomputational, e.g., transiently stabilizing an attractor as representing the external content, neurodynamic, neuropsychological, e.g., carry over of the subjective features to the external contents (see also [119]).

4.6. Neurophenomenal hypothesis Ia—perspectivism and mineness are key phenomenal features of conscious contents

How are the above suggested neurophysiological, neurocomputational, neurodynamic and neuropsychological mechanisms related to the subjective experience of contents as presented by conceptual and phenomenological analysis? According to phenomenologists such as Jean-Paul Sartre, Husserl and Merleau-Ponty, every act of positional consciousness (i.e., being conscious of an object) is accompanied by a non-positional consciousness of that act (i.e., every conscious act is pre-reflectively, non-intentionally aware of itself) [120–122]. This non-voluntary (spontaneous) and non-inferential (it is not a belief, a representation or a judgment) consciousness supported by contemporary phenomenologists [123–125] and some analytic philosophers [126,127] is the so-called “pre-reflective self-awareness” or “pre-reflective self-consciousness”. This means that when we are conscious of a particular content (e.g., an apple), we must be pre-reflectively aware of that act of consciousness; otherwise, there would be nothing it is like to undergo that experience (i.e., that process would remain unconscious).

In this respect, one key subjective feature is the experience of the contents of consciousness in a perspectival way through the first-person perspective, i.e., perspectivism, which refers to the fact that each content of consciousness is given through a specific point of view [128–130]. The key phenomenal feature that refers to the qualitative nature of experience is what Nagel describes as “what it is like to be in a particular state for a particular subject” [128]. With this definition, Nagel refers to the subjective character of experience that should be distinct from any cognitive or functional notion, at least conceptually. Moreover, he thereby directly connects the qualitative features of experience with the point of view as the basis of its perspectivism.

The phenomenal character of consciousness is deeply related to the pre-reflective self-awareness structure of consciousness, since every “what it is like to be conscious of something” is necessarily a “what it is like to be for me.” This implies a strong phenomenological and conceptual relationship between the first-person perspective and what is usually called “mineness,” i.e., the fact that I am the one having an experience within a specific spatiotemporal framework. Finally, and most importantly, pre-reflective self-consciousness does not require any representational or higher-order self-reflection upon the conscious state that explicitly takes the self as an object, e.g., mirror self-recognition, conceptual or narrative self-consciousness [119,123,131–134]: we do not need to constantly check our experience to get a confirmation of who is experiencing that object. Together, perspectivism and mineness are key phenomenal features of our phenomenal experience of the contents of consciousness in terms of pre-reflective self-consciousness.

Note that the concept of self used here in “pre-reflective self-consciousness” does not refer to a bodily-based self or a cognition-based self, e.g., body-image, self-image, cognitive or mental self. Instead, being based on the neuroecological layer of the point of view, it refers to a relational neuroecological self right at the interface of organism and world [135–137]. In other words, prior to engaging in cognitive manipulation of information and symbols or mentally processing external stimuli through representations, and even before physically interacting with the environment through action-perceptions, experience emerges through the temporalization and spatialization of our relationship with things. This shall be described in more detail in the following.

4.7. Neurophenomenal hypothesis Ib—the fractal aperiodic background structure of consciousness constitutes the neuroecological layer of the subject's point of view

Pre-reflective self-consciousness involves a point of view which, following Thomas Nagel [128], is key for the phenomenal qualitative features of consciousness, i.e., qualia, as expressed by him in the famous paper “What is it like to be a bat?”. Nagel refers to the subjective character of experience that should be distinct from any cognitive or functional notion, at least conceptually. The contents of consciousness intrinsically imply the what-it-is-likeness: the main characteristic of experiencing a specific content means that there is something it is like to undergo that event for the experiencing subject. Accordingly, every “what it is like to be conscious of something” is necessarily a “what it is like to be for me”. The “what it is like to be for me” implies a key role of the subject in our experience of contents, namely the self as a point of view as distinguished from any representational or high-order self-reflection upon the conscious state that explicitly takes the self as an object, e.g., mirror self-recognition, conceptual or narrative self-consciousness [119,123,132].

