

## Research



**Cite this article:** Northoff G, Klar P, Bein M, Safron A. 2023 As without, so within: how the brain's temporo-spatial alignment to the environment shapes consciousness. *Interface Focus* **13**: 20220076.  
<https://doi.org/10.1098/rsfs.2022.0076>

Accepted: 2 March 2023

### Subject Areas:

systems biology

### Keywords:

consciousness, temporo-spatial dynamics, spatio-temporal neuroscience

### Author for correspondence:

Georg Northoff  
e-mail: [georg.northoff@theroyal.ca](mailto:georg.northoff@theroyal.ca)

<sup>†</sup>These authors contributed equally.

# As without, so within: how the brain's temporo-spatial alignment to the environment shapes consciousness

Georg Northoff<sup>1,2,3,†</sup>, Philipp Klar<sup>4,†</sup>, Magnus Bein<sup>5</sup> and Adam Safron<sup>6,7,8</sup>

<sup>1</sup>Mind, Brain Imaging and Neuroethics Research Unit, The Royal's Institute of Mental Health Research, University of Ottawa, Ottawa, ON, Canada K1Z 7K4

<sup>2</sup>Mental Health Centre, Zhejiang University School of Medicine, Hangzhou 310053, People's Republic of China

<sup>3</sup>Centre for Cognition and Brain Disorders, Hangzhou Normal University, Hangzhou 310053, People's Republic of China

<sup>4</sup>Medical Faculty, C. & O. Vogt-Institute for Brain Research, Heinrich Heine University of Düsseldorf, 40225 Düsseldorf, Germany

<sup>5</sup>Department of Biology and Department of Psychiatry, McGill University, Quebec, Canada H3A 0G4

<sup>6</sup>Center for Psychedelic and Consciousness Research, Department of Psychiatry & Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD 21205, USA

<sup>7</sup>Cognitive Science Program, Indiana University, Bloomington, IN 47405, USA

<sup>8</sup>Institute for Advanced Consciousness Studies, Santa Monica, CA 90403, USA

MB, 0000-0002-3187-5702; AS, 0000-0002-3102-7623

Consciousness is constituted by a structure that includes contents as foreground and the environment as background. This structural relation between the experiential foreground and background presupposes a relationship between the brain and the environment, often neglected in theories of consciousness. The temporo-spatial theory of consciousness addresses the brain–environment relation by a concept labelled ‘temporo-spatial alignment’. Briefly, temporo-spatial alignment refers to the brain’s neuronal activity’s interaction with and adaption to interoceptive bodily and exteroceptive environmental stimuli, including their symmetry as key for consciousness. Combining theory and empirical data, this article attempts to demonstrate the yet unclear neuro-phenomenal mechanisms of temporo-spatial alignment. First, we suggest three neuronal layers of the brain’s temporo-spatial alignment to the environment. These neuronal layers span across a continuum from longer to shorter timescales. (i) The background layer comprises longer and more powerful timescales mediating topographic-dynamic similarities between different subjects’ brains. (ii) The intermediate layer includes a mixture of medium-scaled timescales allowing for stochastic matching between environmental inputs and neuronal activity through the brain’s intrinsic neuronal timescales and temporal receptive windows. (iii) The foreground layer comprises shorter and less powerful timescales for neuronal entrainment of stimuli temporal onset through neuronal phase shifting and resetting. Second, we elaborate on how the three neuronal layers of temporo-spatial alignment correspond to their respective phenomenal layers of consciousness. (i) The inter-subjectively shared contextual background of consciousness. (ii) An intermediate layer that mediates the relationship between different contents of consciousness. (iii) A foreground layer that includes specific fast-changing contents of consciousness. Overall, temporo-spatial alignment may provide a mechanism whose different neuronal layers modulate corresponding phenomenal layers of consciousness. Temporo-spatial alignment can provide a bridging principle for linking physical-energetic (free energy), dynamic (symmetry), neuronal (three layers of distinct time–space scales) and phenomenal (form featured by background–intermediate–foreground) mechanisms of consciousness.

## 1. Introduction

Consciousness is a phenomenon whose corresponding neuronal mechanisms and connections to various phenomenal aspects of experience remain unclear.

We experience single contents in the foreground of consciousness, while the environment or context constitutes the background of consciousness. A paradigmatic example is single trees that we perceive relative to the forest as a whole [1,2]. Many neuroscientific theories of consciousness focus on the foreground contents of consciousness, and the neuronal mechanisms of the contextual background remain underinvestigated or completely neglected (see [3,4]). Based on the mechanism of temporo-spatial alignment [1,5], our principal aim is to establish a conceptual three-layer neuro-phenomenal model of the structural foreground–background nature of consciousness.

Among the various neuroscientific theories, the temporo-spatial theory of consciousness (TTC) stands out in that it is one of the few—see also integrated world modeling theory [6,7]—that considers the relationship of the brain to the environment as a key feature of consciousness [1,2,8]. In that vein, the TTC proposes a particular mechanism, notably ‘temporo-spatial alignment’ or alignment in short. Alignment is a brain mechanism by which the brain adapts and coordinates its neuronal activity’s dynamics to interoceptive bodily and exteroceptive environmental dynamics.

Alignment concerns how the brain’s spontaneous activity actively, rather than passively [9], processes and encodes extrinsic inputs (see box 1 in [10] for an encompassing notion of inputs). Spontaneous activity refers to the brain’s ongoing intrinsic activity, already discovered and empirically demonstrated in insects and animals by the German physiologist Erich von Holst (1908–1962). Back in the 1930s, the psychological paradigm of behaviourism explained the locomotor or movement behaviour of organisms via reflex chains where environmental stimuli drive and govern the animal’s motor outputs. By surgically cutting distinct nerve connections in insects and animals, von Holst demonstrated that the organisms maintained locomotion or motor outputs, implying that the nervous system produces intrinsic activity irrespective of environmental stimuli or inputs [11]. This observation shifted the brain’s role from a passive transmitter of extrinsic impulses to an active intrinsic organization requiring scientific investigation.

Since the introduction of functional neuroimaging from 1990 to 1992 [12], the investigation of the brain’s spontaneous activity nonetheless lagged many years behind. The first so-called resting-state functional magnetic resonance imaging (fMRI) study by Biswal *et al.* [13] investigated functional connectivity at rest, which occurred in 1995. It nonetheless took another 6 years until 2001, when Raichle *et al.* [14] published their discovery of the resting-state’s default-mode network, until the investigation of the brain’s spontaneous activity via the so-called resting state spread into a mainstream operational research paradigm in fMRI. Consequently, the resting state represents an operational term referring to the empirical investigation of the brain’s intrinsic spontaneous activity, such as via fMRI, without applying specific stimuli or tasks to the subjects. Conversely, the brain’s spontaneous activity describes ongoing and ever-lasting intrinsic brain activity prevalent before, during and after specific environmental stimuli or tasks.

The key assumption is that input processing is strongly shaped by the brain’s intrinsic temporal dynamic and spatial topography hence the name temporo-spatial alignment. Applying various topographic and especially dynamic measures, the neuroimaging modalities of electroencephalography (EEG), magnetoencephalography (MEG) and fMRI,

the TTC is obtaining empirical evidence in support of the alignment hypothesis [15–18].

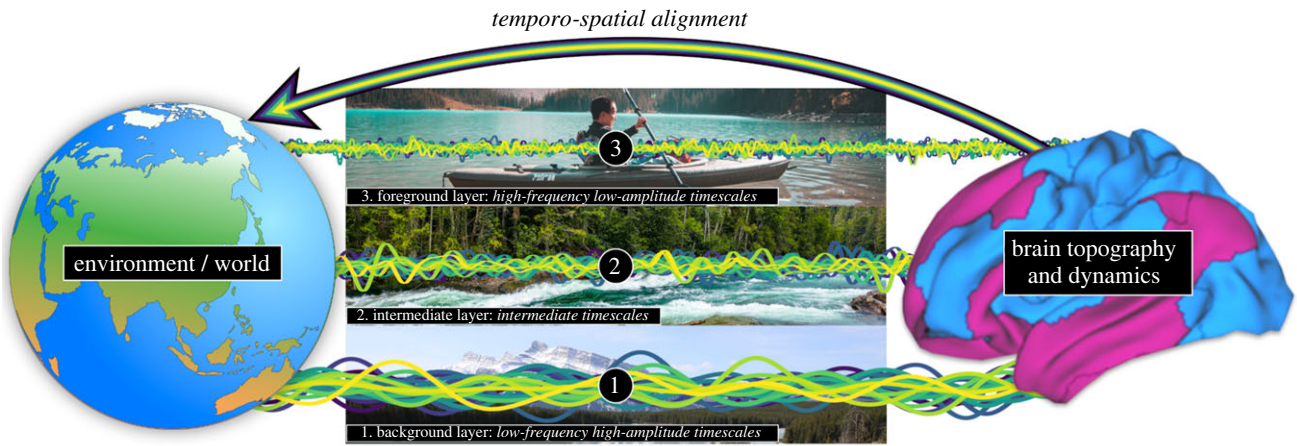
## 1.1. Goal and aims: three-layer structure of the brain’s temporo-spatial alignment shapes phenomenal layers of consciousness

We introduce a conceptual model of alignment where the brain’s shorter timescales or faster frequencies (those related to extrinsic stimulus-induced activity) are nested into and dependent on longer timescales or slower frequencies (primarily provided by intrinsic and ongoing spontaneous activity). We theorize that three distinct neuronal timescales of brain activity correspond to three temporal layers that mediate foreground–background perception in consciousness (see Gestalt psychology for the foreground–background structure [19,20]) as follows. The following hypotheses comprise the three-layer temporal model of alignment:

1. The neuronal activity’s longest timescales, i.e. the slowest frequencies with the highest amplitude and longest phase cycles, drive the process of the background structure of consciousness, such as the scenery of the environmental context (section ‘Background layer: shared cortical topography and neuronal dynamics across subjects’).
2. An intermediate range of intrinsic neuronal timescales (INT) and task-related temporal receptive windows (TRWs) bridge the two other layers, constituting the changing contents of consciousness (section ‘Intermediate layer: stochastic alignment of neuronal to environmental dynamics’).
3. The shortest timescales, i.e. the fastest frequencies with the lowest amplitude and shortest phase cycles, are associated with the foreground of experience, such as the constantly varying contents of social interaction with another person requiring rapid adaptations (section ‘Foreground layer: entrainment as phase-locking of neuronal activity by exteroceptive and interoceptive stimuli’).

