

# Temporo-spatial Theory of Consciousness (TTC) – Bridging the gap of neuronal activity and phenomenal states

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## ABSTRACT

Consciousness and its neural mechanisms remain a mystery. Current neuroscientific theories focus predominantly on the external input/stimulus and the associated stimulus-related activity during conscious contents. Despite all progress, we encounter two gaps: (i) a gap between spontaneous and stimulus-related activity; (ii) a gap between neuronal and phenomenal features. A novel, different, and unique approach, Temporo-spatial Theory of Consciousness (TTC) aims to bridge both gaps. The TTC focuses on the brain's spontaneous activity and how its spatial topography and temporal dynamic shape stimulus-related activity and resurface in the corresponding spatial and temporal features of consciousness, i.e., 'common currency'. The TTC introduces four temporo-spatial mechanisms: expansion, globalization, alignment, and nestedness. These are associated with distinct dimensions of consciousness including phenomenal content, access, form/structure, and level/state, respectively. Following up on the first introduction of the TTC in 2017, we review updates, further develop these temporo-spatial mechanisms, and postulate specific neurophenomenal hypotheses. We conclude that the TTC offers a viable approach for (i) linking spontaneous and stimulus-related activity in conscious states; (ii) determining specific neuronal and neurophenomenal mechanisms for the distinct dimensions of consciousness; (iii) an integrative and unifying framework of different neuroscientific theories of consciousness; and (iv) offers novel empirically grounded conceptual assumptions about the biological and ontological nature of consciousness and its relation to the brain.

## 1. Introduction

Consciousness and its neural mechanisms are one of the few unsolved mysteries in current-day science [1–3]. This includes philosophical debates about the nature and criteria of consciousness such as the 'hard problem' [4] as well as neuroscientific investigations of the neuronal mechanisms of consciousness [3,5]. In that vein, various neuroscientific theories of consciousness have been proposed including Integrated Information Theory (IIT) [6,7], Global Neuronal Workspace Theory (GNWT) [8–10], Recurrent Processing Theory (RPT) [11,12], and Higher-order Thought theory (HOT) [13,14]. Despite their differences (see [5,8] for a review), these theories mainly focus on changes in

stimulus-related activity that are related to conscious content. Specifically, they focus on the minimal neural activations that are sufficient for a specific content of consciousness, the neural correlates of consciousness (NCC) [15].

These theories are complemented by others that propose neural mechanisms and features that extend beyond the stimulus-related activity itself (see [5] for an overview). They focus on anticipation or prediction as in the Predictive Coding Theory (PCT) [16–18], attention as in the Attention Schema Theory (AST) [19–21], embodiment as in the Embodied Theory (ET) [22,23], or/and the brain's spontaneous activity as in the Operational Space-time theory (OST) [24] and the Entropy Hypothesis (EH) [25,26]. These are just some examples of the burgeoning field of neuroscientific theories of consciousness [5]. Despite

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**Nomenclature***Theories of consciousness*

<b>AST</b>	Attention Schema Theory
<b>EH</b>	Entropy Hypothesis
<b>ET</b>	Embodied Theory
<b>GNWT</b>	Global Neuronal Workspace Theory
<b>HOT</b>	Higher-order Thought theory
<b>IIT</b>	Integrated Information Theory
<b>OST</b>	Operational Space-time Theory
<b>PCT</b>	Predictive Coding Theory
<b>RPT</b>	Recurrent Processing Theory
<b>TTC</b>	Temporo-spatial Theory of Consciousness

*Neural conditions*

<b>NPC</b>	Neural predisposition of consciousness
<b>preNCC</b>	Neural prerequisite of consciousness
<b>NCCcont</b>	Neural correlate of conscious contents
<b>NCCcons</b>	Neural consequence of consciousness

*Neural measures and concepts*

<b>ACW</b>	Autocorrelation window
<b>DFA</b>	Detrended fluctuation analysis
<b>GS</b>	Global signal
<b>INT</b>	Intrinsic neural timescales
<b>PLE</b>	Power-law exponent
<b>TRW</b>	Temporal receptive window
<b>TTV</b>	Trial-to-trial variability

the enormous diversity of theories, a truly unifying theory of consciousness that integrates spontaneous and stimulus-related activity and, at the same time, relates them to specific neurophenomenal hypotheses is still lacking in the field.

The Temporo-spatial Theory of Consciousness (TTC) aims to fill that void. Rather than focusing on specific characteristics of information, sensory, or cognitive processing (like IIT, GNWT, RPT, PCT, ET, and HOT), the TTC assumes that the most fundamental characteristics of the brain of its neural activity, namely its spatial topography and temporal dynamic, are key to consciousness. The TTC assumes that the brain is characterized by an intrinsic spatial topography and an intrinsic temporal dynamic that hold in both spontaneous and stimulus-related activity. The temporal dynamic and spatial topography reflect the way the brain constructs its own 'inner time and space' through and within its neural activity [27,28]. Such a construction-based view distinguishes the TTC from other theories of consciousness that understand time and space in terms of perception and cognition, i.e., perceived time and space. Here, the focus is on understanding the neural correlates of the perception of outer time and space in the world whereas the brain's inner time and space are more or less neglected.

Based on this background assumption, the TTC introduces four different temporo-spatial mechanisms: expansion, globalization, alignment, and nestedness [28]. These are supposed to be related to distinct dimensions of consciousness, such as content, access, form/structure, and level/state. Since their original introduction in the 2017 article [28], these mechanisms have gained strong empirical support. The goal of this paper is (i) to update the empirical evidence for the four temporo-spatial mechanisms; (ii) to specify and explicate them with the formulation of specific neuronal hypotheses; (iii) to associate them with specific phenomenal features of consciousness thus developing neurophenomenal hypotheses.

## 2. Phenomenal content of consciousness - Temporo-spatial expansion

### 2.1. Stimulus-evoked activity vs rest/pre-stimulus-stimulus interaction

What are the neural correlates of consciousness? Most theories like IIT, GNWT, HOT, and RPT focus on stimulus-related activity and how its contents become conscious. The TTC takes a more expanded view looking beyond stimulus-related activity to spontaneous activity: stimulus-related activity only reflects the 'tip of the iceberg', i.e., 5%, with the remaining 95% of the brain's neural activity being accounted for by spontaneous activity [29]. The main point of the TTC is that spontaneous activity is key in understanding how and why consciousness is assigned to external (or internal) inputs/stimuli. Rather than the stimulus-related activity itself, the TTC puts a special focus on how the external input/stimuli interact with the brain's spontaneous activity.

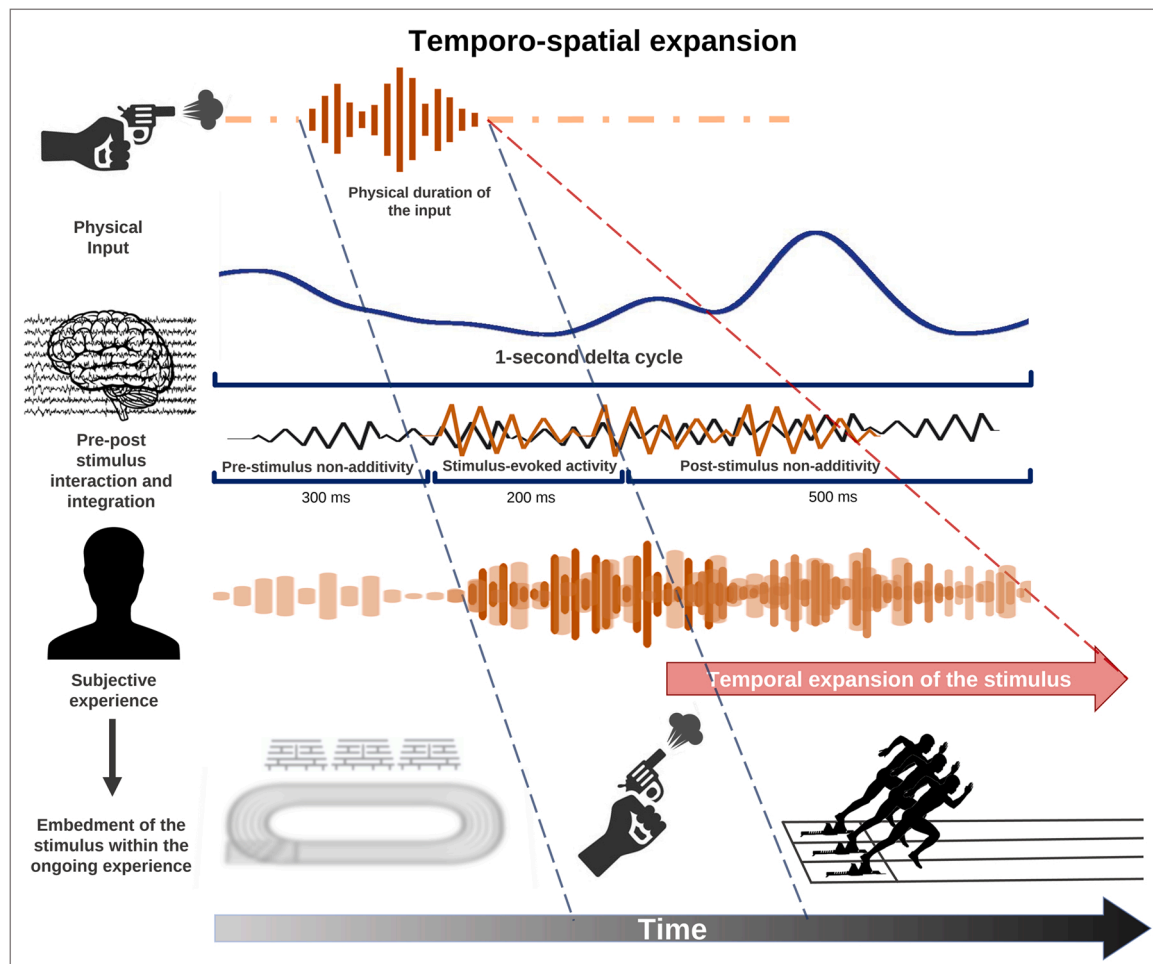
This has been subsumed under the umbrella concept of 'rest-stimulus interaction' which includes the interaction of both resting state and pre-stimulus activity with the external inputs/stimuli [30–32]. The TTC describes this interaction by the mechanism of Temporo-spatial expansion. Temporo-spatial expansion highlights a particular form of the interaction of pre-stimulus and post-stimulus activity that allows for assigning contents to consciousness. We first describe the purely neuronal mechanisms of this interaction, after which we focus on their relevance for consciousness.

#### 2.1.1. Trial-to-trial variability (TTV) I – additive vs non-additive pre- post-stimulus interaction

Traditionally, neuronal activity related to external input/stimulation is supposed to be 'added' or superimposed on the ongoing level of pre-stimulus activity [33–35]. The degree or magnitude to which the external input/stimulus elicits an amplitude in the post-stimulus interval is supposed to remain independent of the pre-stimulus activity level, that is, whether the latter is high or low. This amounts to a model of purely additive pre-stimulus-stimulus interaction [30,33,34,36]. The contents of consciousness are here conceived to remain independent of pre-stimulus activity levels; instead, they are sufficiently and exclusively associated with the magnitude of the post-stimulus amplitude.

However, such an assumption of additive pre-post-stimulus interaction stands counter to various fMRI studies [37–39] and EEG/MEG [40–45] that show the importance of changes in pre-stimulus activity for conscious content (see also [46]). If, for instance, the pre-stimulus activity in the fusiform face area (FFA) is high, subjects are more likely to perceive a face rather than a vase in a bistable perception task [37–39]. The same applies to the pre-stimulus alpha that, if high, is more likely to be followed by conscious perception (rather than unconscious) in the subsequent post-stimulus activity [40–45]. Together, these studies put into doubt the tacit assumption of the exclusive importance of post-stimulus activity for conscious contents [46], including the additive pre-post-stimulus interaction model.