This raises the question what exactly is meant by the concept of the point of view. While the concept of the point of view is often understood on a mental or even cognitive level, e.g., the metacognitive access to the perspectiveness of our experiential states, a recent neurophilosophical elaboration suggests a deeper layer of the point of view, a neuroecological layer [129]. Roughly, the neuroecological layer anchors the point of view within the wider environment. Consider the famous example given by Thomas Nagel, the bat's ability to process ultrasonic waves puts the bat in a different relationship to one and the same overall physical world than humans who do not possess that capacity. Albeit tentatively, we suppose that what we described as pre-reflective self-consciousness presupposes such deeper neuroecological layer of the point of view accounting for both perspectivism and mineness.

To illustrate metaphorically, maintaining the rhythm of music with hands, feet, or the entire body in dance does not necessarily involve cognitively counting time (“one, two, three, four, one...”). Instead, it is typically the body's movement that facilitates alignment with the music. However, preceding the synchronization of the whole body with the rhythm, the brain must initially tune into the beat—it must be receptive to the temporal structure of the sounds and align with the music [130,132]. We assume that consciousness is ultimately based on the relational self and its neuroecological point of view. This implies the possibility of an experience of consciousness without the experience or inclusion of a mental self is possible as, for instance, in non-self centred forms of a most basic and fundamental consciousness as in the non dual experience of proficient meditators [138].

This comparison illustrates some key features of this deeper neuroecological layer of the point of view. The neuroecological layer of the point of view is constituted by its spatial and temporal coordinates of the organism relative to the much broader array of different temporal and spatial scales of the environment, e.g., the natural world as whole. For instance, the bat's ultrasonic features stand in a

different relationship to the natural world than our human capacities. Hence, the neuroecological layer of the point of view can be characterized by its intersection and embedding, e.g., nesting of the organism's spatial and temporal features within the world's spatial and temporal features [129,132,139]. This constitutes the background structure on the phenomenal level of consciousness. Interestingly, we observed an analogous background-foreground distinction in the neurodynamic hypothesis. The brain's neural background is related to the longer timescales of the fractal component of its activity while the neural foreground is more shaped by the shorter timescales of the oscillatory activity (see above).

Taken together dynamic and phenomenal views, we now hypothesize that the neuroecological point of view, that constitutes the background structure of our consciousness including its embedding within the environment through the whole body, is related to the fractal aperiodic component reflecting the structure of the brain's neural background activity [129]. While, the brain's neural foreground activity, e.g., its oscillatory more periodic component, is rather related to the foreground in our consciousness, that is, its distinct contents. Given that the brain's fractal and oscillatory activity operate on different timescales - long and short - we assume that, correspondingly, the background structure and foreground contents in consciousness can also be distinguished by their timescales, e.g., longer and shorter [43].

4.8. Neurophenomenal hypothesis 1c—*intrinsic neural timescales are key in mediating the transition from background structure to the foreground contents of consciousness*

One may yet want to raise another question. How is the fractal aperiodic background neurally connected to the non-additive pre-post-stimulus interaction and its subsequent contents of consciousness. Formulated in a slightly distinct way, this is the question for the neural mechanisms and features that transform the continuously incoming inputs into specific contents at a particular point in time. Albeit tentatively, we assume that the brain's timescales, its intrinsic neural timescales (INT), play a key role here. The INT have been demonstrated to integrate and segregate different inputs out of the continuously ongoing input stream [94,97,98,140]. This segments the input dynamics into different input "chunks" and "pieces" [98] which may form the basis of the foregrounds content as distinct from the background.

We consequently hypothesize that the INT are key in segmenting different contents from the fractal background through their temporal integration and segregation (Fig. 6). In this regard, we further hypothesize that the relationship between temporal integration and segregation of inputs as mediated by INT is altered if not disrupted in states where the contents of consciousness are diminished or lost (e.g., disorders of consciousness, anesthesia, sleep). This is indeed supported as these states show abnormally long ACW which shifts the balance towards excessive temporal integration of inputs at the expense of their temporal segregation [31,32,141]. Albeit tentatively, we subsequently hypothesize that these subjects are no longer able to distinguish the contents from the abnormally strong input integrating background resulting the dedifferentiation and ultimately disappearance of any conscious content.