This three-layer temporal model of alignment opens the possibility to empirically measure environmental dynamics (e.g. the time-series of music or fluctuations of other sensory stimuli), cognitive dynamics (via psychological and behavioural tests recording associated time-series data) [21,22], and neuronal dynamics (via the neuroimaging modalities of EEG, MEG and fMRI). Environmental, cognitive–behavioural and neuronal time-series share dynamics, such as fractal pink noise [15,23–27]. These shared dynamics between environmental, cognitive–behavioural and neuronal levels consequently provide a bridge principle that we call ‘common currency’ allowing the scientific environment–brain linkage for consciousness and behaviour [28,29].

After briefly introducing the concept of alignment in connection to the three timescale layers we visualize in figure 1, the following three subsections elaborate on empirical findings supporting the nervous system’s alignment to the social and natural environment, focusing on the neuronal perspective of the three-layer model. The phenomenal perspective on the three-layer model taking consciousness into consideration follows after introducing the neuronal layers. Finally, we present a brief discussion regarding the implications of



**Figure 1.** Temporo-spatial alignment between environment and brain in a three-layer model. Alignment describes the interaction of the brain's ongoing spontaneous activity with interoceptive bodily and exteroceptive environmental stimuli. The (1) background layer refers to inter-individually shared cortical topography and neuronal dynamics of low-frequency high-amplitude timescales. The (2) intermediate layer refers to a stochastic alignment of INT to environmental dynamics measurable by stimuli- or task-related TRWs. Finally, the (3) foreground layer of high-frequency low-amplitude timescales considers entrainment as phase-locking of neuronal activity by exteroceptive and interoceptive stimuli.

temporo-spatial alignment for other dynamic concepts, such as the free energy principle and symmetry/antisymmetry.

## 2. Temporo-spatial alignment: three neuronal layers of the environment–brain relation

This section aims to link the three conceptualized layers of the brain's neuronal activity ranging from (i) low-frequency high-amplitude timescales associated with the conscious background over (ii) an intermediate layer bridging the first layer with (iii) high-frequency low-amplitude timescales associated with the foreground of consciousness. We propose that these three layers constitute consciousness by modulating various timescales, as in distinct frequency bands of the nervous system, by degrees of symmetry to the environment and its corresponding signals.

### 2.1. Background layer: shared cortical topography and neuronal dynamics across subjects

Functional MRI studies of the brain's ongoing spontaneous activity, often represented by connectivity analyses of the resting state, yielded tremendous evidence for shared topographic network activity across individuals [30,31]. Irrespective of specific stimuli or tasks, human subjects also share functional networks identified by their temporal dynamics, such as via the BOLD's significant temporal correlation across brain regions, in the infra-slow frequency band (0.01–0.1 Hz) of fMRI [32]. Spontaneous BOLD fluctuations are similar between individuals, reflecting the brain's intrinsic functional architecture shared between populations.

#### 2.1.1. Inter-subjective correlation confirms similarity in topography and dynamics

More recently, a novel method labelled inter-subject correlation (ISC) emerged. ISC aims to investigate shared functional states between the brain's topography of the different subjects [33,34]. This method goes beyond functional connectivity analyses that only focus on the temporal correlation between voxels or regions primarily on an intra-

individual level, rather than comparing inter-individually. fMRI studies applying ISC measure responses to naturalistic stimuli, such as movies, stories or auditory narratives [35], where the responses of one brain can even predict responses in other subjects' brains that participated in the same naturalistic paradigm [36,37]. Hasson *et al.* [36] observed significantly shared fMRI voxel-by-voxel inter-individual brain dynamics in viewers of a short movie and found that viewers' brain dynamics could predict those of others. Recent electrophysiological EEG and MEG recordings also show shared spatio-temporal brain dynamics between different subjects [38–40].

The ISC method has found the most application with naturalistic stimuli while neglecting inter-individually shared dynamics of the brain's resting state irrespective of stimuli or tasks. Addressing this gap, recent (i) fMRI (Tumati *et al.* unpublished) and (ii) EEG (unpublished) studies by our group investigated ISC also in the resting state next to task states. We will briefly present the results of both studies in the following, starting with the fMRI analysis.

##### 2.1.1.1. Functional magnetic resonance imaging study

The fMRI study (Tumati *et al.* unpublished) used 3 T data from the Human Connectome Project S1200 release [41] of 974 healthy young subjects obtained from rest and task recordings (TR = 0.72 s). Functional scan acquisition comprised 2 days. On day one, two resting-state scans (14 min 52 s) and three task states ('working memory'; 'gambling'; and 'motor') were acquired. On day two, the two resting-state scans were repeated, including four task states ('emotion'; 'language'; 'relational'; and 'social'). The analysis then parcellated the functional recordings into 360 cortical regions based on the multimodal parcellation atlas [42] to obtain region-of-interest-based mean time-series for each region and in rest and task states.

To investigate subjects' similarity in their brains' topography, the authors assessed the ISC by computing the BOLD's time-series standard deviation (s.d.) for each of the 360 regions.

Healthy physiological processes of the human body, such as heart-rate variability [43], blood flow [44], volumes of breaths [45] and fMRI recordings of human brain activity



under conscious wakefulness [15,46] require a mixture between regularity and variability. The BOLD's s.d. is the square root of the variance and represents a straightforward measurement of the signal's variability. If the BOLD signal's variability has functional implications for consciousness, one expects a substantially shared s.d. across healthy subjects. Conversely, subjects with psychiatric disorders, such as schizophrenia, are expected to show a reduced degree of ISC of the s.d. It is expected that various psychiatric manifestations of schizophrenia on the level of experience and behaviour correspond to the neurodiversity of temporospatial patterns of brain activity, therefore reducing the ISC of the s.d.

Tumati *et al.* (unpublished) hypothesized that (i) the resting-state intra-regional s.d. is topographically shared across the 2 scanning days' recordings within and between subjects and that (ii) the relation between rest and task states s.d. topographies is similar, hence showing a rest-to-task carry-over effect of s.d. topography.

The findings yielded the following results. First, the resting-state s.d. topography showed high overlap across healthy subjects. The within-subject shared s.d. topography between days one and two yielded a high mean correlation across subjects ( $r=0.84$ ), indicating similar intra-individual s.d. topography. The between-subject shared s.d. topography for day one ( $r=0.74$ ) and day two ( $r=0.74$ ) yielded high mean correlations across subjects. Second, the authors analysed the s.d. topography in task states. As hypothesized, the s.d. topography in task states showed high between-subject correlations with the highest mean correlation ( $r=0.74$ ) in the 'relational' (relational contrast) and 'social' (theory of mind contrast) tasks. The results demonstrate that the observed s.d. topography, which showed high within- and between-subject correlations in rest and task states, provides evidence for a more universal, that is, the inter-subjective pattern of the brain's functional organization: the structure is intrinsic to the brain and holds for all subjects, rather than being specific for particular subjects. Figure 2 shows the similar or shared topography between subjects across days in the spontaneous activity during the resting state.

### 2.1.1.2. Electroencephalography study

The EEG study [47] also used spatial ISC methods, aiming to measure the potentially disrupted inter-individual dynamical and spatial distribution of the brain's neuronal activity in the resting state of clinical patient groups with schizophrenia and depression and with healthy control groups. The study analysed three EEG datasets. The first schizophrenia dataset comprised 34 subjects with schizophrenia (mean age/s.d. = 22.12/3.93) and 35 healthy controls (mean age/s.d. = 24.06/3.24) with a recording time of 5 min. The second schizophrenia dataset comprised 24 subjects with schizophrenia (mean age/s.d. = 45.5/8.91) and 25 healthy controls (mean age/s.d. = 45.88/15.79) with a recording time of 3 min. The third depression dataset comprised 44 depressed subjects (mean age/s.d. = 18.7/1.12) with high Beck depression inventory scores and 74 healthy controls (mean age/s.d. = 18.99/1.22) with a recording time of 6 min. A resampling to 250 Hz and a high-pass filter of 1 Hz applied to all datasets resulted in the frequency band 1–250 Hz.

Schizophrenia patients often report a loss of connectedness with the natural and social inter-subjective life-world

of everyday human experience. Instead, they find themselves lost in autistic and aloof reflection on the former. This transformation of conscious experience was famously termed 'the loss of vital contact with reality' by French psychiatrist Eugène Minkowski (1885–1972) [48,49]. Wainio-Theberge *et al.* [47] hypothesized that subjects of the schizophrenia group exhibit a substantially lower ISC in the topography of their scale-free dynamic as measured by the power law exponent (PLE) computed in the frequency band 2–35 Hz. Briefly, the PLE is computed in the frequency domain and indicates the balance of the signal's power between slower and faster frequencies, where a higher steepness of the PLE corresponds to more power in slower than in faster frequencies [46]. (Other measurements included the log-transformed fractal and oscillatory power not reported by us here.) Conversely, the expectation for depressed patients was increased ISC.