How can we measure the impact of pre-stimulus activity on post-stimulus activity? One way is to measure the trial-to-trial variability (TTV) that can be observed on both cellular and regional-systemic activity levels [47–51]. The TTV measures the variation in the amplitude across different trials of the same kind of stimulus. Measuring TTV at each time point during the post-stimulus interval, one can generally observe a decrease in TTV around 100–500 ms in EEG/MEG [30–32,43,50,51] and fMRI [30,36]. The post-stimulus TTV reduction reflects the suppression of the variability in amplitude from trial to trial [32,43,48]. Given that the external stimulus or input remains the same throughout all trials, the variability in the amplitude can only come from the pre-stimulus period itself. Hence, the ongoing variation in the amplitude of the pre-stimulus activity is carried over to the post-stimulus interval where it is transiently suppressed by the external input/stimulus. This



**Fig. 1.** Temporo-spatial expansion of the input/stimulus's original (physical) temporal duration and spatial location during the pre-post stimulus interaction of the brain's neural activity. The stimulus-related activity is non-additively integrated within an ongoing delta cycle of 1 Hz that spills over for another 500 ms into the post-stimulus period. Thus, the original temporal duration of the input is virtually expanded by the neural activity during the pre-post-stimulus interaction. The actual input or stimulus of a firing gun is embedded in the ongoing experience (during the pre-stimulus period) which, after the onset of the input/stimulus is expanded towards the post-stimulus experience. The actual input/stimulus, the firing gun, is thus integrated and embedded within the ongoing experience of the pre-stimulus period, the stadium. Together, pre-stimulus experience (stadium) and the actual input/stimulus (firing gun) amount to the experience of runners starting for a competitive run (as the firing gun in a stadium is usually associated semantically with the start of a run in a competition). If, in contrast, there was a different experience in the pre-stimulus period like a deer in a forest, the same input/stimulus, i.e., firing gun, would elicit a different conscious content, most likely the one of a hunter shooting the deer.

suggests non-additive rather than additive interaction of pre-stimulus and stimulus activity.

Studies in both fMRI [30,36], EEG [31,32,43], and even at the cellular level [47,48] strongly suggest a non-additive rather than additive mechanism. Data show that high post-stimulus TTV suppression, i. e., low TTV, is related to high pre-stimulus variance, while low post-stimulus TTV suppression, i.e., high TTV, is preceded by low pre-stimulus variance [30–32,43,47]. This suggests a non-additive mechanism where the pre-stimulus activity level strongly shapes the level of subsequent post-stimulus activity.

### 2.1.2. Trial-to-trial variability (TTV) II – neural marker (or neural correlate) of conscious contents (NCCcont)

Is non-additive pre-post-stimulus interaction relevant for consciousness? If so, one would expect that the degree of post-stimulus TTV reduction is directly related to the degree to which the contents become conscious. This has indeed been shown especially for the case of visual perception: the stronger the post-stimulus TTV is reduced (for instance, in the dorsolateral prefrontal cortex – DLPFC – and/or alpha band), the more likely the respective contents will become conscious [40–42, 50–56]. These findings strongly suggest that post-stimulus TTV plays a

key role in mediating conscious contents, which, albeit indirectly, implies the presence of non-additive rather than additive pre-post-stimulus interaction.

Sergent et al. [57] demonstrated that the post-stimulus TTV level around 250–300 ms provides a critical threshold: after that, stimulus-related activity may persist and thus be prolonged, showing low TTV during conscious access. If, in contrast, the TTV returns to its high pre-stimulus levels during the post-stimulus period, conscious access is no longer present [57]. The critical role of 250–300 ms post-stimulus is well compatible with a recent intracranial stereo-electroencephalography (sEEG) (with a no-report paradigm) that showed the differential impact of the pre-stimulus activity on early and late post-stimulus activity: pre-stimulus variance strongly shaped the early (0–250/300 ms) than the late (300–600 ms) post-stimulus interval where the impact of the external stimulus was stronger [32] which may provide conscious access [57].

Together, these studies suggest that post-stimulus TTV and its time course may provide a key marker of the contents of consciousness. Future studies are warranted to investigate whether early (0 – 250/300 ms) and late (250/300 – 600 ms) post-stimulus intervals are associated with distinct dimensions of consciousness, i.e., phenomenal and access,

respectively [58]. Moreover, non-additive pre-post-stimulus interaction needs to be explicitly demonstrated to mediate the phenomenal features of conscious contents: the higher the degree of non-additivity, the more likely consciousness including distinct phenomenal features like qualia, intentionality and ipseity [59] may be associated with the respective input/stimulus.

## 2.2. Temporo-spatial expansion I – neural expansion mediates conscious contents

Why and how are the TTV and its non-additive pre-post-stimulus interaction key for contents to become conscious? Given that the temporal and spatial features of the pre-stimulus activity are carried over and thus neurally expanded to especially the early post-stimulus activity (0 – 250/300 ms), the TTC speaks of Temporo-spatial expansion. Expansion is here meant in a purely neural sense, namely, that the spatial and/or temporal features of the spontaneous activity in pre-stimulus activity are carried over and thus expanded during the post-stimulus interval. This allows for their direct interaction with the external input/stimuli in a non-additive (rather than additive) way. For instance, the activity level of a region like the FFA remains the same during pre- and post-stimulus intervals: this temporal expansion of FFA activity from pre- to -post-stimulus intervals, in turn, makes it more likely that one perceives a face rather than a house or else a during the presentation of bistable stimuli [37,38]. The TTC speaks here of ‘spatial expansion’ of FFA activity from pre- to post-stimulus activity.

There is also a temporal expansion related to oscillations. Pre-stimulus variance in slower (delta) and faster (alpha) frequencies entails distinct types of non-additive pre-post-stimulus interaction, i.e., positive (delta) and negative (alpha) [31]. This suggests different types of pre-post-stimulus carry-over of slow and faster frequencies: relative to the length of their ongoing cycle durations across pre- and post-stimulus intervals, slow and fast frequencies with their long and short cycle durations exert a differential impact, that is, positive and negative non-additivity, on post-stimulus activity [31]. If, for instance, a new cycle of delta 1 Hz starts at – 500 ms pre-stimulus, it will be shaping

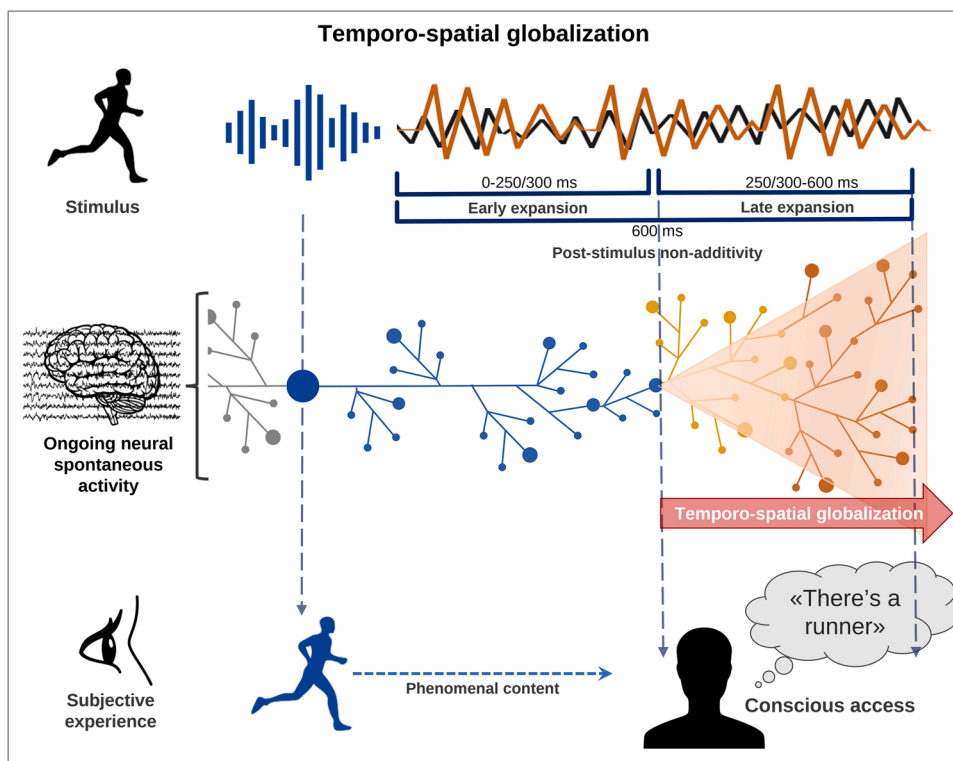
post-stimulus activity for another 500 ms. If, in contrast, a delta cycle starts at – 800 pre-stimulus, it will only be ongoing for another 200 ms in the post-stimulus period.

Is such a temporal expansion of neural activity relevant for conscious contents? Various studies show the relevance of especially pre-stimulus alpha for conscious contents [40–45]. Given that alpha covers the frequency range of 8–12 Hz, these findings suggest that its cycle duration of around 100 ms may be key in linking pre- and post-stimulus activity with each other as well as to consciousness. However, one needs to be careful about some methodological caveats. One must consider the length of the pre-stimulus interval in one analysis: if one only considers 100–200 ms pre-stimulus intervals, one’s focus is necessarily on alpha while excluding slower frequencies with longer cycle durations (like delta or theta) [32,43]. This is indeed supported by Glim et al. [60] who, applying a long pre-stimulus interval of 2 s, demonstrated the importance of slow cortical potentials (0.1–1 Hz with a cycle duration of 10–1 s) in visual consciousness.

### 2.2.1. Temporo-spatial expansion II – from neural expansion to phenomenal features

We so far limited Temporo-spatial expansion to the neural domain while leaving out the phenomenal features of consciousness. The TTC claims that the Temporo-spatial expansion on the neural side of pre- to post-stimulus activity is accompanied by a more or less corresponding expansion of the temporal and spatial features of the external input/stimulus itself: we perceive the external input/stimulus in our consciousness in a temporally and spatially more expanded way when compared to its actual physical duration and location. There is a discrepancy between physical and phenomenal locations/durations of the external input/stimulus – the TTC speaks of a ‘physical-neuronal discrepancy’.

The TTC proposes that this physical-neuronal discrepancy is related to the virtual temporal and spatial expansion of the physical location and duration of the external stimulus. If, for instance, the actual input lasting for about 200 ms is integrated or embedded within an ongoing delta cycle of 1 Hz that spills over for another 500 ms into the post-



**Fig. 2.** Temporo-spatial globalization of an input/stimulus allows for accessing it through cognitive functions, i.e., access consciousness. The input/stimulus of the runner perceived through the eyes is encoded and its information is progressively distributed along the activations of multiple regions and their different time scales; this makes the content available for conscious cognitive access. Neurophenomenally speaking, after an immediate manifestation of an experience of the runner as phenomenal content, i.e., phenomenal consciousness, it is then made available to various cognitive facilities like reasoning, speech, report, behavior, and reflection, i.e., access consciousness.

stimulus period, the temporal duration of the 200 ms lasting input will be expanded by another 300 ms in a virtual, i.e., neuronal way beyond the physical duration of the stimulus (see Fig. 1). This means that, despite lasting only 200 ms by itself, the external input will elicit and thus be processed for a total of 500 ms in brain neural activity. The same may analogously be observed on the spatial side. A simple purely visual stimulus may by itself only elicit neural activity in V1 and V2. However, if V1 and V2 are strongly connected with, for instance, DLPFC in the pre-stimulus period with that transient connection to be carried over to the post-stimulus period, the simple visual stimulus' post-stimulus activity may be expanded beyond V1 and V2 to higher-order regions like MT/V5 and others and ultimately even the DLPFC.

In summary, the TTC claims that the degree to which the physical duration and location of the actual input/stimulus is expanded by the brain's neural activity beyond the physical features of the input/stimulus is directly related to the phenomenal features. Given that the assignment of consciousness supposedly depends on the expansion of the original spatial and temporal features of the input/stimulus, the resulting phenomenal features may be spatial and temporal themselves. Thus, spatial topography and temporal dynamic may be shared as the 'common currency' of brain neural activity and phenomenal features of consciousness [27,61]. Neural topography and dynamic may thus resurface on the phenomenal level in terms of mental topography and dynamic. Finally, Temporo-spatial expansion is a sufficient neural condition of conscious content, i.e., a neural correlate of consciousness (NCCcont). However, it is not a necessary neural condition of conscious content as that is provided by the pre-stimulus activity, namely, its temporal dynamic and spatial topography. For instance, in another spatio-temporal context with different necessary conditions, there may be another neuronal state  $x1$  (or an artificial neural state) to elicit the actual conscious content  $y$ . Logically speaking, being in Rome is a sufficient condition for being in Italy, but it is not necessary, as I could, for instance, also be in Milan or elsewhere to be in Italy [62].