Moreover, we hypothesize that INT also shape the pre-stimulus activity including its non-additive interaction with the respectively integrated or segregated inputs as basis of the contents, this presumed modulation of the non-additive pre-post-stimulus interaction by the brain's INT is supposed to be key in associating the contents and their specific timescales with the wider range of timescales in the brain's neural background. Following the TTC, such integration and nesting of the content's more limited timescales within the brain's wider range of timescales is for rendering the content conscious. Such nesting and embedding of shorter within longer timescales may be disrupted in those states where the conscious contents are lost, e.g., disorders of consciousness. This is indeed supported on empirical grounds as for instance the longer timescales of the ACW no longer correlate with the shorter timescales of the alpha peak frequency in anesthesia and unresponsive wakefulness [141].

Conceived in a more general neurophenomenal way, this means that the content, as mediated by the shorter timescales of trial-to-trial variability and alpha, is no longer related to the neuroecological layer of the subject's point of view as constituted by the dynamic repertoire and larger range of timescales of the brain's ongoing spontaneous activity. If, however, the content can no longer be related to the point of view, it means that the subject can no longer associate the content with consciousness anymore, that is, the subject can no longer experience the content, even if there were one.

Together, we assume two key neurophenomenal mechanisms mediating the transition from background structure to foreground content in consciousness. First, we assume that there is differentiation of the content in the foreground of consciousness from the fractal aperiodic background activity through the INT. Secondly, we assume that the content's shorter timescales must be linked to and thus embedded within the longer timescales of the neuroecological layer of the subject's point of view [129] (Fig. 6). We assume that both neurophenomenal mechanisms are disrupted in states without any conscious contents, e.g., disorders of consciousness. While in other states like meditation, we assume that the first mechanism is topographically and dynamically reorganized with less content background differentiation. While the second mechanism, the embedding of the actual processing within the subject's point of view, is still preserved rendering the subject able to experience the background structure by itself as the content of their consciousness [138].

4.9. Neurophenomenal hypothesis 1d—*non-additive pre-post-stimulus interaction mediates the association of perspectivism and mineness with the contents of consciousness*

We are now ready to come back to the foreground contents of consciousness including its phenomenal features. Building on the neuroecological point of view and its background structure, we now suggest the following neurophenomenal hypotheses for the foreground contents of consciousness featured by mineness and perspectivism.

We hypothesize that the non-additive pre-post-stimulus interaction, especially in the alpha frequency band, may be fundamental to

Box 1

Extending and broadening the focus of current theories of consciousness

The Integrated Information Theory (IIT) [5,148,149] assumes that information integration is key for consciousness of contents. Mathematically, the phi index is supposed to account for information integration while empirically it can be measured with for instance the Lempel-Ziv complexity (LZC). One could say that the here suggested non-additive pre-post-stimulus interaction reflects information integration, that is, the information of the pre-stimulus period is integrated with the information of the external stimulus. That is well in accordance with the IIT. The IIT operates on very short timescales around 100–300 ms which at best represent only the early part of post-stimulus activity, though [43]. In contrast, the non-additive pre-post-stimulus interaction requires longer timescales like between 500 and 1000 ms as to temporally connect pre- and post-stimulus activity; that, in turn, first makes possible the non-additive nature of their interaction [10,17,43]. Accordingly, the main difference of the current approach to IIT is the necessity of including longer timescales that allow for temporally connecting pre- and post-stimulus activity.

The Global Neuronal Workspace theory (GNWT) [7,150–153] posits that external stimuli need to gain access to the global neuronal workspace through ignition in order to become conscious [7,151]. For that, the prefrontal cortex and somewhat late activity around 300–400 ms (P3b) are supposedly critical. A recent study investigated TTV in both empirical data and computational models associating it with the access to conscious contents around 300 ms [13]. This is indeed in accordance with the timing of the TTV which usually reaches its peak reduction around 200–400 ms post-stimulus [10–12,14,15].