Since EEG lacks voxel-based time-series, the authors assessed the time-series of each of the 30 electrodes for ISCs. Wainio-Theberge *et al.* [47] implemented a 'topography vector' of the PLE computation at each electrode and for each subject. The vectors encapsulated the subjects' EEG dynamics and were compared between subjects through Pearson correlation, resulting in the following correlation matrices: (i) healthy–healthy correlation; (ii) schizophrenia–schizophrenia correlation; (iii) depression–depression correlation and (iv) healthy–schizophrenia or healthy–depression correlations. The authors obtained the following results.

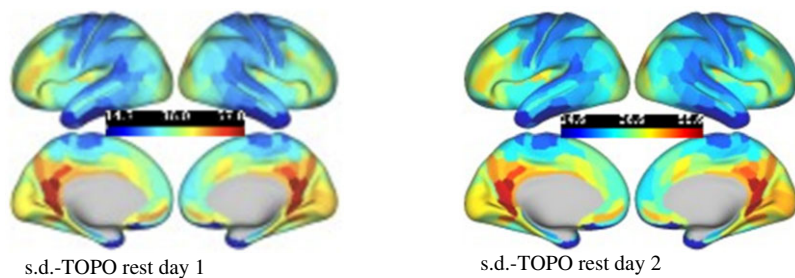
*Schizophrenia dataset 1:* As hypothesized, the schizophrenia patients had lower ISCs compared to the healthy controls ( $p=0.05$ ). Conversely, the ISC within the healthy control group resulted in non-significant ( $p=0.12$ ) inter-subject differences for the PLE, hence indicating that PLE levels are shared between healthy subjects. The findings support that healthy subjects share a significant degree of ISC, measured via the PLE, whereas schizophrenia patients showed a loss of inter-subject neuronal dynamics.

*Schizophrenia dataset 2:* Based on the topography vector of the EEG recordings, the authors again observed a lower spatial ISC of the PLE in schizophrenia patients ( $p=0.024$ ). Furthermore, the ISC of the PLE turned out significantly higher among healthy controls than in the comparison between schizophrenia patients and healthy controls ( $p=0.016$ ). The results of the second dataset thus followed the results of the first dataset for schizophrenia and healthy subjects.

*Depression dataset:* Compared to schizophrenia, the ISC of the PLE yielded no differences ( $p=0.84$ ). Interestingly, the PLE ISC comparisons healthy versus depressed–healthy ( $p=0.89$ ) and depressed versus depressed–healthy ( $p=0.59$ ) resulted in non-significant differences. The authors concluded that ISC abnormalities occurred in depression, albeit in the opposite direction compared to schizophrenia, precisely because the ISC increased across depressed patients.

Wainio-Theberge *et al.* [47] demonstrated that the brain's ongoing spontaneous activity here measured via the PLE of the resting state exhibits a high ISC across healthy subjects. Conversely, schizophrenia patients showed abnormally reduced levels of ISCs of neuronal dynamics across the brain's topography assessed. Within the schizophrenia patient group, there was less ISC of the PLE, theoretically in line with historical [48] and contemporary views [50,51] on the psychopathology of schizophrenia, namely the disconnectedness to the social inter-subjective life-world that healthy subjects share.

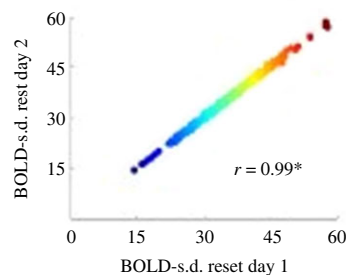
(a) topography of resting state SD-TOPO



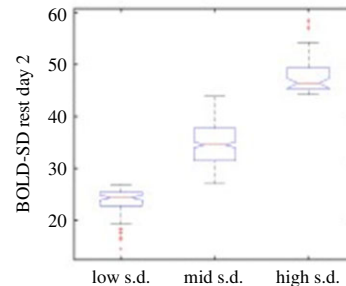
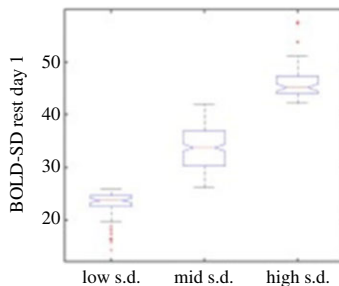
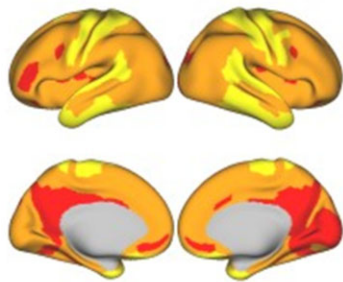
s.d.-TOPO rest day 1

s.d.-TOPO rest day 2

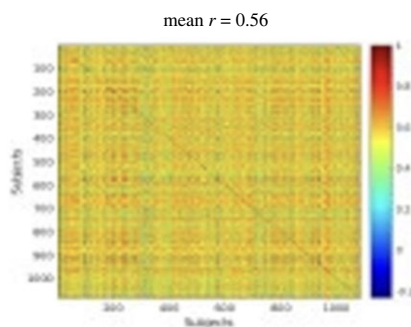
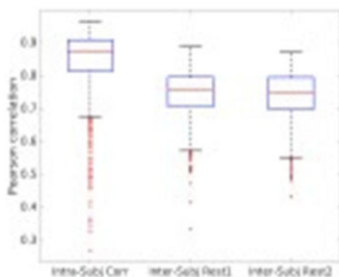
(b) spatial correlation of SD-TOPO topography on day 1 and day 2



(c)



(d)



**Figure 2.** ISC of the BOLD time-series standard deviation (s.d.) in the resting state. (a) Variability of the spontaneous BOLD signal measured in 360 regions across 974 subjects on days one and two. (b) Spatial or topographic correlation of the BOLD s.d. between days one and two. (c) Statistical comparison between regional differences into three groups: low, mid and highly shared s.d. The accompanying boxplots display the difference between the three group-based regions. (d) s.d. topography at the single subject level. The mean s.d. correlation between days one and two across all subjects yielded a high Pearson correlation ( $r = 0.84$ ). The correlation of each subject's s.d. topography to the rest of the group on both days yielded high Pearson correlations (day 1:  $r = 0.74$ ; day 2:  $r = 0.74$ ). Finally, the correlation between the topography of each subject to every other subject yielded moderate results (day 1:  $r = 0.56$ ; day 2:  $r = 0.55$ ).

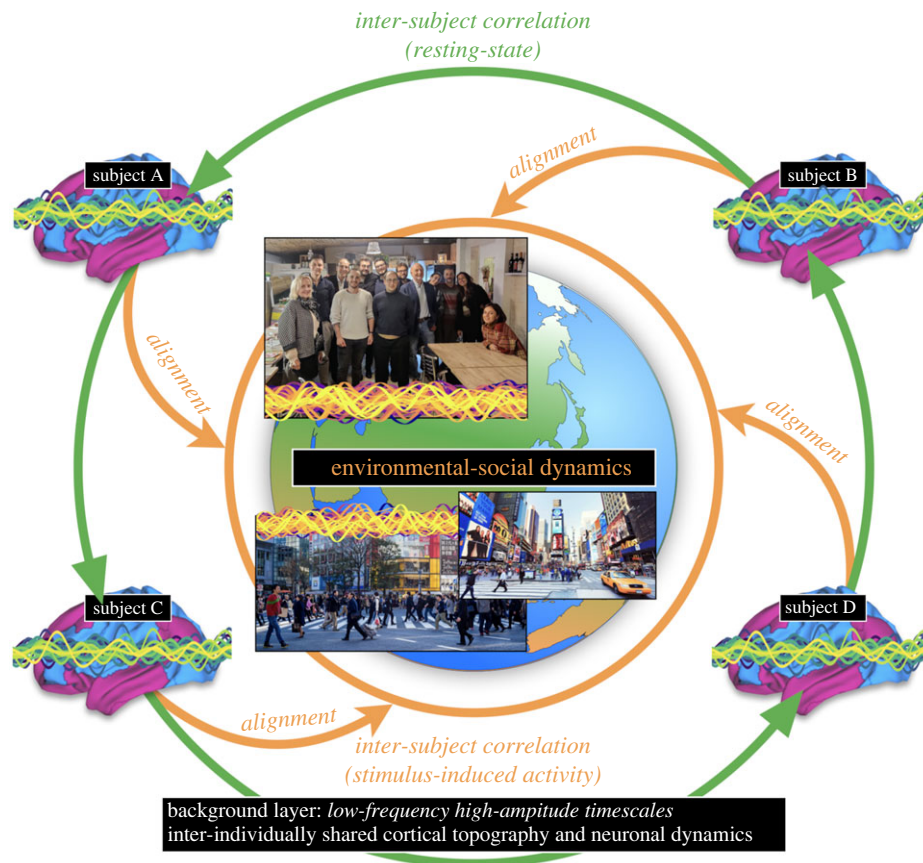
*Theoretical conclusions of the fMRI and EEG studies:* The fMRI study expanded the results of earlier resting-state functional connectivity studies that demonstrated shared networks across subjects irrespective of specific stimuli or tasks [52–54]. Tumati *et al.* (unpublished) highlight the concordant inter-individual variability, primarily measured via the standard deviation of the BOLD time-series. Notably, the same temporal dynamics spatially re-occurred in the same voxels and regions over different days, showing the stability of the brain's spontaneous activity that is not only intra-individually bound but also shared across subjects.

Further studies from our group support that spontaneous temporal brain dynamics and their spatial distribution across brains show a highly inter-individually shared nature (as measured in both rest and task states). Related studies from our group include fMRI and MEG analyses that investigated scale-free activity in the cerebral cortex's twofold division into higher order transmodal association and unimodal somatosensory regions [10,15,55]; a threefold topographic hierarchy of interoceptive, exteroceptive and cognitive processing stages of the self [56], and the manifestation of different sensory input regions measured via the PLE and

sample entropy [57]. These neuroimaging studies and analyses underlined that topographical and dynamic properties are all substantially shared across subjects.