### 3. Accessing contents of consciousness – Temporo-spatial globalization

We already highlighted that later stimulus-related activity around 300–600 ms and recruitment of the DLPFC are associated with conscious contents (as distinct from unconscious contents). There has been considerable debate among especially IIT/RPT and GNWT/HOT whether such later higher-order recruitment is associated with the phenomenal or cognitive/access features of consciousness [1,3,6,8,63,64]. The TTC does not participate in this debate nor takes a stance here. Instead, it proposes a distinct mechanism, Temporo-spatial globalization, which can be conceived as a continuation of Temporo-spatial expansion by providing the latter's link to cognitive functions.

Temporo-spatial globalization refers to the global recruitment of regions and frequencies that are important for specifically access consciousness [65,66]: this happens when some content is processed and made dispositionally available to cognitive functions such as reasoning, speech, report, and behavior. This is a final stage or result of a chain of various preceding temporo-spatial mechanisms closely related to the spontaneous activity itself, i.e., its Temporo-spatial expansion, nestedness, and alignment. Conceived in this way, the external input/stimulus supposedly only triggers or accentuates (rather than causes) an already ongoing neural activity change that by itself predisposes or makes it impossible to associate consciousness with the external stimulus (see Fig. 2). Thus, Temporo-spatial globalization can be related to the neural consequences of consciousness (NCCcons), that is, to those sufficient neural conditions that allow cognitive accessing and (successively) reporting conscious contents [5,67,68].

This is where TTC and other theories of consciousness such as GNWT, RPT, and HOT diverge. In fact, to fully understand how the temporal-spatial mechanisms of expansion and globalization work, it is necessary to step back and focus not only on the neural correlates and neural

(or better neuro-cognitive) consequences of the content and access of consciousness per se (i.e., the actual consciousness) but on the intrinsic spatial-topographic and temporal-dynamic features of the neural activity that precedes them, that is, the brain's spontaneous activity as manifest in pre-stimulus and also in the resting-state activity [59]. This leads to Temporo-spatial alignment and nestedness that, as the TTC claims, provide the necessary neural conditions of possible consciousness, that is, the neural capacity or neural predisposition (NPC) and prerequisite (preNCC) of consciousness [5,69,70]. Complementing the content and access of consciousness, NPC and preNCC are key for its additional dimensions like the level/state and form/structure of consciousness.

### 4. Form or structure of consciousness – Temporo-spatial alignment

One key component of consciousness is its inclusion of multiple layers in our experience. Most prominent is the attempt by Gestalt Psychology to characterize perception in terms of figure and background. We experience or are conscious of a particular content (as figure) within a context (as background), with the latter itself being conscious, preconscious, or subliminally perceived (see also [46]). This has been picked up somewhat by the IIT in especially its axioms, which, taken roughly, are different organizational constellations between context (background) and content (figure) in phenomenal consciousness ([6]; see [71,72] for a critical evaluation). Where and how is the background or context of the contents of consciousness coming from? The TTC assumes here a particular mechanism, namely, Temporo-spatial alignment. Temporo-spatial alignment means that the brain encodes the context by adapting (and thereby aligning) its own neural activity to the various inputs/stimuli that shape the context [28].

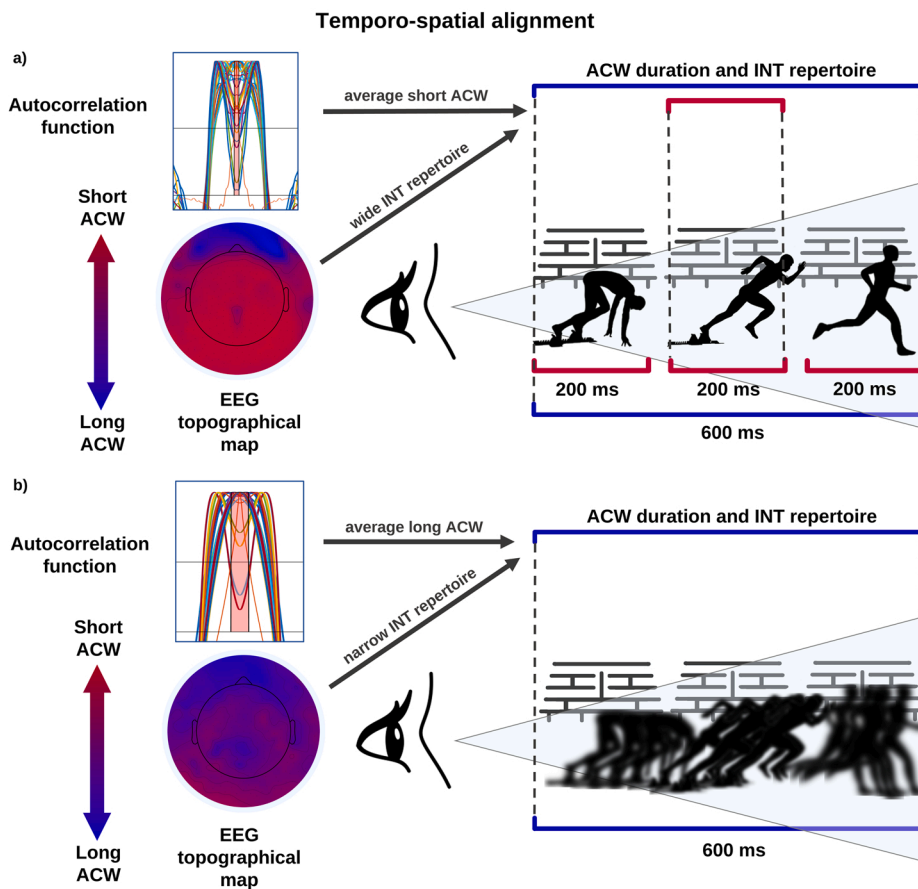
#### 4.1. Intrinsic neural timescales (INT) I – difference-based coding and context

Our environment bombards the brain with a variety of regular and irregular inputs on different timescales. Consider one of the temporally most complex inputs, music. We are able to simultaneously perceive the different timescales of music and, even better, integrate them into one meaningful whole, like a melody that, moreover, can be distinguished from the ongoing accompaniment in the background. How can our brain process and integrate such multi-scale inputs? Recent evidence suggests that the brain itself exhibits 'intrinsic neural timescales' (INT) [73–83].

Measured by the autocorrelation window (ACW) [73,76,83], the brain exhibits temporal windows (INT) of different lengths or duration in the resting state. Interestingly, unimodal regions such as primary sensory cortices show shorter ACW, while transmodal regions such as the default mode network (DMN) show longer timescales, i.e., long ACW [74,76,83–86]. Hence, the temporal distinction of shorter and longer timescales converges with the spatial topography of uni- and transmodal regions [85,86] that amounts to a core-periphery organization [76,87,88].

What is the role of the brain's INT? A variety of studies by the group around Hasson demonstrated that longer and shorter timescales are related to corresponding temporal differences in the input sequences [73,77,81,89]; for instance, single tones are related to neural activity in the unimodal primary auditory cortex while sequences of tones and a whole melody are more related to neural activity in transmodal higher-order regions with the DMN at the top of the hierarchy [73,80,90]. Therefore, they characterize INT as 'temporal receptive windows' (TRW) as they receive and organize input sequences by temporal segmentation [77,89]. This is well compatible with a recent study showing that the INT change during the transition from rest to task by showing task-specific effects in both uni- and transmodal regions [76].

Together, these findings suggest a key role for INT in the brain input processing [83] and, more generally, the brain's encoding of its external



**Fig. 3.** Temporo-spatial alignment of the brain's intrinsic activity to ongoing environmental stimuli. In the upper part of the figure (a), the autocorrelation window (ACW) of the subject shows the different lengths of the INT repertoire and its topographic distribution (EEG map). In particular, the temporal dynamic of the subject are sufficiently short to allow sampling the start of the runners in a fine-grained and temporally precise and differentiated way. Neurophenomenally speaking, every detail of the competition (figure-runner and background-bleachers) is well parsed across multiple levels of duration. On the contrary, in the lower part of figure (b), the mildly sedated subject has a reduced and generally longer INT repertoire. This corresponds to the loss of the ability to segment the input series in detail, resulting in the coarse-grained integration of all stimuli into long time windows. Instead of perceiving the input in a temporally precise way (as in the first case), the subject now perceives the same input in a temporally imprecise or smoothed way – the perceived image of the runner is blurred with the other inputs/stimulus of the same scene or context. The ACW representations are taken from the datasets investigated in [93].

context. Through its own INT, the brain formats the input stochastics in a temporal way; this allows it to process and encode the multitude of inputs in their temporal stochastics. Therefore, one input is processed and encoded relative to the other – this requires difference-based coding [91].

Difference-based coding must be distinguished from another possible encoding strategy, namely stimulus-based coding [91]. In that case, the single input is encoded in an absolute way, as a stimulus or input by itself in isolation from the other inputs/stimuli. However, this is not empirically supported by the data [91] nor is it compatible with the temporal windows of the INT (as these lump or pool and thus relate distinct inputs together; [83]). In summary, input encoding and processing as mediated by INT is difference-based and therefore intrinsically contextual. This has major implications for consciousness.

#### 4.1.1. Intrinsic neural timescales (INT) I – key role in consciousness

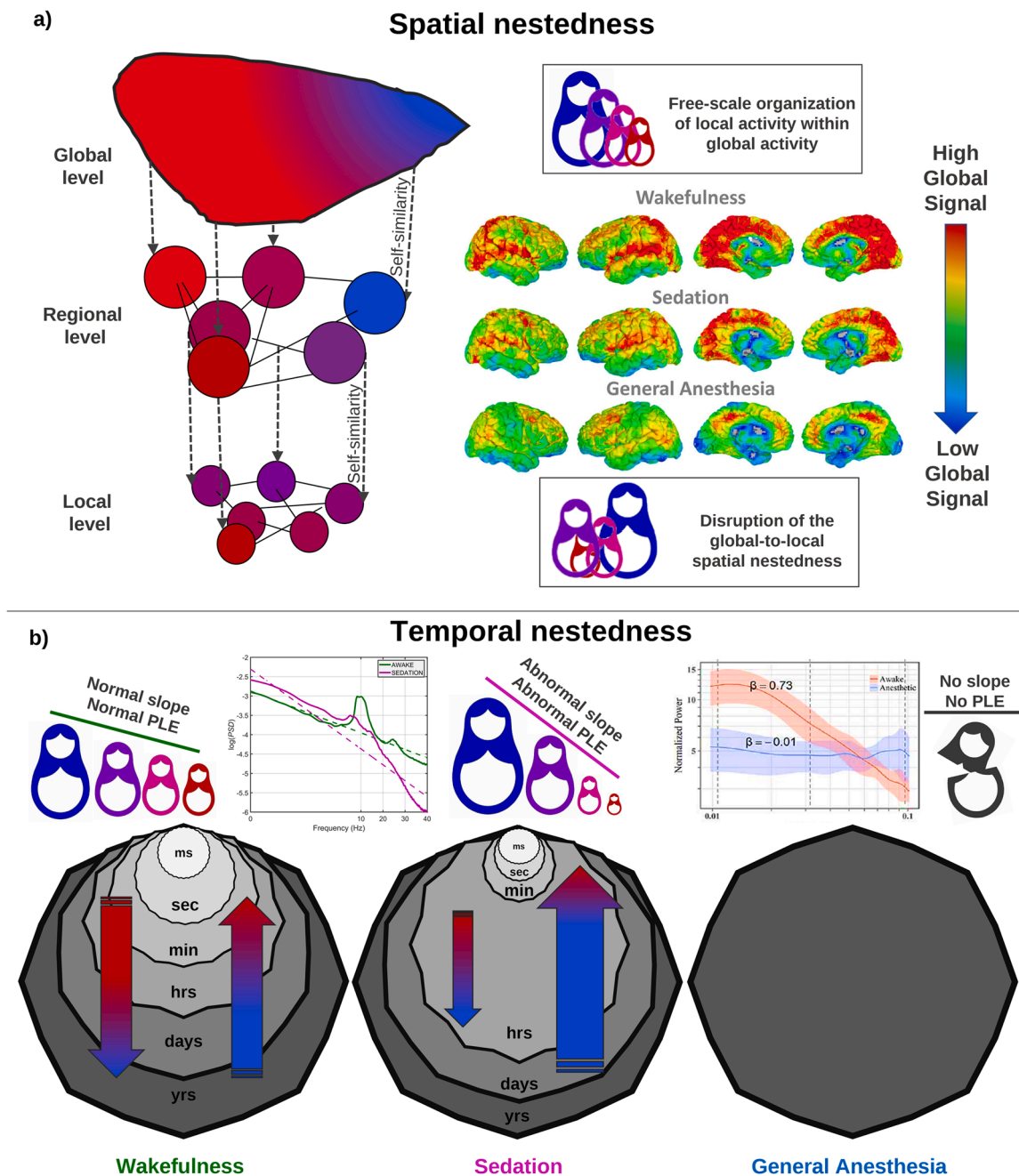
Are INTs important for consciousness? Some recent studies have investigated INT in various disorders of consciousness. Conducting an fMRI resting state, Huang et al. [54] investigated the autocorrelation function (as an index of INT) in subjects undergoing graded propofol sedation. They observed a prolonged temporal autocorrelation in these subjects accompanied by a shift towards slow frequencies, i.e., lower median frequency, while, at the same time, global functional connectivity decreased.