Are TTV and non-additive pre-post-stimulus interaction related to prefrontal ignition and the access to conscious content as postulated by the GNWT? What is clear is that, unlike in the GNWT that emphasizes later time points like around 300 ms, the non-additive pre-post-stimulus interaction already operates in early post-stimulus intervals (like 0–300 ms) [10,12] where it may be related more with the phenomenal rather than access features of consciousness. Accordingly, unlike IIT whose timescales are too short, the ones of GNWT are too long and thus too late for yielding conscious contents when considered from the perspective non-additive pre-post-stimulus interaction. Hence, inclusion of the pre-stimulus activity may help to expand the timescales of both IIT and GNWT to include a broader repertoire of shorter and longer timescales.

In addition to these task-focused theories of consciousness, other theories put a stronger emphasis on the spontaneous activity like the Entropy hypothesis [154] and the Operational space-time theory (OST) [155]. Briefly, the Entropy hypothesis assumes that the degree of order/disorder or regularity/irregularity, e.g., entropy, in the brain's spontaneous activity is directly related to the order/disorder of contents in consciousness. This concerns mainly the number of contents and their organisation or structure, e.g., their order or disorder. In contrast, it leaves open why and how these contents are associated with consciousness (rather than remaining unconscious) and its phenomenal features. The same applies to the OST where the exact neurophenomenal mechanisms also remain open. Non-additive pre-post-stimulus interaction addresses this neurophenomenal gap. It delineates specific neurophysiological, neurocomputational, neuropsychological and neurophenomenal mechanisms which allow associating external contents with the subjective features of consciousness.

the phenomenal structuring of the contents of consciousness as featured by perspectivism and mineness. One would consequently expect that the post-stimulus TTV quenching, as index of the degree of negative non-additive pre-post-stimulus interaction, is closely related to the phenomenal features of pre-reflective self-awareness, such as mineness and perspectiveness. If, in contrast, there were merely additive interaction of pre-post-stimulus activity without any post-stimulus TTV reduction, one would expect that neither mineness nor perspectiveness would be present anymore. In that case, the external stimulus would no longer be integrated and embedded within the spatiotemporal structure of the ongoing pre-stimulus and spontaneous activity that constitute the subject's pre-reflective self-awareness as the background structure of consciousness. The latter's phenomenal features such as mineness and perspectiveness would consequently also remain absent; this is indeed empirically supported by data showing the absence of post-stimulus TTV reduction in both unresponsive wakefulness [69] and anesthesia [22].

Formulated in a more general way, the spontaneous brain activity, including its manifestation in the pre-stimulus period, shape the spatiotemporal background structure within which the contents in the foreground of consciousness are situated and experienced. If, for instance, the fractal aperiodic background activity is dominated more strongly by slower than faster frequencies with a steep fractal-aperiodic slope, the contents related to the oscillatory foreground may be experienced in an abnormally slow way. This may, for instance, be the case in major depressive disorder where subjects experienced an abnormal slowness with decreased speed in the change of contents in their consciousness [142–144]. The opposite may occur in mania where subjects experience an abnormally high speed in the change of the contents in their consciousness which is related to corresponding changes in the speed of their neural activity, e.g., neural variability [145].

Going final step further, we tentatively suppose direct relation of the temporal and also spatial features on the neuronal level with the experience of time and space on the phenomenal level. The latter may constitute the spatiotemporal background context within which we experience the contents in the foreground of consciousness. Just as we always perceive individual contents as integrated within an experiential context and by an experiencing subject, so the way processed stimuli can emerge to contents of consciousness depends on their integration within the spatiotemporal structure of the spontaneous brain activity preceding the external stimulus, i.e., the pre-stimulus. We suppose that this spatio-temporality may ultimately be shared by both the brain's spontaneous activity on the neural level and our conscious experience on the phenomenal level as their "common currency" [146,147]. This stands at the core of

Box 2

Temporo-spatial theory of consciousness (TTC) I—integrating neuronal and phenomenal features through linking spontaneous and task-related activity

The main critique of both task- and spontaneous activity-focused theories of consciousness [3] is that they do not link spontaneous and task-related activity in an integrated way, that is, they remain more or less on either side of the divide. This is different in and therefore renders unique the Temporo-spatial theory of consciousness (TTC) [29,30,43]. The TTC supposes that a special mechanism operating across and directly connecting the divide of spontaneous and task-related activity, namely temporo-spatial expansion, is key in constituting the contents of consciousness. Temporospatial expansion is proposed by the TTC as mechanism for specifically the contents of consciousness. Unlike in the other theories of consciousness, TTC suggests different mechanisms for the different dimensions of consciousness like temporospatial alignment for the form of consciousness while temporospatial nestedness accounts for the level or state of consciousness [29,30,43]. Given that our focus here is on the contents of consciousness, we here mostly discuss temporospatial expansion, while neglecting these additional mechanisms in the TTC.