The EEG study highlighted the absence of significant ISCs in the clinical group of schizophrenia patients. This contrasts to traditional methods that often compared group-based mean values, neglecting possible inter-individual differences in healthy versus psychiatric groups. Notably, the schizophrenia group lost a shared ISC that, in turn, was not replaced by a shared abnormal PLE topography. We interpret this to mean that the healthy phenomenological life-world of ordinary human experience is not replaced by an inter-subjectively shared world of pathological experiences. Instead, there is higher neurodiversity among schizophrenia subjects who are neuronally disconnected from both healthy and other schizophrenia subjects—this may be manifest in the clinical observation that each schizophrenia subject develops idiosyncratic life-world experiences.

These empirical findings suggest that a form of temporospatial alignment already occurs in the brain's ongoing spontaneous activity irrespective of specific stimuli or tasks, hence providing a degree of preadaptation to social interactions and



**Figure 3.** The background layer is constituted by low-frequency high-amplitude timescales. These long timescales show a high degree of inter-individual overlap across the brain's topography in rest and task states. The background layer thus provides a common shared ground between subjects for alignment with the social and natural world.

conditioning to environmental phenomena. This preadaptive form of alignment may correspond to our first suggested background layer primarily constituted by low-frequency high-power timescales of the brain that appear to be a phenotype that exhibits limited variation within groups sharing sociocultural and environmental contexts given inter-individual similarity and stability over days (see, paradigmatically, [58] for inter-subjective and cultural layers of the brain). Figure 3 visualizes the ISC of the brain's neuronal dynamics across its topography for the environment–brain relation, namely temporo-spatial alignment on inter-subjective social grounds.

## 2.2. Intermediate layer: stochastic matching of neuronal to environmental dynamics via alignment

The suggested alignment mechanism requires the empirical testing of the brain's spontaneous activity interaction with or modulation by environmental stimulus- or task-evoked activity. One possible investigation is testing the shared nature of TRWs of electrophysiological and hemodynamic signals across subjects in response to the same environmental inputs.

### 2.2.1. Temporal receptive windows

The TRW, initially suggested by Hasson *et al.* [59], describes the time required for a stimulus to elicit measurable responses in neuronal activity. Hasson and colleagues hypothesized that a hierarchy of increasing TRWs exists in the human cerebral cortex. This hierarchy supposedly starts with the cerebral cortex's unimodal somatosensory areas with relatively short TRWs allowing for rapid processing and temporal alignment to sensory

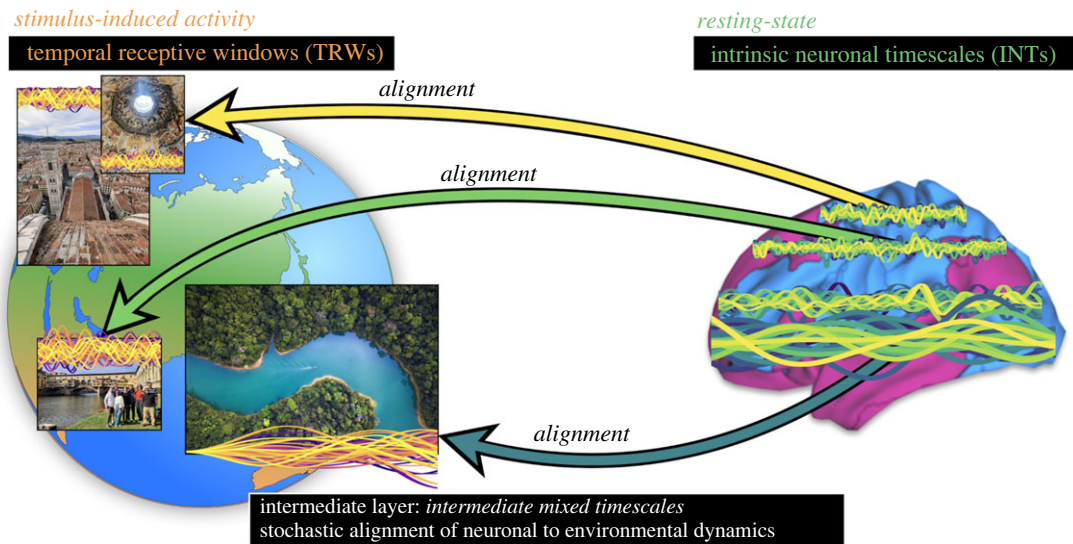
inputs, to higher order association cortices with significantly longer TRWs that support the integration of various inputs over more extended periods, albeit at the cost of longer response delays. Hasson *et al.* [59] thus shifted the focus from response magnitudes, such as the amplitude in electrophysiological EEG and the power of fMRI BOLD recordings, to the dynamics of the ongoing signal in the time domain. Applying naturalistic visual stimuli (silent films), Hasson and colleagues indeed found a hierarchy of TRWs from primarily instantaneous responses in the early visual cortex (V1 and MT+), over intermediate timescales of 12 s in the superior temporal sulcus and precuneus, to longer timescales of 36 s in the posterior lateral sulcus, the temporo-parietal junction, and the frontal eye field.

Further studies expanded the knowledge of TRWs [60–62]. Paradigmatically, Lerner *et al.* [63] demonstrated a TRW hierarchy in auditory and language areas where early auditory areas, such as A1+, showed responses driven by momentary short-scaled inputs up to parietal and frontal areas that only reliably responded to intact sentences up to paragraphs presented in meaningful sequences. These results highlighted the functional relevance of TRWs and their expanding topographical distribution with increasing TRW lengths across the cerebral cortex for the brain's relating to various features of incoming stimuli, such as single words to more complex paragraphs.

### 2.2.2. From temporal receptive windows to intrinsic neuronal timescales

Inter-individually shared hierarchy of TRWs in the cerebral cortex raises the question as to what extent TRWs are rooted





**Figure 4.** The intermediate layer provides stochastic alignment by modulating a repertoire of the brain's INT, measured in the resting state, to a range of environmental dynamics resulting in TRWs, measured in naturalistic stimuli paradigms.

in the brain's intrinsic functional organization, as represented by spontaneous or resting-state activity through INT. INT refer to the length of timescales of the brain's ongoing spontaneous activity (or resting state) irrespective of specific stimuli or tasks. Empirically, INT can be measured by the length of the autocorrelation function, specified by a chosen time lag, e.g.  $1/e$ , 50, or 0, for computing the autocorrelation statistic. The three paradigmatic time lags above refer to autocorrelation corresponding to each specific time lag. Furthermore, the time lag specification is also possible in seconds, as shown by Wolff *et al.* [64]. The autocorrelation's specification is sometimes labelled the autocorrelation window (ACW) in neuroimaging [10,65–67]. Paradigmatically, the ACW 0 describes a window length of the autocorrelation's first zero crossing ( $r=0$ ). Longer INT correspond to higher ACW values and vice versa: slower and powerful timescales decay slowly and carry temporal correlations in the signal over long periods compared with fast and less powerful timescales, mirroring the properties of task-related TRWs.

Recordings of INT spanning from single unit [68] over electrocorticography [69,70] and MEG [10,71] to fMRI [72] demonstrated that INT, like TRWs, vary following an anatomical hierarchy. Furthermore, the fMRI study by Huang *et al.* [73] provided evidence for the functional relevance of INT for consciousness, where the BOLD signal showed abnormally prolonged INT and regional synchronization under propofol-induced light and deep sedation compared to conscious wakefulness. In addition to ACW measurements of INT in the time domain, environment–brain matching is also observable in the frequency domain. An fMRI analysis by Klar *et al.* [15] demonstrated that the brain's power law distribution, measured by the PLE, significantly increased power in slower frequencies while simultaneously decreasing power in faster frequencies in task states with inter-trial intervals of 52–60 s (frequency band of 0.016–0.019 Hz). Consequently, the slope (PLE) of the least-squares linear regression in the frequency domain on a logarithmic scale increased.

### 2.2.3. Theoretical inferences

These observations of TRWs in response to extrinsic stimuli or task-related activity and INT that measure the temporal dynamics of the brain's ongoing spontaneous activity

suggest a functional capacity of the brain to match its neuronal with environmental dynamics in two main ways. First, the brain's mechanism to align to environmental fluctuations is provided by the repertoire of INT across the cerebral cortex, from faster and less powerful INT of unimodal somatosensory cortices or areas to slower and more powerful INT of higher order and transmodal association cortices [10,67].

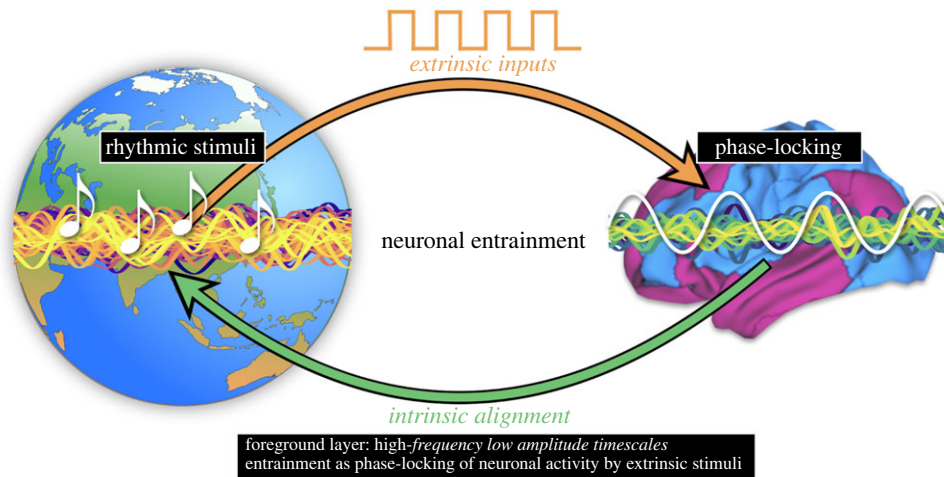
The second way of organization of the brain's matching of neuronal and environmental dynamics is the carry-over effect of the brain's intrinsic spatio-temporal INT organization from rest to task states. The processing of inputs requires their temporal integration, as provided by longer and more powerful timescales, and segregation, as provided by faster and less powerful timescales, of the brain's ongoing spontaneous activity and their alignment in TRWs [10,67,74]. The brain's intrinsic temporal and spatial features, building on a repertoire of timescales, provide a topography for organizing input processing, namely temporo-spatial alignment [75]. Given our findings of inter-subjective similarity in topography and dynamics, we suppose that such temporal and spatial shaping of input processing is shared between subjects, i.e. inter-individually (figure 4).