Unlike graded nonsurgical sedation with propofol, subjects with deep or surgical anaesthesia, as well as those in an unresponsive wakefulness state (UWS), showed a major reduction, i.e., a shortening in temporal autocorrelation [54,92]. The authors conclude that during sedated states, the INTs are prolonged, which disrupts the global functional connectivity between regions, while in the deep unconscious state, i.e., surgical anaesthesia and UWS, both timescales and functional

connectivity are completely disrupted and basically broken down [54].

In another fMRI study, Huang et al. [92] observed that, when becoming unconscious, intra-regional temporal autocorrelation does indeed increase while interregional functional connectivity decreases. In contrast, during recovery from unconsciousness, there is a sudden restoration of the cortical INT with restoration of subcortical-cortical functional connectivity. Together, these findings demonstrate the relevance of INT for consciousness in the infraslow frequency range (0.01–0.1 Hz) of fMRI, as well as their dynamic changes across different degrees or levels/states of consciousness.

Although these findings establish a role for INT in consciousness, i.e., level/state, they leave open whether they are specifically related to changes in input processing. This was addressed by Zilio et al. [93] in a recent EEG study, albeit indirectly. They investigated ACW in resting-state EEG in subjects with physiological, pharmacological, and pathological alterations of consciousness. Under such conditions, input processing is known to be altered in distinct ways, i.e., progressive decrease (NREM sleep stages N1, N2, N3), isolation from external inputs but preserved capacity for processing of internal inputs (from the own body and brain) (REM sleep and ketamine), and extreme deficiency or complete absence of both external and internal inputs (unresponsive wakefulness syndrome, sevoflurane). Additionally, they included subjects with complete loss of motor function, e.g., output processing, while input processing and consciousness are preserved (Locked-in syndrome (LIS) and amyotrophic lateral sclerosis (ALS)). The results show an abnormally long ACW in the unresponsive wakefulness syndrome, through abnormal strengthening of slow frequency power (and a concurrent weakening of fast frequency power). Both anaesthesia and sleep showed abnormal prolongation of the ACW, which is in line with the progressive decrement of the capacity of input processing in the different behavioral states. Motor conditions, on the contrary, exhibited



**Fig. 4.** Visual illustration of spatial (a) and temporal (b) nestedness. The spatial nestedness represented by the brain’s global cortical and subcortical signal shows how the various levels of activity (global, regional, and local) are spatially nested within each other in a scale-free way. Similarly, on the temporal level, the fastest frequencies are nested within the slowest frequencies following the power-law distribution (slow frequencies-high power; fast frequencies-low power). The disruption of the global-to-local spatial relationship and/or the unbalance of the relationship between slow-fast frequencies corresponds to the decline of the level/state of consciousness, up to the complete loss of consciousness as in deep anaesthesia, which is related to the complete disruption of the nested structure of spontaneous brain activity. GS representations are taken from [103]; the PLE representations are taken from the data sets investigated in [93] and [111].

‘normal’ ACW with a preserved balance of slow and fast frequencies in the power spectrum.

Together, these findings support the involvement of intrinsic neural timescales specifically in input processing rather than output processing, including their relevance for consciousness. If, in contrast, the ACW was involved in both input and output processing, it should have changed in both types of conditions, altered states of consciousness and motor conditions. However, that was not the case, as only disorders of consciousness exhibit major changes in INT (see also [76]). In summary, we tentatively assume that input encoding through INT in terms of

difference-based coding (rather than in a stimulus-based way) is key for the presence of consciousness.

**4.1.2. Intrinsic neural timescales (INT) II – from Temporo-spatial alignment to the phenomenal context/background of consciousness**

We are now ready to address our question of where the context or background of consciousness is coming from. The INT encode contents within their respective contexts, i.e., input stochastics through difference-based coding. Such context-dependent encoding of single inputs/stimuli allows the brain to attune, synchronize or entrain and,

more generally speaking, and match; i.e., complexity matching; [94] to its respective environmental context. Therefore, the TTC speaks of ‘temporo-spatial alignment’.

How is Temporo-spatial alignment as a purely neuronal mechanism related to the phenomenal experience of context or background of consciousness? When we are conscious, we are constantly aligned to some degree with the continuous flow of external stimuli. Let us consider the example of dancing. During dancing, we synchronize and align the temporo-spatial stochastics of our own brain and the body movements to the temporo-spatial stochastics of music. We consequently become conscious not only of single tones, but of tones in their respective context like a melody. As mentioned previously, studies by the group around Hasson on the TRW demonstrate that the topographical differences in the length of the INT are key in segmenting the input into shorter and longer sequences (see Fig. 3). Temporal segmentation may thus constitute the context for a single note of which we become conscious – we then perceive the single note as part of and being integrated within a sequence of ongoing tones, i.e., the melody.

Temporal segmentation requires both temporal integration and segregation [75,83,95]. Their balance may be key for distinguishing context (i.e., the sequence of tones as background) and content (i.e., the single tone as a figure within the sequence of tones). The experience of a single content requires high temporal precision, while temporally segregating it from others. In contrast, the concurrent experience of the context with its multitude of contents may be more related to a high degree of temporal integration and subsequently temporal smoothing (rather than temporal precision) [83]. We consequently assume that temporal segmentation with temporal integration vs segregation (and associated temporal smoothing vs precision) is a key neurophenomenal (rather than just purely neuronal) mechanism of Temporo-spatial alignment.

Temporal integration and segregation constitute the form or structure of the context within which the contents are embedded and integrated. The TTC claims that the temporal-dynamic and spatial-topographic form or structure of the brain’s spontaneous activity is also manifest, in more or less corresponding ways, on the phenomenal or mental level of consciousness: spatial topography and temporal dynamic are shared by the brain’s neural activity and the mental states of consciousness as their ‘common currency’ [27,61,96,97]. This is manifest, for instance, in subjective time and space experience, i.e., temporality and spatiality [98] or, more generally, mental dynamic and mental topography.

## 5. Level or state of consciousness - Temporo-spatial nestedness

### 5.1. Level/state of consciousness I – spatial nestedness

In addition to its INT, the spontaneous activity exhibits a certain temporal and spatial structure, which the TTC refers to as Temporo-spatial nestedness. Roughly, Temporo-spatial nestedness refers to a particular type of organisation of different spatial and temporal scales of neural activity. Rather than operating in parallel, unconnected, or causally connected but separate ways, the different spatial and temporal scales of neural activity are contained or nested within each other.

The most typical example of spatial nestedness is the Russian dolls. Here, smaller dolls are contained, and thus nested within the next larger one, and so forth. While the different dolls exhibit different sizes, i.e., large and small, they nevertheless show the same shape, i.e., self-similarity. This means that they are organized in a scale-free way: self-similarity in their shape or structure across different spatial scales. Such scale-free activity typically characterizes ubiquitous systems in nature, from seismic earth waves to stock market fluctuations [99–101].

Scale-free activity with spatial nestedness also characterizes the brain. Spatially, regions are nested within networks that, among the latter, constitute a small-world topography [102]. This is, for instance, manifest in a particular topography with different degrees of global

spatial activity representation in particular regions/networks: the local activity of particular regions is spatially nested within the global activity of the whole brain. The key assumption of the TTC is that such spatial nestedness is a key mechanism of the level or state of consciousness, namely, its arousal.

In a multigroup fMRI study, Tanabe et al. [103] investigated global functional connectivity (Global signal/GS) in both rat and human anaesthesia as well as in human sleep and UWS. They observed that the decrease in GS is directly related to the decrease in the level/state of consciousness: the lower the GS, the lower the level/state [103] (see also [104,105] for further support) (see Fig. 4a). This establishes a direct relationship between the degree of global brain activity and the level/state of consciousness across different disruptions (anaesthesia, sleep, UWS) and species (humans, rats).

Importantly, changes in global brain activity were accompanied by a differential topography of GS (as measured by correlating GS with each regions’ time series, i.e., GSCORR) during different consciousness states: for instance, sleep stages (N1–N2–N3, REM) exhibited a differential regional distribution pattern of GS, i.e., GS topography, than distinct stages of sedation/anaesthesia [103] despite showing similar levels of global activity, i.e., GS in, for instance, N3 and deep sedation. This suggests that the global activity level, i.e., GS, and global-to-local activity representation, i.e., GS topography, can, at least in part, dissociate from each other: the same level/state of consciousness may be related to a distinct structure or form of consciousness leading to distinct phenomenology as mediated by the different spatial topographies (GSCORR).

### 5.2. Level/state of consciousness II – temporal nestedness

We so far focused on spatial nestedness; how about temporal nestedness? The short cycle durations of the less powerful faster frequencies like gamma and beta are contained and thus nested within much longer cycle durations of more power slower frequencies, such as theta and delta; the latter ones, in turn, are nested within slow cortical potentials (0.1–1 Hz) and infraslow frequencies (0.01–0.1 Hz). Such temporal nestedness can be measured by the power-law exponent (PLE) [100,101,104,106] or by the detrended fluctuation analysis (DFA) [107,108].

Various studies in both fMRI [109–111] and EEG [93,112] (see also [28] as well as [5] for extensive reviews) show abnormal scale-free activity in different behavioral states. During the early stages of loss of consciousness, for instance, in mild sedation or N1/2 sleep, the power shifts towards slower frequencies at the expense of power in the faster frequencies, resulting in higher PLE [54,93,112]. In contrast, during the complete and irreversible absence of consciousness like in chronic UWS or surgical anaesthesia, the basic structure of the power spectrum (slow-fast frequencies related to high-low power) is lost completely: it is now completely flat without any temporal nestedness anymore [54,111].

Together, one may assume that an average dynamic range of temporal nestedness with a certain structure or balance of slow and fast frequency power may be optimal for the maximal expression of the level/state of consciousness [113]: ‘average is good, extremes are bad’ (see Fig. 4b). If that structure is shifted to some degree, the possibility of consciousness is preserved even if it is not actually realized. This marks scale-freeness with temporal nestedness as the neural predisposition of consciousness (NPC) rather than as its neural correlate: it constitutes the necessary non-sufficient neural conditions that make possible consciousness (‘possible consciousness’), while not realizing its actual manifestation through specific contents (‘actual consciousness’) [5,28,59,70].