Temporo-spatial expansion assumes that the wider time-space scales of the intrinsic pre-stimulus activity allow integrating the external stimulus' more restricted timescales within a broader and thereby more subjective context. This, so the TTC, leads to a virtual expansion of the external stimulus' more narrow timescales and its contents beyond themselves within the wider timescale array of the brain's neural activity. Such virtual expansion of the shorter timescales of the stimuli towards longer ones, in turn, makes it more likely that the originally rather short external stimulus becomes conscious. For instance, the actual physical duration of the external stimulus may be, let's say, 20 ms which, due to its integration into the ongoing pre-stimulus activity, is now expanded to 200 ms in the post-stimulus activity—this prolongation, as the data suggest, renders the stimulus conscious, even though its original physical duration of 20 ms would by itself be too short for the external stimulus to become conscious. Such temporo-spatial expansion requires direct interaction of the external stimulus' shorter timescales with the longer ones of the ongoing spontaneous activity—this is accounted for by non-additive pre-post-stimulus interaction.

Accordingly, the discussion of non-additive pre-post-stimulus interaction can be seen as a specification of what is described as temporospatial expansion in TTC. We described the neurophysiological, neurodynamic, neurocomputational, neuropsychological and neurophenomenal mechanisms of non-additive pre-post-stimulus interaction as mediating temporospatial expansion. These mechanisms are supposed to mediate the virtual temporal and also spatial expansion of the contents beyond their original purely physical spatial extension and temporal duration. The current paper thus sets the stage for detailed experimental testing of temporospatial expansion on the different levels of its mechanisms, neurophysiological, neurodynamic, neurocomputational, neuropsychological, and neurophenomenal.

One may now raise the question why the TTC so much emphasizes the temporal and spatial features which distinguishes it from all other theories of consciousness do. This leads us to the most important background assumption of TTC. The key background assumption is that neuronal and phenomenal (or mental states share some similarity which, following the TTC, consists in their commonly shared spatial and temporal features as their “common currency” [147]). For instance, if the neural activity is abnormally slow, subjects may experience a corresponding slowness in their inner time consciousness, this is the case in depression [144,145]. This marks the TTC an integrated brain-mind theory. Due to the assumption of space and time being shared by both neural and mental features as their “common currency”, the TTC can bridge the gap of neuronal and phenomenal features by connecting them in a necessary way (chapter 10 in Northoff [139]). This carries major conceptual philosophical implications for the mind body problem and others like the hard problem [139]. While, empirically, we assume the here described neurophysiological, neurocomputational, neurodynamic, neuropsychological, and neurophenomenal levels with all focusing on spatial and temporal features.

the Temporo-spatial theory of consciousness (TTC) which therefore can be considered an intrinsically integrated brain-mind approach to consciousness (see Box 2) as it allows for necessary connection of neural and mental features [139].

5. Conclusion

What are the neural correlates of the contents of consciousness? Reviewing recent data, we hypothesize that the dynamic negative non-additive interaction of pre- and post-stimulus activity in specifically alpha is a key mechanism in modulating conscious contents including their subjective features. This is demonstrated on distinct levels including neurophysiological, neurocomputational, neurodynamical, neuropsychological and neurophenomenal. Neurophysiologically, we suppose that negative non-additive interaction of the pre-stimulus activity level, e.g., its alpha power and variability, with the external stimulus allows rendering the latter to become a content of consciousness. While neurocomputationally, the occurrence of both pre-stimulus noise suppression and post-stimulus attractor stabilization may be key in shifting the balance from internal to external contents in consciousness. Neurodynamically, we suppose that fractal background activity and oscillatory foreground activity are related to the distinction between the background structure or stream and the foreground content in consciousness. Neuropsychologically, the non-additive interaction may allow for the carry over of the subjective features from the pre-stimulus period to the external stimulus by which, as we assume, the latter is rendered conscious. Finally, we also assume specific neurophenomenal mechanisms focusing on phenomenal features like perspectivalness and mineness as being mediated by non-additive pre-post-stimulus interaction and its various timescales.