## 2.3. Foreground layer: phase-locking of neuronal activity to exteroceptive and interoceptive inputs

The previous section introduced stimulus-related TRWs and INT in neuronal activity to match environmental dynamics. This section examines the question of how the brain's ongoing spontaneous activity aligns with the fluctuations of extrinsic or interoceptive stimuli.

### 2.3.1. Neuronal entrainment

One mechanism by which INT potentially align to extrinsic stimuli-induced TRWs is through entrainment. Ongoing neuronal activity comprises a mixture between variability (fluctuations) and regularity (periodicity) [76,77]. Brain activity also exhibits rhythmic patterns that allow alignment via entrainment of neuronal activity by extrinsic stimuli, where the former are temporally aligned to the latter [78]. In entrainment, intero- and exteroceptive stimuli force



**Figure 5.** The foreground layer focuses on fast timescales (high-frequency low-amplitude) by stimulus- or task-evoked activity. Interoceptive bodily and exteroceptive environmental stimuli can entrain the brain's neuronal activity by phase-locking the intrinsic spontaneous activity's oscillatory phase angles to the extrinsic stimuli's oscillations, establishing alignment on rapid timescales.

periodic delays in neuronal activity that locks their phase to that of the stimuli [78]. Hence entrainment reflects the neuronal activity's unidirectional alignment to rhythms extrinsic to the brain by phase-locking to the environmental dynamics. That contrasts with synchronization where the oscillators are bidirectionally coupled with each other.

One example of entrainment is rhythms between the nervous system's motor output, such as speech, and auditory perception of speech comprising shared frequencies [79]. Neuronal entrainment supports perception and behaviour such as music perception [80,81], auditory detection [82] or visual contrast sensitivity [83]. The brain aligns to the rhythmic environmental dynamics by matching neuronal oscillations in its frequency repertoire (delta, theta, alpha, beta and gamma) with those in the environment to subsequently increase the amplitude or gain of stimulus-induced activity [84].

### 2.3.2. Rhythmic versus continuous mode

To further unpack the environment-brain relation on the grounds of entrainment, we elaborate two suggested mechanisms by Schroeder & Lakatos [85]: (i) a 'rhythmic mode' of brain activity and (ii) a 'continuous mode' of brain activity regarding the environment-brain interaction (see also [86]). The rhythmic and continuous modes of brain activity can represent two extreme endpoINT on a mutual and quantitative continuum [87] that, paradigmatically, is shifted to one of the poles such as in the neuropsychiatric disorder of schizophrenia [88].

- (i) The rhythmic mode of neuronal activity can apply when environmental stimuli exhibit a significant degree of temporal regularity. In the rhythmic mode of neuronal activity, the brain's low-frequency high-amplitude oscillations can align their phase onsets to the unpredictable environmental stimuli, paradigmatically exemplified by the temporal occurrences or frequency rate of the stimuli. The rhythmic mode allows neuronal activity to quasi-follow environmental stimuli by phase-locking or aligning the stimuli's rhythmic high-frequency low-amplitude oscillations to the brain's intrinsic low-frequency oscillations. Metaphorically speaking, the

brain dynamics follow and track environmental dynamics in the rhythmic mode.

- (ii) The continuous mode of neuronal activity comes into play when environmental stimuli show high degrees of randomness with lack of rhythmic statistical or frequency patterns that render difficult successful entrainment by phase-locking the spontaneous activity's phase angles to the stochasticity of stimuli. High-frequency low-amplitude fluctuations of environmental stimuli are now no longer aligned to the spontaneous activity's low-frequency oscillations, such as delta waves (1–4 Hz) measured by cross-frequency coupling [89]. Instead, the neuronal activity's low-frequency high-amplitude oscillations undergo suppression. The continuous mode thus represents the reverse of the rhythmic one, where low-frequency high-amplitude oscillations phase lock with rhythmic environmental high-frequency low-amplitude oscillations.

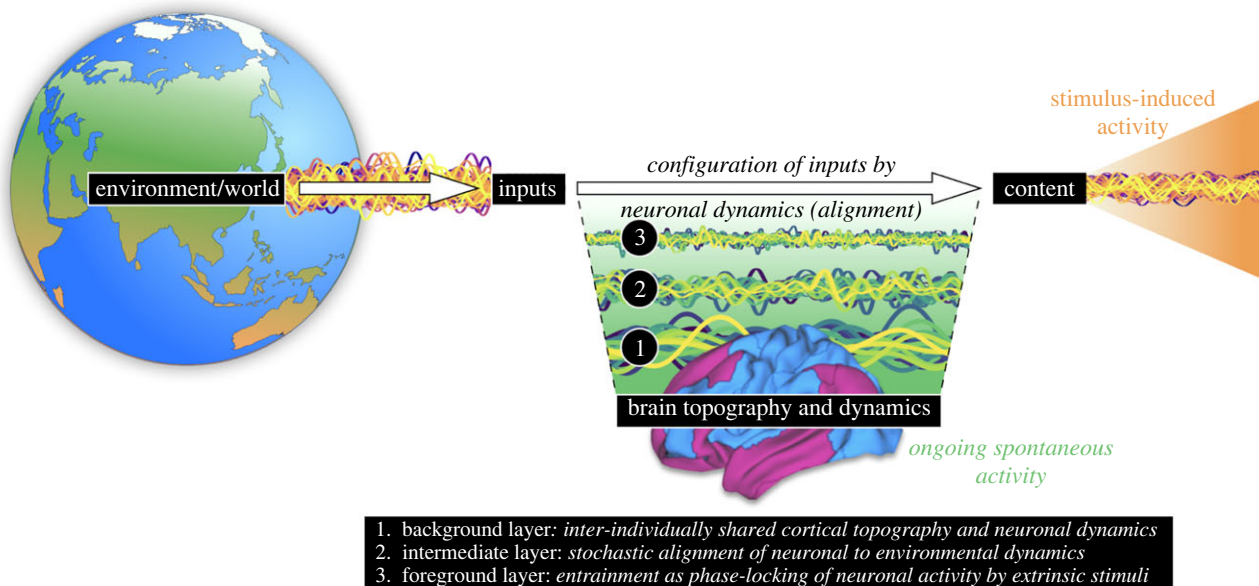
Summarizing the discussed findings, the brain's alignment with the environment is not an all-or-nothing mechanism. Instead, alignment of the brain's intrinsic neuronal activity to extrinsic stimuli operates on a continuum of the degree of changing environmental contexts, such as by confronting the organism with a relatively high degree of rhythmic or more arrhythmic temporal patterns, displayed in figure 5.

### 2.4. Neuronal aspects of the three-layer organization

Summarizing the three subsections above, we suggest three layers of the brain's temporo-spatial alignment with the environment. Layer one introduced an inter-individually shared cortical topography of neuronal dynamics. ISC in fMRI and EEG neuroimaging studies demonstrated a stable resting state irrespective of distinct inputs and occur at low-frequency high-amplitude fluctuations and oscillations.

The intermediate second layer focused on a stochastic alignment between neuronal and environmental dynamics. Layer two elaborated on TRWs related to stimulus- or task-evoked activity and subsequently on INT of the brain's ongoing spontaneous activity as operationally measured via





**Figure 6.** The summary of the three-layer organization displays temporo-spatial alignment starting from environmental stimuli or inputs over the interaction with the three layers of the neuronal activity's ongoing spontaneous activity to stimulus-induced activity associated with the contents of consciousness.

the resting state. The second layer suggested conceiving TRWs as a result of modulated INT: INT, just like TRWs, exhibit a systematic distribution across the brain's cortical topography allowing various degrees or balances of integration and segregation. We suggested that the ever-changing temporal integration–segregation balance results from the brain's alignment with the environment. The intrinsic spatio-temporal INT configuration may allow alignment to environmental stimuli, which, in turn, is then measured by stimulus-related TRWs.

The final third layer briefly introduced the electrophysiological concept of entrainment. Entrainment describes the neuronal activity's phase-locking to interoceptive bodily and exteroceptive environmental stimuli. Brain dynamics unidirectionally align with environmental stimuli where the former's phase angles adapt to the latter's rhythmic oscillations.

In conclusion, the three layers of consciousness are primarily distinguishable by their respective timescales and manifest themselves by spatially shared properties across subjects, shown by the ISC studies [33,34]. The resting-state measurements of the first layer focus on low-frequency and high-amplitude timescales of the brain's spontaneous activity that provide long-range correlations and stability over extended periods. These timescales reliably recur across days in inter-individually shared temporal dynamics and topography of subjects and are potentially associated with the background of conscious experience. The second layer includes a mixture of intermediate timescales and frequencies that span across a wide spatio-temporal range of brain activity and topography, depending on more specific environmental demands that are met by distinctive INT and TRWs systematically distributed across the brain's topography from unimodal somatosensory to heteromodal association cortices. The third layer exhibits highly specialized brain dynamics where distinct timescales or frequencies, including their phase angles, precisely align with bodily and environmental stimuli potentially associated with the foreground of conscious experience [57,90]. Figure 6 provides an overview of the three-layer organization.