The TTC postulates that such Temporo-spatial nestedness on the neuronal level is also neurophenomenally relevant for consciousness. The different temporo-spatial scales or ranges of the various layers of context/background and contents of our experience are linked and unified with each other through their temporo-spatial nestedness – this



**Table 1**  
The Temporo-spatial mechanisms and their respective neural conditions and dimensions of consciousness.

Temporo-spatial mechanisms	Neural conditions	Dimensions of consciousness	
Nestedness	Predispositions (NPC)	Level/state	Possible consciousness
Alignment	Prerequisites (preNCC)	Form/structure	
Expansion	Correlates (NCCcont)	Phenomenal content	Actual consciousness
Globalization	Consequences (NCCcons)	Conscious access	

may result in the experience of unity as a phenomenal key feature of consciousness [59,114,115]: the higher the degree of temporo-spatial nestedness of the different temporal and spatial scales of the brain's neural activity, the higher the degree of their nestedness or unity in our experience. Thus, unity in the gestalt of temporo-spatial nestedness may be shared by both the brain and consciousness as their 'common currency' [27,61,97].

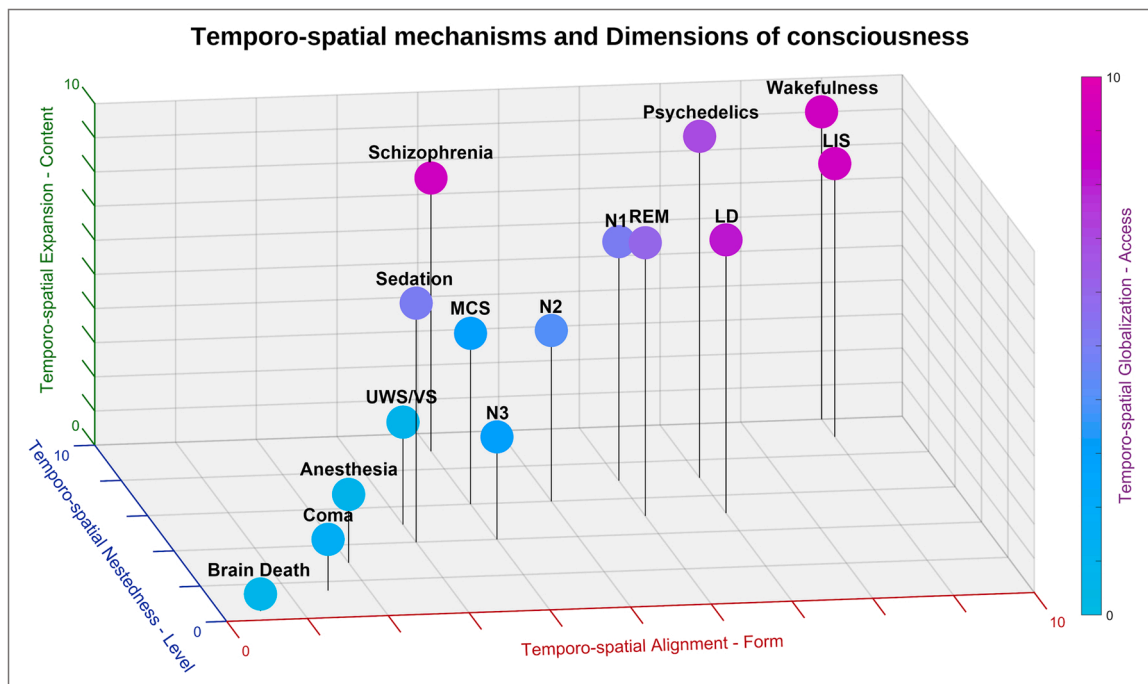
**6. Conclusion**

We introduced the TTC as a different approach to consciousness compared to various other theories. The key difference is that TTC takes into account the most basic features of the brain's neural activity, namely, its spatial topography and temporal dynamic. Both spatial and temporal features are supposed to be shared by neural and phenomenal activity, that is, the brain and consciousness as their 'common currency' [27,61]. This provides a direct (e.g., necessary a posteriori; [116]) link of neuronal and phenomenal features resulting in the here postulated neurophenomenal hypotheses.

The four temporo-spatial mechanisms correspond to four specific neuronal conditions related to consciousness: correlates, consequences,

prerequisites, and predispositions. Neural predisposition (Temporo-spatial nestedness) and neural prerequisite (Temporo-spatial alignment) refer to those temporo-spatial conditions of the brain's neural activity that provide the ground for and thus make possible (without yet actually realizing) the association of specific contents with consciousness - they refer to what conceptually can be described as 'possible consciousness' [59,91]. While the neural correlates (Temporo-spatial expansion) and neural consequences (Temporo-spatial globalization) refer to those neural conditions that realize the content of consciousness in a precise spatio-temporal context (e.g., the consciousness of a table in front of the subject) - they refer to what conceptually is described as 'actual consciousness' [59,91] (see Table 1 below) [59,116].

To make the four-dimensional structure of consciousness more understandable, starting this time from NPC to NCCcons, we could use the metaphor of a room: the floor corresponds to the level/state of activation (nestedness); the arrangement of the furniture to the form/structure of consciousness (alignment); the presence of various objects to the phenomenal contents (expansion); finally, the relation between the single objects (e.g., the table with the chair, the fork with the knife) to the access consciousness (globalization). The floor (nestedness-level/state) and the furniture (alignment-form/structure) work as a condition



**Fig. 5.** Four-dimensional (three dimensions + color bar) representation of different physiological, pathological, and pharmacological states of consciousness, through temporo-spatial mechanisms and their related dimensions of consciousness. Nestedness-level and alignment-form function constitute the neural predisposition and neural prerequisite of consciousness, i.e., possible consciousness. While expansion-content and globalization-access realize the content of actual consciousness, the neural correlates and consequences of consciousness. Generally, most conditions of consciousness are located along the diagonal from the minimum to the maximum degree of consciousness. However, some conditions show important dissociations between mechanisms-dimensions, such as schizophrenia, REM sleep, lucid dreams, sedation, and psychedelic state. Abbreviations: UWS/VS = Unresponsive wakefulness syndrome/vegetative state; MCS = Minimally conscious state; REM = Rapid eye movement sleep; N1-2-3 = non-REM sleep 1-2-3; LD = Lucid dreams; LIS = Locked-in syndrome. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Box 1**

Relationship of the four mechanisms of TTC to other neuroscientific theories of consciousness.

**Temporo-spatial expansion:** Temporo-spatial expansion is a unique mechanism compared to the ones assumed in other theories of consciousness. Current theories of consciousness focus predominantly on post-stimulus activity, such as RPT, GNWT, and HOT, or they highlight the role of spontaneous brain activity, such as EH or OST. However, the bridge or link of spontaneous and stimulus-evoked activity is missing in either of these theories. This bridge or link is provided by Temporo-spatial expansion.

On the one hand, Temporo-spatial expansion picks up the intrinsic features of the brain's spontaneous activity, including pre-stimulus activity, namely, its temporal dynamic and spatial topography. On the other hand, Temporo-spatial expansion conceives stimulus-evoked activity relative to the pre-stimulus activity's temporal dynamic and spatial topography. Hence, temporal dynamic and spatial topography provide the link or 'glue' between pre- and post-stimulus activity.

While the mechanism of Temporo-spatial expansion is primarily spatial and temporal, it is well compatible with the more cognitive and stochastic view of the PCT. The PCT assumes the prediction of the input, the prior, to be key in how the external input/stimulus, the posterior, is processed [16,17]. The degree to which the prior and posterior differ or match yields a prediction error. Most interestingly, predictive coding assumes a temporal basis, 'deep temporal models' [120–122] or 'temporal thickness' [123] – this may be found in the temporal dynamic of pre-stimulus activity. How such a temporal basis looks in detail and how it shapes pre-post-stimulus interaction, including the prediction error and conscious content, remains yet unclear.

**Temporo-spatial globalization:** We compare Temporo-spatial expansion and globalization with the neural mechanisms of other theories to flesh out their similarities and differences. Like the IIT, the TTC considers integration a key feature of phenomenal consciousness, namely, through Temporo-spatial expansion and globalization. However, the TTC takes on a more sophisticated view of integration (see also [124]).

Integration in TTC refers to the degree to which the pre-stimulus spatial topography and temporal dynamic are carried over and thereby expanded to and integrated within the post-stimulus interval through their non-additive (rather than additive) interactions. Integration is thus understood in a temporo-spatial sense rather than as a causal integration in a discrete point in time. How such a temporo-spatial sense of integration can be linked to the more abstract and mathematical sense of integration in IIT through, for instance, category theory [125] remains to be investigated in the future.

The connection of Temporo-spatial globalization to cognitive function is shared with especially the GNWT. GNWT argues for the existence of recurrent and competitive top-down/bottom-up loops that accumulate information from perceptual, motor, attention, memory, and value networks, then sharing and broadcasting information back to lower-level processors. This broadly distributed network permits conscious access to the unified and synthesized information, i.e., the consciousness of some specific content [126]. We assume that Temporo-spatial globalization makes possible such global access as highlighted by GNWT.

**Temporo-spatial alignment:** Due to their involvement in the brain's processing of the inputs of both the body [127] and environment [83,93], we regard the INT as key for the stochastic matching of brain dynamics with the input dynamic of the body [22,23] and environment [93]. This converges the Temporo-spatial alignment with especially embodied theories of consciousness [22]. However, the Temporo-spatial alignment extends beyond the embodied theories in that it explicitly speaks of alignment to the environment as key for consciousness.

Temporo-spatial alignment may also be related to the concept of free energy in PCT (see also [75]); free energy describes the degree of discrepancy in the brain's energy relative to that in its respective environmental context [16]. One would assume that high degrees of Temporo-spatial alignment provide an optimal reduction or minimization of free energy and henceforth a high degree of homeostasis of brain and environment. If, in contrast, the degree of Temporo-spatial alignment is low, their energetic discrepancy may be high as manifested in high degrees of free energy.

There are major differences in TTC from other theories in both empirical and conceptual terms. The TTC proposes that Temporo-spatial alignment constitutes a particular dimension, namely, the form or structure of consciousness. The form or structure of consciousness refers to the organisation of its contents relative to each other [59,69]. The TTC assumes that such a form or structure is constituted by the temporal-dynamic and spatial-topographic features of the brain's spontaneous activity.

This distinguishes the TTC from all other theories like IIT, GNWT, RPT, and HOT, which neither consider the spontaneous activity (or, if they do, they consider it only as a background condition [6128,129]) nor its intrinsic spatial topography and temporal dynamic. That makes it impossible for them to take into view the form or structure of consciousness as a third dimension besides content and level/state. Moreover, it also distinguishes the TTC from other resting state-based approaches such as EH [26] and OST [24] where the direct or intrinsic link of the brain's spontaneous activity to consciousness remains more indirect (or extrinsic).

**Temporo-spatial nestedness:** Temporo-spatial nestedness distinguishes the TTC from those theories that focus mainly on early and/or late stimulus-evoked activity such as IIT, RPT, GNWT, and HOT. Unlike these theories, the TTC explicitly takes into consideration the key role of the brain's spontaneous activity for consciousness. This puts the TTC on par with other theories that focus on spontaneous activity, such as OST [24] and EH [25,26], including its recent cognitive version, REBUS (RELaxed Beliefs Under pSychedelics [130]).

Through Temporo-spatial nestedness, the TTC conceives the intrinsic spatial-topographic and temporal-dynamic organisation of the brain's spontaneous activity as key for consciousness. If we lose its basic intrinsic spatial topography and temporal dynamic as in the case of a flat power spectrum, we lose our capacity for consciousness, i.e., its neural predisposition (NPC) [54,70,111]. In that case, we lose the level or state of consciousness.

If, alternatively, the intrinsic spatial topography and temporal dynamic are still preserved but shifted in atypical ways, the level or state of consciousness is preserved too. In contrast, the form or structure of consciousness becomes abnormal such that the contents of consciousness are integrated and embedded within an abnormal context. That is, for instance, the case in psychedelics where the structure or form of consciousness becomes abnormal. Here, the entropy of the brain's spontaneous activity increases leading to more disordered states as during psychedelics, such as LSD or psilocybin; that, in turn, changes our cognition to more relaxed belief states, i.e., REBUS [25,130].