Box 3**Temporo-spatial theory of consciousness (TTC) II—converging with predictive coding**

Another theory of consciousness is the predictive coding theory [2]. Briefly, this theory states that the contents of consciousness are closely related to the brain's constitution of a prediction error as based on its own prediction, the empirical prior [25, 156–159]. The empirical prior can be related to the neural activity in the pre-stimulus period [18,19,21,159], that is, its amplitude/power and variance, while the prediction error is manifest in post-stimulus measures like TTV and amplitude [2,25]. Most importantly, predictive coding assumes direct non-additive relationship between empirical prior and posterior resulting in the prediction error—this is well in accordance with the present approach of non-additive pre-post-stimulus interaction.

Moreover, similar to the present approach, the post-stimulus prediction error is constituted by a balance or hybrid of internally predicted contents, e.g., the empirical prior, and the actual external incoming contents, e.g., the posterior. If the former is stronger, it will dominate the prediction error, while a strong external stimulus is more likely to override the impact of the internal one, the mostly unconscious perceptual prior [158]. Accordingly, we see strong convergence of the predictive coding approach with the here supposed various neuronal mechanisms of non-additive pre-post-stimulus interaction with respect to the contents of consciousness. Hence, future studies want to link the predictive coding formalism to the here supposed different level mechanisms of non-additive pre-post-stimulus interaction including their much broader repertoire of different timescales.

Let us be more specific in converging temporospatial expansion with non-additive interaction with the predictive coding model. The level of pre-stimulus activity and variance can be linked to the empirical prior in both the spatial domain, e.g., structural prior, and the temporal domain, e.g., dynamical prior [160]. While the predicted level of post-stimulus activity may be related with the posterior with the degree of post-stimulus TTV quenching probably indexing the degree of the prediction error. Future studies are thus warranted that relate the here proposed focus on the dynamic mechanisms of pre-post-stimulus interaction with the computational mechanisms of predictive coding, including both its structural and dynamical priors.

We consider negative non-additive pre-post-stimulus interaction in alpha a strong candidate to serve as neural correlate of consciousness, understood as neural correlate of conscious content. Specifically, we consider the inclusion of both pre- and post-stimulus periods as the temporal NCC addressing the question for “when do the NCCs occur”. As discussed above, non-additive interaction can occur in various regions along a posterior to anterior gradient accounting for the spatial NCCs, the “where are the NCCs”. While the question for the mechanism, the “how are the NCCs mediated”, is answered by negative non-additive pre-post-stimulus interaction in alpha which, as we showed, can be explicated on different levels including neurophysiological, neurodynamical, neurocomputational, neuropsychological, and neurophenomenological. In contrast, we left open the questions for the “why are there NCCs”, the neural predispositions of consciousness (NPC) [29,34], and the “what are the biological substrates of the NCC” [46,47].

Our view of the NCCs allows for a broader view of neural activity beyond the post-stimulus period and its task related activity as being key for consciousness [9]. We may not only want to take into view the brain's spontaneous activity including its manifestation in the pre-stimulus period but, even more important, the exact mechanisms of its interaction with the external stimulus, e.g., non-additive pre-post-stimulus interaction. This extends leading neuroscientific theories of consciousness like the Integrated Information theory (IIT) [5] and the Global Neuronal Workspace theory (GNWT) [7] beyond their current focus on post-stimulus task-related activity [9] to pre-stimulus activity ([3] for general overview) and, more generally, spontaneous activity. At the same time, such pre-post-stimulus view of the NCCs lends additional support to theories that attribute a key role to pre-stimulus activity like predictive processing [25] and the Temporo-spatial theory of consciousness (TTC) [29,30,43] (see Boxes 1–3).

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.

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