### 3. Temporo-spatial alignment and consciousness: from neuronal to phenomenal layers

An open question concerns the association between the neuronal perspective on the three layers and their respective counterparts on the phenomenal perspective of consciousness. Therefore, the following three sections represent a conceptual attempt to link neuronal with phenomenal dynamics, converging both levels into one coherent three-layer model.

#### 3.1. From an inter-individually shared topographic-dynamic resting-state structure to the shared stable contextual structure of consciousness

We posit that the task-irrespective prevalence of specific dynamics across the brain's topography implies that neuronal activity is preadapted to the social and natural environment or context. Healthy subjects share this form of preadaptation in their resting state's cortical topographic and dynamic organization. When expanding the perspective from resting-state to task-related activity, it is feasible that subjects share common grounds or capacities for input processing, possibly from a phylogenetic origin [10,91]. The inter-individually shared topographic and dynamical properties of the brain's spontaneous activity may establish a contextual neuro-ecological point of view within a pre-given, self-evident and natural life-world that is widely shared across healthy human beings [92,93]. This, in turn, provides the background of consciousness, paradigmatically termed 'vital contact with reality' by psychiatrist Minkowski [48].

We suppose that the inter-individually shared degree of inter-subjective neuronal topographic-dynamic overlaps should be mirrored in the degree of inter-subjective phenomenal overlaps in the contextual background of consciousness. The contextual background structure of consciousness remains relatively stable over time compared to the ever-changing contents of the experiential foreground, and we

suggest that the background's temporal stability is associated with the spontaneous activity's long and powerful timescales including their topographic organization.

### 3.2. Functional magnetic resonance imaging study on consciousness and long intrinsic timescales

Previously presented neuroimaging studies provide support for the long timescales of the brain's spontaneous activity as a shared background experience in healthy subjects (see [1,2,8]). Zhang *et al.* [55] demonstrate the function of the long timescales in the background of consciousness, irrespective of specific conscious contents. With fMRI, they confirmed and extended previous findings [94,95] by showing a global decrease of inter-individually shared brain topography and dynamics, measured by the PLE as an indicator of the signal's noise colour and long-range temporal correlations, under propofol- and sevoflurane-induced unconsciousness.

The awake subjects in Zhang *et al.* [55] showed a statistically significant shared voxel-based topography of the s.d. and the PLE under conscious wakefulness. Conversely, the loss of these inter-individually shared topographies was accompanied by the loss of consciousness in anaesthesia which, as we assume, is related to the loss of shared input processing capacities based on the loss of shared resting-state topographic dynamics.

### 3.3. Phenomenal implications: background structure of consciousness in schizophrenia

The background structure of consciousness is also altered in schizophrenia. Our findings demonstrate a decrease in the inter-subjectively shared topographic dynamic among schizophrenia subjects compared to healthy subjects. This suggests that schizophrenia patients no longer share the same background structure in their consciousness as the healthy subjects share it among themselves. The early psychiatrist Minkowski, therefore, spoke of a 'loss of vital contact with reality' in the consciousness of schizophrenia [48], indicating the loss of preadaptation to the social and ecological environmental context. Accordingly, the case of schizophrenia, albeit indirectly, lends further support to the assumption of the fundamental role of the brain's inter-subjectively shared topographic-dynamic organization for the background structure of consciousness.

#### 3.3.1. Intermediate layer of consciousness: from the inputs' temporal integration—segregation to the relationships between contents in consciousness

While the background layer of consciousness is maintained by neuronal activity on long timescales and is relatively more stable, the intermediate layer is more flexible and can be associated with the changing contents of consciousness. A repertoire of INT that can form TRWs under stimulus- or task-related activity allows temporal integration and segregation balances of environmental inputs [10,67]. Temporal integration [61] allows connecting several inputs into one coherent content, while temporal segregation differentiates input clusters from each other, distinguishing contents of consciousness [2]. Long timescales can establish a stable background, while simultaneously, intermediate timescales

may encode a variety of changing contents in conscious experience. Two recent studies provide some evidence that the changing pattern of internally versus externally oriented thoughts operate on timescales around 10–30 s [21,96]. Taken together these results identify timescales of the intermediate layer on the neuronal level, and although tentative, may be related to the timescales in the dynamic pattern of the changing contents of consciousness.

Indirect support comes from schizophrenia studies with fMRI and EEG. Recent studies [97–99] demonstrated abnormal length of the INT during rest or task states. This suggests that different temporal inputs are abnormally integrated and segregated. That, in turn, results in abnormal relationships between different contents of these subjects' consciousness where, for instance, different inputs from different external events are bound that usually are not perceived in the external environment. The intermediate layer of temporo-spatial alignment may thus be dysfunctional in schizophrenia leading to abnormal relationships between different contents in consciousness—this further underlines the importance of the intermediate layer of temporo-spatial alignment for the relationship between the various contents in consciousness.

#### 3.3.2. Foreground layer of consciousness: from input sampling to specific contents in the foreground

The foreground layer focused on the entrainment of the brain's ongoing activity by environmental signals and fluctuations on timescales within the millisecond to the second range. Accordingly, the particular contents of consciousness come with a fleeting character, constantly varying over short timescales below 3 s and within the millisecond range [100,101]. We suggest that fast and short timescales of the brain's neuronal level are related to the faster timescales of specific contents within conscious experience that are sensed and perceived in the environment. In this layer of consciousness, the brain's intrinsic neural dynamics and its sensory apparatus become entrained through phase-locking by extrinsic environmental dynamics.

Various studies support the role of phase-locking in accounting for specific contents of consciousness [3,78]. A recent EEG study demonstrated how task-on and -off thoughts encounter sampling via phase-related processes in faster alpha (8–13 Hz) and slower theta (5–8 Hz) frequency bands, respectively [22]. The distinct types of thoughts can thus be related to different timescales in the faster and shorter range, e.g. theta frequency for off-thoughts and the faster alpha frequency for on-thoughts [22]. Based on these findings, we suggest that specific phase cycles may allow the sampling of specific contents as in input sampling, which, like the tones of a melody, are thereby highlighted and shifted into the foreground as the specific contents of consciousness [2,78].

This is further supported by observations in studies of schizophrenia. Schizophrenia patients show major deficits phase-locking to external stimuli. For instance, they exhibit decreased inter-trial phase coherence (ITPC) in response to rhythmic stimuli like in an auditory oddball paradigm [67,88]. Their foreground layer of neuronal alignment operating on short timescales is thus deficient as input sampling is unable to lead to entrainment of neural dynamics. These patients operate more in a continuous mode than a rhythmic mode (section 'Foreground layer: phase-locking of neuronal

activity to exteroceptive and interoceptive inputs'). On the phenomenal side, this may be related to their abnormal contents of consciousness: environmental signals are often replaced by internal contents in their consciousness which they experience as external contents, for instance experience of auditory hallucinations and delusions (see also [102]). This is supported by the fact that the ITPC deficits strongly correlate with positive symptoms [67,88]. Albeit indirectly, these data support the assumption that the faster and shorter timescales of the foreground layer are related to the foreground of consciousness, that is, its specific contents.

Together, the three phenomenal layers of consciousness including its background structure, relationships between contents and specific foreground contents allow the association with their respective neuronal layers based on shared temporal alignment between environment and brain [28]. We summarize the suggested three-layer concept as follows: (i) the background layer is relatively stable on long-range and global spatio-temporal scales; this layer manifests itself in the experience of a shared and stable contextual background of the environment; (ii) the intermediate layers comprise a mixture of timescales that allow stochastic matching of environmental inputs and brain dynamics through the latter's temporal integration and segregation; this is associated with changes in contents in conscious experience; (iii) the foreground layers are bound to specific temporal, e.g. specific time poINT, and spatial, e.g. specific locations, of environmental inputs; this neuronal layer of high frequencies is related to specific foreground contents of consciousness at specific poINT in time.

## 4. Discussion: temporo-spatial alignment, free energy and symmetry

### 4.1. 'Common currency' of world, brain and consciousness: temporo-spatial alignment and free energy

The framing of mental processes in terms of physical forces, a 'common currency' of world, brain and consciousness, as established by temporo-spatial alignment may be a primary factor allowing for coherently integrated functioning of minds based on the creation and annihilation of informational (and to varying extents, thermodynamic) free energy gradients. In such physics-inspired models, the regularities (or invariances) observed are modelled as being maintained in the face of disturbances by symmetry-preserving gauge fields. With respect to nervous systems, the maintenance of these regularities—e.g. the establishment of coherent ego-centric perspective, or the preservation of enduring self-processes—could be thought of as 'force fields' over conjoined neural and environmental dynamics [103].

More specifically, the ability to create aligned inner and outer (wave)forms can be understood as a kind of predictive modelling, where these symmetries may be understood as establishing homomorphic (and perhaps diffeomorphic) relationships between models and that which they model. TTC proposes that perhaps the most important feature for establishing this kind of functional linkage is for a system's attracting states to evolve on timescales that correspond with the world's dynamics it attempts to model/couple or align with. As such,

we suggest that the primary task of these sources of 'fictitious' force (or control energy) is the constitution, maintenance and promotion of temporo-spatial alignment.

Slower (relative to faster) timescales may have uniquely powerful roles in establishing temporal and spatial contexts (or reference frames). These, in turn, may make major contribution to constructing unified fields of consciousness, and perhaps to varying extents, coherently integrated selfhood, that is, a basic subjectivity or sense of self as point of view on a lived world [93,104]. From this perspective, various timescales with their self-processes would represent an essential source of background for contents in the foreground of experience, that is, the predominant source of force that determines the flow of the stream as the background of consciousness.