Together, albeit in the early stages, the direct link of neuronal topography and mental topography and, analogously, of neuronal dynamic and mental dynamic, distinguishes TTC from other theories of consciousness such as OST [24] and EH [25,26]. The TTC extends beyond these approaches by providing a specific mechanism, i.e., Temporo-spatial nestedness, that bridges the gap and intrinsically connects brain and consciousness (and thus, conceptually put, in a necessary a posteriori way [116,131]).

of possibility for the room itself (possible consciousness): without a floor, there would be no furniture or objects, and without specific furniture, it would just be an empty room. The objects (expansion-content) and their position (globalization-access) in relation to the furniture enrich and characterize the room (actual consciousness).

Through this differentiation of mechanisms, it is also possible to understand how some cases, both pathological and physiological, can induce dissociation between various dimensions (see Fig. 5). For instance, the REM state during sleep might be represented as a room with a confused arrangement of furniture and objects, while in non-REM sleep the furniture may be extremely sparse if not lost completely (N3). Unresponsive wakefulness syndrome/vegetative state, on the other hand, can be conceived as an unstable vanishing floor that leads to a general disorder that makes it impossible any consistent relationship between objects and furniture. The psychedelic state might correspond to a room rich in furniture and objects with a solid but sloping floor that makes the relationship or organization among the objects chaotic and highly entropic. Finally, schizophrenia might be represented by a room with a solid but unstable variable floor that mixes furniture and objects from different parts of the house (the bathtub next to the bed or the fork next to the toothbrush).

Together, the four temporo-spatial core mechanisms mark the TTC as a viable candidate theory to bridge the two key gaps in our current view of consciousness. First, it bridges the gap between spontaneous and stimulus-related activity by intimately linking them together as, for instance, in Temporo-spatial expansion. Together with its focus on the most basic features of the brain's neural activity, its spatial topography, and temporal dynamic, the TTC may provide a unifying neuronal framework for various neuroscientific theories of consciousness.

Second, TTC bridges the gap between neuronal and phenomenal features by assuming that both share their most basic and fundamental spatial-topographic and temporal-dynamic organisation, i.e., 'common currency' [27,61]. The assumption of such shared features provides an intrinsic (and necessary a posteriori) connection of brain and consciousness [116–119]. The intrinsic (necessary a posteriori; [116], Chapter 10) connection of neural and phenomenal states allows the TTC to also address some of the basic and fundamental philosophical problems. For instance, the assumption of time and space as 'common currency' of brain and mind may provide a novel answer to – if not a resolution – of perennial philosophical issues like the 'Hard problem of consciousness' and the mind-brain problem [62,116]. This marks the TTC not only as a viable empirical and, therefore, neuroscientific theory of consciousness but also as a promising conceptual approach to ontological issues in philosophy Box 1.

#### CRediT authorship contribution statement

**Georg Northoff:** Conceptualization, Writing – original draft. **Federico Zilio:** Writing – review & editing, Visualization.

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#### Declarations of interest

none.

#### References

- [1] C. Koch, M. Massimini, M. Boly, G. Tononi, Neural correlates of consciousness: progress and problems, *Nat. Rev. Neurosci.* 17 (2016) 307–321, <https://doi.org/10.1038/nrn.2016.22>.
- [2] C. Koch, What is consciousness? *Nature* 557 (2018) S8–S12, <https://doi.org/10.1038/d41586-018-05097-x>.
- [3] L. Melloni, L. Mudrik, M. Pitts, C. Koch, Making the hard problem of consciousness easier, *Science* 372 (2021) 911–912.
- [4] D.J. Chalmers, Facing up to the problem of consciousness, *J. Conscious. Stud.* 2 (1995) 200–219.
- [5] G. Northoff, V. Lamme, Neural signs and mechanisms of consciousness: Is there a potential convergence of theories of consciousness in sight, *Neurosci. Biobehav. Rev.* 118 (2020) 568–587, <https://doi.org/10.1016/j.neubiorev.2020.07.019>.
- [6] G. Tononi, M. Boly, M. Massimini, C. Koch, Integrated information theory: from consciousness to its physical substrate, *Nat. Rev. Neurosci.* 17 (2016) 450–461, <https://doi.org/10.1038/nrn.2016.44>.
- [7] G. Tononi, The integrated information theory of consciousness: an outline, in: M. Velmans, S. Schneider (Eds.), *The Blackwell Companion to Consciousness*, II, Blackwell Publisher, Malden, MA, 2017, pp. 243–256.
- [8] G.A. Mashour, P. Roelfsema, J.-P. Changeux, S. Dehaene, Conscious processing and the global neuronal workspace hypothesis, *Neuron* 105 (2020) 776–798, <https://doi.org/10.1016/j.neuron.2020.01.026>.
- [9] S. Dehaene, L. Charles, J.-R. King, S. Marti, Toward a computational theory of conscious processing, *Curr. Opin. Neurobiol.* 25 (2014) 76–84, <https://doi.org/10.1016/j.conb.2013.12.005>.
- [10] S. Dehaene, H. Lau, S. Kouider, What is consciousness, and could machines have it? *Science* (2017) <https://doi.org/10.1126/science.aan8871>.
- [11] V.A.F. Lamme, Visual functions generating conscious seeing, *Front. Psychol.* 11 (2020) 83, <https://doi.org/10.3389/fpsyg.2020.00083>.
- [12] V.A.F. Lamme, Can we see without knowing that we see? Challenges for two theories of consciousness 1, in: *Beyond Neural Correlates of Consciousness*, Routledge, 2020, pp. 62–86.
- [13] H. Lau, D. Rosenthal, Empirical support for higher-order theories of conscious awareness, *Trends Cogn. Sci.* 15 (2011) 365–373, <https://doi.org/10.1016/j.tics.2011.05.009>.
- [14] M. Michel, H. Lau, Higher-order theories do just fine, *Cogn. Neurosci.* 12 (2021) 77–78.
- [15] F. Crick, C. Koch, A framework for consciousness, *Nat. Neurosci.* 6 (2003) 119–126, <https://doi.org/10.1038/nn0203-119>.
- [16] K. Friston, The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11 (2010) 127, <https://doi.org/10.1038/nrn2787>.
- [17] J. Hohwy, *The Predictive Mind*, Oxford University Press, 2013, <https://doi.org/10.1093/acprof:oso/9780199682737.001.0001>.
- [18] A. Clark, *Surfing Uncertainty: Prediction, Action, and the Embodied Mind*, Oxford University Press, 2015.
- [19] M.S.A. Graziano, S. Kastner, Human consciousness and its relationship to social neuroscience: a novel hypothesis, *Cogn. Neurosci.* 2 (2011) 98–113, <https://doi.org/10.1080/17588928.2011.565121>.
- [20] M.S.A. Graziano, T.W. Webb, The attention schema theory: a mechanistic account of subjective awareness, *Front. Psychol.* 6 (2015) 500.
- [21] M.S.A. Graziano, The attention schema theory: a foundation for engineering artificial consciousness, *Front. Robot. AI* 4 (2017) 60.
- [22] C. Tallon-Baudry, F. Campana, H.D. Park, M. Babo-Rebello, The neural monitoring of visceral inputs, rather than attention, accounts for first-person perspective in conscious vision, *Cortex* 102 (2018) 139–149, <https://doi.org/10.1016/j.cortex.2017.05.019>.
- [23] D. Azzalini, I. Rebollo, C. Tallon-Baudry, Visceral signals shape brain dynamics and cognition, *Trends Cogn. Sci.* 23 (2019) 488–509, <https://doi.org/10.1016/j.tics.2019.03.007>.
- [24] A.A. Fingelkurts, A.A. Fingelkurts, C.F.H. Neves, Natural world physical, brain operational, and mind phenomenal space-time, *Phys. Life Rev.* 7 (2010) 195–249, <https://doi.org/10.1016/j.plrev.2010.04.001>.
- [25] R.L. Carhart-Harris, Serotonin, psychedelics and psychiatry, *World Psychiatry* 17 (2018) 358–359, <https://doi.org/10.1002/wps.20555>.
- [26] R.L. Carhart-Harris, R. Leech, P.J. Hellyer, M. Shanahan, A. Feilding, E. Tagliazucchi, D.R. Chialvo, D. Nutt, The entropic brain: a theory of conscious states informed by neuroimaging research with psychedelic drugs, *Front. Hum. Neurosci.* 8 (2014) 20.
- [27] G. Northoff, S. Wainio-Theberge, K. Evers, Is temporo-spatial dynamics the "common currency" of brain and mind? In *Quest of spatiotemporal neuroscience*, *Phys. Life Rev.* 33 (2020) 34–54, <https://doi.org/10.1016/j.plrev.2019.05.002>.
- [28] G. Northoff, Z. Huang, How do the brain's time and space mediate consciousness and its different dimensions? Temporo-spatial theory of consciousness (TTC), *Neurosci. Biobehav. Rev.* 80 (2017) 630–645, <https://doi.org/10.1016/j.neubiorev.2017.07.013>.
- [29] M.E. Raichle, M.A. Mintun, Brain work and brain imaging, *Annu. Rev. Neurosci.* 29 (2006) 449–476, <https://doi.org/10.1146/annurev.neuro.29.051605.112819>.
- [30] Z. Huang, J. Zhang, A. Longtin, G. Dumont, N.W. Duncan, J. Pokorny, P. Qin, R. Dai, F. Ferri, X. Weng, G. Northoff, Is There A Nonadditive Interaction between Spontaneous and Evoked Activity? Phase-dependence and Its Relation to the Temporal Structure of Scale-free Brain Activity, *Cereb. Cortex* 27 (2017) 1037–1059, <https://doi.org/10.1093/cercor/bhv288>.
- [31] S. Wainio-Theberge, A. Wolff, G. Northoff, Dynamic relationships between spontaneous and evoked electrophysiological activity, *Commun. Biol.* 4 (2021) 1–17.