### 4.2. Temporo-spatial alignment and dynamics: symmetries constitute the form or structure of consciousness

Finally, in terms of interpersonal symmetries, we can think of how individuals who couple with the world may also find themselves mutually entrained in processes of shared sense-making [105]. These may not only be enhanced by integrative world models, but in many ways may be required for such modelling processes to be successfully bootstrapped in an inter-subjective fashion [106]. That is, with respect to schizophrenia, disrupted temporo-spatial alignment and integrated world modelling contribute to disrupted socioemotional coupling. Additionally, such disruptions in shared sense-making could further compromise the brain's aligning and integrating processes which, in turn, disrupt the form or structure of consciousness.

In sum, the temporo-spatial alignment is closely related to the notion of symmetry in several ways. (i) Firstly, processes of temporo-spatial alignment result in symmetry between inner and outer states, (ii) with aligning processes understood as governed by informational-gauge fields [103,107,108] that preserve essential symmetries of brain and environment through their various sources of temporal and spatial coherence [7,28].

(iii) These, in turn, provide the basis for constituting an environmentally based point of view, (iv) which makes possible the constitution of consciousness. (v) Such temporo-spatial alignment across individuals results in a substantially symmetric consciousness across subjects as based on their shared embedding within the same (physical, biological, social and cultural) environment. For more details on the abstract physics-informed and dynamic description of the neuronal mechanisms of temporo-spatial alignment (i,ii), we refer interested readers to other articles in this collection while the more neuro-phenomenal mechanisms of point of view and consciousness (iii–v) are detailed in Northoff & Smith [93].

## 5. Conclusion

Rather than representing or modelling (or simulating) the world, the brain aligns to the environment by embedding and nesting its temporo-spatial structure to the one of the environment. This is made possible by temporo-spatial alignment as the brain through its different neuronal layers, that is, background, intermediate and foreground layers.



The temporal and spatial dynamics of the neuronal layers, in turn, manifest in more or less corresponding phenomenal layers of consciousness, e.g. background structure, intermediate layers with the relationship between different contents and specific contents in the foreground of experience (see [2,100,101]). This further supports the assumption that the brain's three neuronal layers of temporo-spatial alignment to the world/environment provide an intimate link among environmental, neuronal and phenomenal levels of consciousness—they share their temporo-spatial dynamic as 'common currency' [28]. Going beyond the brain, that makes it possible to consider the deeper roots of temporo-spatial alignment in both basic physical-energetic mechanisms like free energy and the more dynamic processes of symmetry formation.

## References

- Northoff G, Zilio F. 2022 Temporo-spatial theory of consciousness (TTC): bridging the gap of neuronal activity and phenomenal states. *Behav. Brain Res.* **424**, 113788. (doi:10.1016/j.bbr.2022.113788)
- Northoff G, Zilio F. 2022 From shorter to longer timescales: converging integrated information theory (IIT) with the temporo-spatial theory of consciousness (TTC). *Entropy* **24**, 270. (doi:10.3390/e24020270)
- Northoff G, Lamme V. 2020 Neural signs and mechanisms of consciousness: is there a potential convergence of theories of consciousness in sight? *Neurosci. Biobehav. Rev.* **118**, 568–587. (doi:10.1016/j.neubiorev.2020.07.019)
- Seth AK, Bayne T. 2022 Theories of consciousness. *Nat. Rev. Neurosci.* **23**, 439–452. (doi:10.1038/s41583-022-00587-4)
- Northoff G. 2013 *Unlocking the brain, vol. 1: coding*. New York, NY: Oxford University Press.
- Safran A. 2020 An Integrated World Modeling Theory (IWMT) of consciousness: combining integrated information and global neuronal workspace theories with the free energy principle and active inference framework; toward solving the hard problem and characterizing agentic causation. *Front. Artif. Intell.* **3**, 30. (doi:10.3389/frai.2020.00030)
- Safran A. 2022 Integrated World Modeling Theory expanded: implications for the future of consciousness. *Front. Comput. Neurosci.* **16**, 642397. (doi:10.3389/fncom.2022.642397)
- Northoff G, Huang Z. 2017 How do the brain's time and space mediate consciousness and its different dimensions? Temporo-spatial theory of consciousness (TTC). *Neurosci. Biobehav. Rev.* **80**, 630–645. (doi:10.1016/j.neubiorev.2017.07.013)
- Northoff G. 2018 *The spontaneous brain: from the mind-body to the world-brain problem*. Cambridge, MA: MIT Press.
- Golesorkhi M, Gomez-Pilar J, Tumati S, Fraser M, Northoff G. 2021 Temporal hierarchy of intrinsic neural timescales converges with spatial core-periphery organization. *Commun. Biol.* **4**, 277. (doi:10.1038/s42003-021-01785-z)
- von Holst E. 1939 Über die nervöse Funktionsstruktur des rhythmisch tätigen Fischrückenmarks. *Pflügers Arch.* **241**, 569–611. (doi:10.1007/BF01766126)
- Bandettini PA, Wong EC, Hinks RS, Tikofsky RS, Hyde JS. 1992 Time course EPI of human brain function during task activation. *Magn. Reson. Med.* **25**, 390–397. (doi:10.1002/mrm.1910250220)
- Biswal B, Yetkin FZ, Haughton VM, Hyde SJ. 1995 Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn. Reson. Med.* **34**, 537–541. (doi:10.1002/mrm.1910340409)
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL. 2001 A default mode of brain function. *Proc. Natl Acad. Sci. USA* **98**, 676–682. (doi:10.1073/pnas.98.2.676)
- Klar P, Çatal Y, Langner R, Huang Z, Northoff G. 2022 Scale-free dynamics of the core-periphery topography. *Hum. Brain Mapp.* **44**, 1997–2017. (doi:10.1002/hbm.26187)
- Wainio-Theberge S, Wolff A, Northoff G. 2021 Dynamic relationships between spontaneous and evoked electrophysiological activity. *Commun. Biol.* **4**, 741. (doi:10.1038/s42003-021-02240-9)
- Wolff A, Yao L, Gomez-Pilar J, Shoaran M, Jiang N, Northoff G. 2019 Neural variability quenching during decision-making: neural individuality and its prestimulus complexity. *Neuroimage* **192**, 1–14. (doi:10.1016/j.neuroimage.2019.02.070)
- Zilio F *et al.* 2021 Are intrinsic neural timescales related to sensory processing? Evidence from abnormal behavioral states. *Neuroimage* **226**, 117579. (doi:10.1016/j.neuroimage.2020.117579)
- Köhler W. 1967 Gestalt psychology. *Psychol. Forsch.* **31**, 18–30. (doi:10.1007/bf00422382)
- Wagemans J, Elder JH, Kubovy M, Palmer SE, Peterson MA, Singh M, von der Heydt R. 2012 A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure-ground organization. *Psychol. Bull.* **138**, 1172–1217. (doi:10.1037/a0029333)
- Rostami S, Borjali A, Eskandari H, Rostami R, Scalabrini A, Northoff G. 2022 Slow and powerless thought dynamic relates to brooding in unipolar and bipolar depression. *Psychopathology* **55**, 258–272. (doi:10.1159/000523944)
- Hua J, Wolff A, Zhang J, Yao L, Zang Y, Luo J, Ge X, Liu C, Northoff G. 2022 Alpha and theta peak frequency track on- and off-thoughts. *Commun. Biol.* **5**, 209. (doi:10.1038/s42003-022-03146-w)
- Gisiger T. 2001 Scale invariance in biology: coincidence or footprint of a universal mechanism? *Biol. Rev. Camb. Phil. Soc.* **76**, 161–209. (doi:10.1017/s1464793101005607)
- Gilden DL, Thornton T, Mallon MW. 1995 1/f noise in human cognition. *Science* **267**, 1837–1839. (doi:10.1126/science.7892611)
- Halley JM, Inchausti P. 2004 The increasing importance of 1/f-noises as models of ecological variability. *Fluctuation Noise Lett.* **04**, R1–R26. (doi:10.1142/S0219477504001884)
- Riley MA, Shockley K, van Orden G. 2011 Learning from the body about the mind. *Top. Cogn. Sci.* **4**, 21–34. (doi:10.1111/j.1756-8765.2011.01163.x)
- Voss RF, Clarke J. 1975 1/f noise in music and speech. *Nature* **258**, 317–318. (doi:10.1038/258317a0)
- Northoff G, Wainio-Theberge S, Evers K. 2020 Is temporo-spatial dynamics the 'common currency' of brain and mind? In quest of 'spatiotemporal neuroscience'. *Phys. Life Rev.* **33**, 34–54. (doi:10.1016/j.plrev.2019.05.002)
- Kolvoort IR, Wainio-Theberge S, Wolff A, Northoff G. 2020 Temporal integration as 'common currency' of brain and self-scale-free activity in resting-state EEG correlates with temporal delay effects on self-relatedness. *Hum. Brain Mapp.* **41**, 4355–4374. (doi:10.1002/hbm.25129)
- Fox MD, Raichle ME. 2007 Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat. Rev. Neurosci.* **8**, 700–711. (doi:10.1038/nrn2201)
- Mitra A, Raichle ME. 2016 How networks communicate: propagation patterns in spontaneous brain activity. *Phil. Trans. R. Soc. Lond. B* **371**, 20150546. (doi:10.1098/rstb.2015.0546)