- [32] A. Wolff, L. Chen, S. Tumati, M. Goleosorkhi, J. Gomez-Pilar, J. Hu, S. Jiang, Y. Mao, A. Longtin, G. Northoff, Prestimulus dynamics blend with the stimulus in neural variability quenching, *NeuroImage* 238 (2021), 118160.
- [33] M.D. Fox, A.Z. Snyder, J.M. Zacks, M.E. Raichle, Coherent spontaneous activity accounts for trial-to-trial variability in human evoked brain responses, *Nat. Neurosci.* 9 (2006) 23–25.
- [34] M.D. Fox, A.Z. Snyder, J.L. Vincent, M.E. Raichle, Intrinsic fluctuations within cortical systems account for intertrial variability in human behavior, *Neuron* 56 (2007) 171–184.
- [35] A. Arieli, A. Sterkin, A. Grinvald, A.D. Aertsen, Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses, *Science* 273 (1996) 1868–1871.
- [36] B.J. He, Spontaneous and task-evoked brain activity negatively interact, *J. Neurosci.* 33 (2013) 4672–4682.
- [37] S. Sadaghiani, R. Scheeringa, K. Lehongre, B. Morillon, A.-L. Giraud, A. Kleinschmidt, Intrinsic connectivity networks, alpha oscillations, and tonic alertness: a simultaneous electroencephalography/functional magnetic resonance imaging study, *J. Neurosci.* 30 (2010) 10243–10250.
- [38] S. Sadaghiani, J.-B. Poline, A. Kleinschmidt, M. D'Esposito, Ongoing dynamics in large-scale functional connectivity predict perception, *Proc. Natl. Acad. Sci.* 112 (2015) 8463–8468.
- [39] G. Hesselmann, C.A. Kell, E. Eger, A. Kleinschmidt, Spontaneous local variations in ongoing neural activity bias perceptual decisions, *Proc. Natl. Acad. Sci.* 105 (2008) 10984–10989.
- [40] C.S.Y. Benwell, C.F. Tagliabue, D. Veniero, R. Cecere, S. Savazzi, G. Thut, Prestimulus EEG power predicts conscious awareness but not objective visual performance, *ENEuro* 4 (2017), <https://doi.org/10.1523/ENEURO.0182-17.2017>.
- [41] C.S.Y. Benwell, A. Coldea, M. Harvey, G. Thut, Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity, *Eur. J. Neurosci. N/a* (2021), <https://doi.org/10.1111/ejn.15166>.
- [42] V. Romei, V. Brodbeck, C. Michel, A. Amedi, A. Pascual-Leone, G. Thut, Spontaneous fluctuations in posterior  $\alpha$ -band EEG activity reflect variability in excitability of human visual areas, *Cereb. Cortex* 18 (2008) 2010–2018.
- [43] A. Wolff, J. Gomez-Pilar, T. Nakao, G. Northoff, Interindividual neural differences in moral decision-making are mediated by alpha power and delta/theta phase coherence, *Sci. Rep.* 9 (2019) 4432, <https://doi.org/10.1038/s41598-019-40743-y>.
- [44] E. Podvalny, M.W. Flounders, L.E. King, T. Holroyd, B.J. He, A dual role of prestimulus spontaneous neural activity in visual object recognition, *Nat. Commun.* 10 (2019) 3910, <https://doi.org/10.1038/s41467-019-11877-4>.
- [45] H. Van Dijk, J.-M. Schoffelen, R. Oostenveld, O. Jensen, Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability, *J. Neurosci.* 28 (2008) 1816–1823.
- [46] S. Dehaene, J.P. Changeux, L. Naccache, J. Sackur, C. Sergent, Conscious, preconscious, and subliminal processing: a testable taxonomy, *Trends Cogn. Sci.* 10 (2006) 204–211, <https://doi.org/10.1016/j.tics.2006.03.007>.
- [47] W. Braun, Y. Matsuzaka, H. Mushiki, G. Northoff, A. Longtin, Non-additive activity modulation during a decision making task involving tactic selection, *Cogn. Neurodyn* (2021) 1–17.
- [48] M.M. Churchland, M.Y. Byron, J.P. Cunningham, L.P. Sugrue, M.R. Cohen, G. S. Corrado, W.T. Newsome, A.M. Clark, P. Hosseini, B.B. Scott, Stimulus onset quenches neural variability: a widespread cortical phenomenon, *Nat. Neurosci.* 13 (2010) 369–378.
- [49] E. Daniel, T. Meindertsma, A. Arazi, T.H. Donner, I. Dinstein, The relationship between trial-by-trial variability and oscillations of cortical population activity, *Sci. Rep.* 9 (2019) 1–11.
- [50] A. Arazi, N. Censor, I. Dinstein, Neural variability quenching predicts individual perceptual abilities, *J. Neurosci.* 37 (2017) 97–109.
- [51] A. Arazi, G. Gonen-Yaacovi, I. Dinstein, The magnitude of trial-by-trial neural variability is reproducible over time and across tasks in humans, *ENEuro* 4 (2017).
- [52] B. van Vugt, B. Dagnino, D. Vartak, H. Safaai, S. Panzeri, S. Dehaene, P. R. Roelfsema, The threshold for conscious report: signal loss and response bias in visual and frontal cortex, *Science* 360 (2018) 537–542.
- [53] A. Schurger, I. Sarigiannidis, L. Naccache, J.D. Sitt, S. Dehaene, Cortical activity is more stable when sensory stimuli are consciously perceived, *Proc. Natl. Acad. Sci. USA* 112 (2015) E2083–E2092, <https://doi.org/10.1073/pnas.1418730112>.
- [54] Z. Huang, X. Liu, G.A. Mashour, A.G. Hudetz, Timescales of Intrinsic BOLD signal dynamics and functional connectivity in pharmacologic and neuropathologic states of unconsciousness, *J. Neurosci.* 38 (2018) 2304–2317.
- [55] C.S.Y. Benwell, C. Keitel, M. Harvey, J. Gross, G. Thut, Trial-by-trial co-variation of pre-stimulus EEG alpha power and visuospatial bias reflects a mixture of stochastic and deterministic effects, *Eur. J. Neurosci.* 48 (2018) 2566–2584.
- [56] A.T. Baria, M.V. Centeno, M.E. Ghanousi, P.C. Chang, D. Proccisi, A.V. Apkarian, BOLD temporal variability differentiates wakefulness from anesthesia-induced unconsciousness, *J. Neurophysiol.* 119 (2018) 834–848.
- [57] C. Sergent, M. Corazzol, G. Labouret, F. Stockart, M. Wexler, J.-R. King, F. Drenth, D. Pressnitzer, Bifurcation in brain dynamics reveals a signature of conscious processing independent of report, *Nat. Commun.* 12 (2021) 1–19.
- [58] N. Block, Two neural correlates of consciousness, *Trends Cogn. Sci.* 9 (2005) 46–52, <https://doi.org/10.1016/j.tics.2004.12.006>.
- [59] G. Northoff, *Unlocking the Brain. Volume II: Consciousness*, Oxford University Press, New York, 2014. (<https://doi.org/10.1093/acprof:oso/9780199826995.001.0001>).
- [60] S. Glim, A. Ries, C. Sorg, A.M. Wohlschläger, The temporal evolution of pre-stimulus slow cortical potentials is associated with an upcoming stimulus' access to visual consciousness, *Conscious. Cogn.* 84 (2020), 102993, <https://doi.org/10.1016/j.concog.2020.102993>.
- [61] G. Northoff, S. Wainio-Theberge, K. Evers, Spatiotemporal neuroscience—what is it and why we need it, *Phys. Life Rev.* 33 (2020) 78–87.
- [62] F. Zilio, *Consciousness and World. A Neurophilosophical and Neuroethical Account*, Edizioni ETS, Pisa, 2020.
- [63] J.F. Storm, M. Boly, A.G. Casali, M. Massimini, U. Olcese, C.M.A. Pennartz, M. Wilke, Consciousness regained: disentangling mechanisms, brain systems, and behavioral responses, *J. Neurosci.* 37 (2017) 10882–10893, <https://doi.org/10.1523/JNEUROSCI.1838-17.2017>.
- [64] C. Koch, M. Massimini, M. Boly, G. Tononi, Posterior and anterior cortex — where is the difference that makes the difference? *Nat. Rev. Neurosci.* 17 (2016) 666, <https://doi.org/10.1038/nrn.2016.105>.
- [65] N. Block, On a confusion about a function of consciousness, *Behav. Brain Sci.* 18 (1995) 227–247, <https://doi.org/10.1017/S0140525X00038188>.
- [66] M. Overgaard, Phenomenal consciousness and cognitive access, *Philos. Trans. R. Soc. B Biol. Sci.* 373 (2018), 20170353, <https://doi.org/10.1098/rstb.2017.0353>.
- [67] J. Aru, T. Bachmann, W. Singer, L. Melloni, Distilling the neural correlates of consciousness, *Neurosci. Biobehav. Rev.* 36 (2012) 737–746, <https://doi.org/10.1016/j.neubiorev.2011.12.003>.
- [68] P. Schröder, T. Nierhaus, F. Blankenburg, Dissociating perceptual awareness and postperceptual processing: the P300 is not a reliable marker of somatosensory target detection, *J. Neurosci.* 41 (2021) 4686–4696, <https://doi.org/10.1523/JNEUROSCI.2950-20.2021>.
- [69] G. Northoff, What the brain's intrinsic activity can tell us about consciousness? A tri-dimensional view, *Neurosci. Biobehav. Rev.* (2013), <https://doi.org/10.1016/j.neubiorev.2012.12.004>.
- [70] G. Northoff, W.D. Heiss, Why is the distinction between neural predispositions, prerequisites, and correlates of the level of consciousness clinically relevant?: functional brain imaging in coma and vegetative state, *Stroke* 46 (2015) 1147–1151, <https://doi.org/10.1161/STROKEAHA.114.007969>.
- [71] T. Bayne, On the axiomatic foundations of the integrated information theory of consciousness, *Neurosci. Conscious.* 2018 (2018), <https://doi.org/10.1093/nc/niy007>.
- [72] B. Merker, K. Williford, D. Rudrauf, The integrated information theory of consciousness: a case of mistaken identity, *Behav. Brain Sci.* (2021) 1–72, <https://doi.org/10.1017/S0140525X21000881>.
- [73] C.J. Honey, T. Thesen, T.H. Donner, L.J. Silbert, C.E. Carlson, O. Devinsky, W. K. Doyle, N. Rubin, D.J. Heeger, U. Hasson, Slow cortical dynamics and the accumulation of information over long timescales, *Neuron* 76 (2012) 423–434, <https://doi.org/10.1016/j.neuron.2012.08.011>.
- [74] J.D. Murray, A. Bernacchia, D.J. Freedman, R. Romo, J.D. Wallis, X. Cai, C. Padoa-Schioppa, T. Pasternak, H. Seo, D. Lee, X.J. Wang, A hierarchy of intrinsic timescales across primate cortex, *Nat. Neurosci.* 17 (2014) 1661–1663, <https://doi.org/10.1038/nn.3862>.
- [75] A. Wolff, N. Berberian, M. Goleosorkhi, J. Gomez-Pilar, F. Zilio, G. Northoff, Intrinsic neural timescales: temporal integration and segregation, *Trends Cogn. Sci.* 26 (2022) 159–173, <https://doi.org/10.1016/j.tics.2021.11.007>.
- [76] M. Goleosorkhi, J. Gomez-Pilar, S. Tumati, M. Fraser, G. Northoff, Temporal hierarchy of intrinsic neural timescales converges with spatial core-periphery organization, *Commun. Biol.* 4 (2021) 277, <https://doi.org/10.1038/s42003-021-01785-z>.
- [77] U. Hasson, J. Chen, C.J. Honey, Hierarchical process memory: memory as an integral component of information processing, *Trends Cogn. Sci.* 19 (2015) 304–313, <https://doi.org/10.1016/j.tics.2015.04.006>.
- [78] L.L. Gollo, A. Zalesky, R. Matthew Hutchison, M. Van Den Heuvel, M. Breakpear, Dwelling quietly in the rich club: brain network determinants of slow cortical fluctuations, *Philos. Trans. R. Soc. B Biol. Sci.* 370 (2015), 20140165, <https://doi.org/10.1098/rstb.2014.0165>.
- [79] L.L. Gollo, J.A. Roberts, L. Cocchi, Mapping how local perturbations influence systems-level brain dynamics, *NeuroImage* 160 (2017) 97–112, <https://doi.org/10.1016/j.neuroimage.2017.01.057>.
- [80] J. Chen, U. Hasson, C.J. Honey, Processing timescales as an organizing principle for primate cortex, *Neuron* 88 (2015) 244–246, <https://doi.org/10.1016/j.neuron.2015.10.010>.
- [81] Y. Yeshurun, M. Nguyen, U. Hasson, Amplification of local changes along the timescale processing hierarchy, *Proc. Natl. Acad. Sci. USA* 114 (2017) 9475–9480, <https://doi.org/10.1073/pnas.1701652114>.
- [82] G. Deco, J. Cruzat, M.L. Kringelbach, Brain songs framework used for discovering the relevant timescale of the human brain, *Nat. Commun.* 10 (2019) 583, <https://doi.org/10.1038/s41467-018-08186-7>.
- [83] M. Goleosorkhi, J. Gomez-Pilar, F. Zilio, N. Berberian, A. Wolff, M.C.E. Yagoub, G. Northoff, The brain and its time: intrinsic neural timescales are key for input processing, *Commun. Biol.* 4 (2021) 1–16, <https://doi.org/10.1038/s42003-021-02483-6>.
- [84] R. Chaudhuri, K. Knoblauch, M.A. Gariel, H. Kennedy, X.J. Wang, A large-scale circuit mechanism for hierarchical dynamical processing in the primate cortex, *Neuron* 88 (2015) 419–431, <https://doi.org/10.1016/j.neuron.2015.09.008>.
- [85] R.V. Raut, A.Z. Snyder, M.E. Raichle, Hierarchical dynamics as a macroscopic organizing principle of the human brain, *Proc. Natl. Acad. Sci.* 117 (2020) 20890–20897, <https://doi.org/10.1073/pnas.2003383117>.
- [86] T. Ito, L.J. Hearn, M.W. Cole, A cortical hierarchy of localized and distributed processes revealed via dissociation of task activations, connectivity changes, and intrinsic timescales, *NeuroImage* 221 (2020), 117141.
- [87] D.S. Margulies, S.S. Ghosh, A. Goulas, M. Falkiewicz, J.M. Huntenburg, G. Langs, G. Bezzin, S.B. Eickhoff, F.X. Castellanos, M. Petrides, E. Jefferies, J. Smallwood,

- Situating the default-mode network along a principal gradient of macroscale cortical organization, *Proc. Natl. Acad. Sci.* 113 (2016) 12574–12579, <https://doi.org/10.1073/pnas.1608282113>.
- [88] J.M. Huntenburg, P.-L. Bazin, D.S. Margulies, Large-scale gradients in human cortical organization, *Trends Cogn. Sci.* 22 (2018) 21–31, <https://doi.org/10.1016/j.tics.2017.11.002>.
- [89] Y. Yeshurun, M. Nguyen, U. Hasson, The default mode network: where the idiosyncratic self meets the shared social world, *Nat. Rev. Neurosci.* 22 (2021) 181–192.
- [90] J. Chen, Y.C. Leong, C.J. Honey, C.H. Yong, K.A. Norman, U. Hasson, Shared memories reveal shared structure in neural activity across individuals, *Nat. Neurosci.* 20 (2017) 115–125, <https://doi.org/10.1038/nn.4450>.
- [91] G. Northoff, *Unlocking the Brain*, in: *Coding*, 1, Oxford University Press, 2014, <https://doi.org/10.1093/acprof:oso/9780199826988.001.0001>.
- [92] Z. Huang, V. Tarnal, P.E. Vlisides, E.L. Janke, A.M. McKinney, P. Picton, G. A. Mashour, A.G. Hudetz, Asymmetric neural dynamics characterize loss and recovery of consciousness, *NeuroImage* 236 (2021), 118042, <https://doi.org/10.1016/j.neuroimage.2021.118042>.
- [93] F. Zilio, J. Gomez-Pilar, S. Cao, J. Zhang, D. Zang, Z. Qi, J. Tan, T. Hiroimi, X. Wu, S. Fogel, Z. Huang, M.R. Hohmann, T. Fomina, M. Synofzik, M. Grosse-Wentrup, A.M. Owen, G. Northoff, Are intrinsic neural timescales related to sensory processing? Evidence from abnormal behavioral states, *NeuroImage* 226 (2021), 117579, <https://doi.org/10.1016/j.neuroimage.2020.117579>.
- [94] A.F.T. Borges, A.-L. Giraud, H.D. Mansvelder, K. Linkenkaer-Hansen, Scale-free amplitude modulation of neuronal oscillations tracks comprehension of accelerated speech, *J. Neurosci.* 38 (2018) 710–722.
- [95] K.D. Himberger, H.Y. Chien, C.J. Honey, Principles of Temporal Processing Across the Cortical Hierarchy, *Neuroscience* 389 (2018) 161–174, <https://doi.org/10.1016/j.neuroscience.2018.04.030>.
- [96] G. Northoff, “Common currency” between experience and brain: spatiotemporal psychopathology of the resting state in depression, *Major Depress Disord. Rethink. Underst. Recent Discov.* (2021) 71–84.
- [97] G. Northoff, K.E. Sandsten, J. Nordgaard, T.W. Kjaer, J. Parnas, The self and its prolonged intrinsic neural timescale in schizophrenia, *Schizophr. Bull.* (2020), <https://doi.org/10.1093/schbul/sbaa083>.
- [98] L. Kent, M. Wittmann, Time consciousness: the missing link in theories of consciousness, *Neuroscience of Consciousness*. 2021 (2021) niab011.
- [99] D.R. Chialvo, Emergent complex neural dynamics, *Nat. Phys.* 6 (2010) 744–750, <https://doi.org/10.1038/nphys1803>.
- [100] B.J. He, J.M. Zempel, A.Z. Snyder, M.E. Raichle, The temporal structures and functional significance of scale-free brain activity, *Neuron* 66 (2010) 353–369, <https://doi.org/10.1016/j.neuron.2010.04.020>.
- [101] B.J. He, Scale-free brain activity: past, present, and future, *Trends Cogn. Sci.* 18 (2014) 480–487, <https://doi.org/10.1016/j.tics.2014.04.003>.
- [102] J. Zhang, Z. Huang, S. Tumat, G. Northoff, Rest-task modulation of fMRI-derived global signal topography is mediated by transient coactivation patterns, *PLOS Biol.* 18 (2020), e3000733, <https://doi.org/10.1371/journal.pbio.3000733>.
- [103] S. Tanabe, Z. Huang, J. Zhang, Y. Chen, S. Fogel, J. Doyon, J. Wu, J. Xu, J. Zhang, P. Qin, Altered global brain signal during physiologic, pharmacologic, and pathologic states of unconsciousness in humans and rats, *Anesthesiology* 132 (2020) 1392–1406.
- [104] Z. Huang, N. Obara, H. (Hap) Davis, J. Pokorny, G. Northoff, The temporal structure of resting-state brain activity in the medial prefrontal cortex predicts self-consciousness, *Neuropsychologia* 82 (2016) 161–170, <https://doi.org/10.1016/j.neuropsychologia.2016.01.025>.
- [105] G. Hahn, G. Zamora-López, L. Uhrig, E. Tagliazucchi, H. Laufs, D. Mantini, M. L. Kringelbach, B. Jarraya, G. Deco, Signature of consciousness in brain-wide synchronization patterns of monkey and human fMRI signals, *NeuroImage* 226 (2021), 117470.
- [106] Z. Huang, J. Zhang, A. Longtin, G. Dumont, N.W. Duncan, J. Pokorny, P. Qin, R. Dai, F. Ferri, X. Weng, G. Northoff, Is there a nonadditive interaction between spontaneous and evoked activity? phase-dependence and its relation to the temporal structure of scale-free brain activity, *Cereb. Cortex* 27 (2017) 1037–1059, <https://doi.org/10.1093/cercor/bhv288>.
- [107] K. Linkenkaer-Hansen, V.V. Nikouline, J.M. Palva, R.J. Ilmoniemi, Long-range temporal correlations and scaling behavior in human brain oscillations, *J. Neurosci.: Off. J. Soc. Neurosci.* 21 (2001) 1370–1377.
- [108] R. Hardstone, S.-S. Poil, G. Schiavone, R. Jansen, V.V. Nikulin, H.D. Mansvelder, K. Linkenkaer-Hansen, Detrended fluctuation analysis: a scale-free view on neuronal oscillations, *Front. Physiol.* 3 (2012) 450.
- [109] E. Tagliazucchi, L. Roseman, M. Kaelin, C. Orban, S.D. Muthukumaraswamy, K. Murphy, H. Laufs, R. Leech, J. McGonigle, N. Crossley, E. Bullmore, T. Williams, M. Bolstridge, A. Feilding, D.J. Nutt, R. Carhart-Harris, Increased global functional connectivity correlates with LSD-induced ego dissolution, *Curr. Biol.* 26 (2016) 1043–1050, <https://doi.org/10.1016/j.cub.2016.02.010>.
- [110] E. Tagliazucchi, F. von Wegner, A. Morzelewski, V. Brodbeck, S. Borisov, K. Jahnke, H. Laufs, Large-scale brain functional modularity is reflected in slow electroencephalographic rhythms across the human non-rapid eye movement sleep cycle, *NeuroImage* 70 (2013) 327–339, <https://doi.org/10.1016/j.neuroimage.2012.12.073>.
- [111] J. Zhang, Z. Huang, Y. Chen, J. Zhang, D. Ghinda, Y. Nikolova, J. Wu, J. Xu, W. Bai, Y. Mao, Z. Yang, N. Duncan, P. Qin, H. Wang, B. Chen, X. Weng, G. Northoff, Breakdown in the temporal and spatial organization of spontaneous brain activity during general anesthesia, *Hum. Brain Mapp.* 39 (2018) 2035–2046, <https://doi.org/10.1002/hbm.23984>.
- [112] J.D. Lendner, R.F. Helfrich, B.A. Mander, L. Romundstad, J.J. Lin, M.P. Walker, P. G. Larsson, R.T. Knight, An electrophysiological marker of arousal level in humans, *Elife* 9 (2020), e55092.
- [113] G. Northoff, S. Tumat, “Average is good, extremes are bad” – non-linear inverted U-shaped relationship between neural mechanisms and functionality of mental features, *Neurosci. Biobehav. Rev.* 104 (2019) 11–25, <https://doi.org/10.1016/j.neubiorev.2019.06.030>.
- [114] T. Bayne, J. Hohwy, A.M. Owen, Are there levels of consciousness? *Trends Cogn. Sci.* 20 (2016) 405–413, <https://doi.org/10.1016/j.tics.2016.03.009>.
- [115] T. Bayne, The unity of consciousness, Oxford University Press, 2010.
- [116] G. Northoff, *The spontaneous. Brain: From the Mind–Body to the World–Brain Problem*, The MIT Press, Cambridge, MA, 2018.
- [117] S. Kripke, *Naming and Necessity*, Harvard University Press, 1980.
- [118] T. Nagel, What is it like to be a bat? *Philos. Rev.* 83 (1974) 435, <https://doi.org/10.2307/2183914>.
- [119] T. Nagel, Conceiving the impossible and the mind-body problem, *Philosophy* 73 (1998) 337–352, <https://doi.org/10.1017/s0031819198000035>.
- [120] K.J. Friston, R. Rosch, T. Parr, C. Price, H. Bowman, Deep temporal models and active inference, *Neurosci. Biobehav. Rev.* 90 (2018) 486–501.
- [121] S.J. Kiebel, J. Daunizeau, K.J. Friston, A hierarchy of time-scales and the brain, *PLoS Comput. Biol.* 4 (2008), 1000209, <https://doi.org/10.1371/journal.pcbi.1000209>.
- [122] S.J. Kiebel, J. Daunizeau, K.J. Friston, Perception and hierarchical dynamics, *Front. Neuroinformatics* 3 (2009) 20.
- [123] A.K. Seth, K.J. Friston, Active interoceptive inference and the emotional brain, *Philos. Trans. R. Soc. B Biol. Sci.* 371 (2016), 20160007.
- [124] L. Mudrik, N. Faivre, C. Koch, Information integration without awareness, *Trends Cogn. Sci.* 18 (2014) 488–496, <https://doi.org/10.1016/j.tics.2014.04.009>.
- [125] G. Northoff, N. Tsuchiya, H. Saigo, Mathematics and the brain: a category theoretical approach to go beyond the neural correlates of consciousness, *Entropy* 21 (2019) 1234, <https://doi.org/10.3390/e21121234>.
- [126] S. Dehaene, J.P. Changeux, L. Naccache, The global neuronal workspace model of conscious access: from neuronal architectures to clinical applications, in: S. Dehaene, Y. Christen (Eds.), *Characterizing Consciousness: From Cognition to the Clinic?*, Springer, 2011, [https://doi.org/10.1007/978-3-642-18015-6\\_4](https://doi.org/10.1007/978-3-642-18015-6_4).
- [127] S. Tumat, M.P. Paulus, G. Northoff, Out-of-step: brain-heart desynchronization in anxiety disorders, *Mol. Psychiatry* 26 (2021) 1–12.
- [128] M. Oizumi, L. Albantakis, G. Tononi, From the phenomenology to the mechanisms of consciousness: integrated information theory 3.0, *PLoS Comput. Biol.* 10 (2014) 1–25, <https://doi.org/10.1371/journal.pcbi.1003588>.
- [129] M. Boly, M. Massimini, N. Tsuchiya, B.R. Postle, C. Koch, G. Tononi, Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? clinical and neuroimaging evidence, *J. Neurosci.* 37 (2017) 9603–9613, <https://doi.org/10.1523/JNEUROSCI.3218-16.2017>.
- [130] R.L. Carhart-Harris, K.J. Friston, REBUS and the anarchic brain: toward a unified model of the brain action of psychedelics, *Pharmacol. Rev.* 71 (2019) 316–344.
- [131] F. Zilio, A sketch of a Kripkean theory of consciousness, *Universa. Recensioni di filosofia* 10 (3) (2021) 273–292, <https://doi.org/10.14658/pupj-urdf-2021-3-15>.