32. Bijsterbosch J, Smith S, Beckmann C. 2007 *Introduction to resting state fMRI functional connectivity*. Oxford, UK: Oxford University Press.
33. Nastase SA, Gazzola V, Hasson U, Keysers C. 2019 Measuring shared responses across subjects using intersubject correlation. *Soc. Cogn. Affect. Neurosci.* **14**, 668–685. (doi:10.1093/scan/nsz037)
34. Yeshurun Y, Nguyen M, Hasson U. 2021 The default mode network: where the idiosyncratic self meets the shared social world. *Nat. Rev. Neurosci.* **22**, 181–192. (doi:10.1038/s41583-020-00420-w)
35. Simony E, Honey CJ, Chen J, Lositsky O, Yeshurun Y, Wiesel A, Hasson U. 2016 Dynamic reconfiguration of the default mode network during narrative comprehension. *Nat. Commun.* **7**, 12141. (doi:10.1038/ncomms12141)
36. Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R. 2004 Intersubject synchronization of cortical activity during natural vision. *Science* **303**, 1634–1640. (doi:10.1126/science.1089506)
37. Hasson U, Frith CD. 2016 Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions. *Phil. Trans. R. Soc. Lond. B* **371**, 20150366. (doi:10.1098/rstb.2015.0366)
38. Chang WT, Jääskeläinen IP, Belliveau JW, Huang S, Hung AY, Rossi S, Ahveninen J. 2015 Combined MEG and EEG show reliable patterns of electromagnetic brain activity during natural viewing. *Neuroimage* **114**, 49–56. (doi:10.1016/j.neuroimage.2015.03.066)
39. Chen Y, Farivar R. 2020 Natural scene representations in the gamma band are prototypical across subjects. *Neuroimage* **221**, 117010. (doi:10.1016/j.neuroimage.2020.117010)
40. Hasson U, Ghazanfar AA, Galantucci B, Garrod S, Keysers C. 2012 Brain-to-brain coupling: a mechanism for creating and sharing a social world. *Trends Cogn. Sci.* **16**, 114–121. (doi:10.1016/j.tics.2011.12.007)
41. Van Essen DC, Smith SM, Barch DM, Behrens EJ, Yacoub E, Ugurbil K. 2013 The WU-Minn human connectome project: an overview. *Neuroimage* **80**, 62–79. (doi:10.1016/j.neuroimage.2013.05.041)
42. Glasser MF *et al.* 2016 A multi-modal parcellation of human cerebral cortex. *Nature* **536**, 171–178. (doi:10.1038/nature18933)
43. Lipsitz LA, Goldberger AL. 1992 Loss of ‘complexity’ and aging. Potential applications of fractals and chaos theory to senescence. *JAMA* **267**, 1806–1809. (doi:10.1001/jama.1992.03480130122036)
44. Bassingthwaite JB, van Beek JHGM. 1988 Lightning and the heart: fractal behavior in cardiac function. *Proc IEEE Inst. Electr. Electron. Eng.* **76**, 693–699. (doi:10.1109/5.4458)
45. Hoop B, Kazemi H, Liebovitch LS. 1993 Rescaled range analysis of resting respiration. *Chaos* **3**, 27–29. (doi:10.1063/1.165976)
46. Huang Z *et al.* 2017 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**, 1037–1059. (doi:10.1093/cercor/bhv288)
47. Wainio-Theberge S, Wolff A, Gomez-Pilar J, Zhang J, Northoff G. 2022 Variability and task-responsiveness of electrophysiological dynamics: scale-free stability and oscillatory flexibility. *Neuroimage* **256**, 119245. (doi:10.1016/j.neuroimage.2022.119245)
48. Minkowski E. 1927 *La schizophrénie. Psychopathologie des schizoïdes et des schizophrènes*. Paris, France: Payot.
49. Klar P, Northoff G. 2021 When the world breaks down: a 3-stage existential model of nihilism in schizophrenia. *Psychopathology* **54**, 169–192. (doi:10.1159/000516814)
50. Parnas J, Sass LA. 2001 Self, solipsism, and schizophrenic delusions. *Phil. Psychiatry Psychol.* **8**, 101–120. (doi:10.1353/ppp.2001.0014)
51. Parnas J. 2012 The core gestalt of schizophrenia. *World Psychiatry* **11**, 67–69. (doi:10.1016/j.wpsyc.2012.05.002)
52. Friston KJ. 2011 Functional and effective connectivity: a review. *Brain Connect.* **1**, 13–36. (doi:10.1089/brain.2011.0008)
53. Cole DM, Smith SM, Beckmann CF. 2010 Advances and pitfalls in the analysis and interpretation of resting-state fMRI data. *Front. Syst. Neurosci.* **4**, 8. (doi:10.3389/fnsys.2010.00008)
54. Raichle ME. 2015 The brain’s default mode network. *Annu. Rev. Neurosci.* **38**, 433–447. (doi:10.1146/annurev-neuro-071013-014030)
55. Zhang J *et al.* 2018 Breakdown in the temporal and spatial organization of spontaneous brain activity during general anesthesia. *Hum. Brain Mapp.* **39**, 2035–2046. (doi:10.1002/hbm.23984)
56. Qin P, Wang M, Northoff G. 2020 Linking bodily, environmental and mental states in the self—a three-level model based on a meta-analysis. *Neurosci. Biobehav. Rev.* **115**, 77–95. (doi:10.1016/j.neubiorev.2020.05.004)
57. Catal Y, Gomez-Pilar J, Northoff G. 2022 Intrinsic dynamics and topography of sensory input systems. *Cereb. Cortex* **32**, 4592–4604. (doi:10.1093/cercor/bhab504)
58. Scalabrini A, Xu J, Northoff G. 2021 What COVID-19 tells us about the self: the deep intersubjective and cultural layers of our brain. *Psychiatry Clin. Neurosci.* **75**, 37–45. (doi:10.1111/pcn.13185)
59. Hasson U, Yang E, Vallines I, Heeger DJ, Rubin N. 2008 A hierarchy of temporal receptive windows in human cortex. *J. Neurosci.* **28**, 2539–2550. (doi:10.1523/jneurosci.5487-07.2008)
60. Lerner Y, Honey CJ, Katkov M, Hasson U. 2014 Temporal scaling of neural responses to compressed and dilated natural speech. *J. Neurophysiol.* **111**, 2433–2444. (doi:10.1152/jn.00497.2013)
61. Himberger KD, Chien HY, Honey CJ. 2018 Principles of temporal processing across the cortical hierarchy. *Neuroscience* **389**, 161–174. (doi:10.1016/j.neuroscience.2018.04.030)
62. Jääskeläinen IP, Sams M, Gleason E, Ahveninen J. 2021 Movies and narratives as naturalistic stimuli in neuroimaging. *Neuroimage* **224**, 117445. (doi:10.1016/j.neuroimage.2020.117445)
63. Lerner Y, Honey CJ, Silbert LJ, Hasson U. 2011 Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *J. Neurosci.* **31**, 2906–2915. (doi:10.1523/jneurosci.3684-10.2011)
64. Wolff A, Di Giovanni DA, Gomez-Pilar J, Nakao T, Huang Z, Longtin A, Northoff G. 2019 The temporal signature of self: temporal measures of resting-state EEG predict self-consciousness. *Hum. Brain Mapp.* **40**, 789–803. (doi:10.1002/hbm.24412)
65. Gao R, van den Brink RL, Pfeffer T, Voytek B. 2020 Neuronal timescales are functionally dynamic and shaped by cortical microarchitecture. *Elife* **9**, e61277. (doi:10.7554/elife.61277)
66. Golesorkhi M, Gomez-Pilar J, Zilio F, Berberian N, Wolff A, Yagoub MCE, Northoff G. 2021 The brain and its time: intrinsic neural timescales are key for input processing. *Commun. Biol.* **4**, 970. (doi:10.1038/s42003-021-02483-6)
67. Wolff A, Berberian N, Golesorkhi M, Gomez-Pilar J, Zilio F, Northoff G. 2022 Intrinsic neural timescales: temporal integration and segregation. *Trends Cogn. Sci.* **26**, 159–173. (doi:10.1016/j.tics.2021.11.007)
68. Murray JD *et al.* 2014 A hierarchy of intrinsic timescales across primate cortex. *Nat. Neurosci.* **17**, 1661–1663. (doi:10.1038/nn.3862)
69. Cavanagh SE, Hunt LT, Kennerley SW. 2020 A diversity of intrinsic timescales underlie neural computations. *Front. Neural Circuits* **14**, 615626. (doi:10.3389/fncir.2020.615626)
70. Honey CJ *et al.* 2012 Slow cortical dynamics and the accumulation of information over long timescales. *Neuron* **76**, 423–434. (doi:10.1016/j.neuron.2012.08.011)
71. Demirtaş M *et al.* 2019 Hierarchical heterogeneity across human cortex shapes large-scale neural dynamics. *Neuron* **101**, 1181–1194. (doi:10.1016/j.neuron.2019.01.017)
72. Raut RV, Snyder AZ, Raichle ME. 2020 Hierarchical dynamics as a macroscopic organizing principle of the human brain. *Proc. Natl Acad. Sci. USA* **117**, 20 890–20 897. (doi:10.1073/pnas.2003383117)
73. Huang Z, Liu X, Mashour GA, Hudetz AG. 2018 Timescales of intrinsic BOLD signal dynamics and functional connectivity in pharmacologic and neuropathologic states of unconsciousness. *J. Neurosci.* **38**, 2304–2317. (doi:10.1523/jneurosci.2545-17.2018)
74. Hasson U, Chen J, Honey CJ. 2015 Hierarchical process memory: memory as an integral component of information processing. *Trends Cogn. Sci.* **19**, 304–313. (doi:10.1016/j.tics.2015.04.006)
75. Safron A, Klimaj V, Hipólito I. 2022 On the importance of being flexible: dynamic brain networks and their potential functional significances. *Front. Syst. Neurosci.* **15**, 688424. (doi:10.3389/fnsys.2021.688424)
76. Schirner M, Kong X, Yeo BTT, Deco G, Ritter P. 2022 Dynamic primitives of brain network interaction. *Neuroimage* **250**, 118928. (doi:10.1016/j.neuroimage.2022.118928)
77. Waschke L, Kloosterman NA, Obleser J, Garrett DD. 2021 Behavior needs neural variability. *Neuron* **109**, 751–766. (doi:10.1016/j.neuron.2021.01.023)
78. Lakatos P, Gross J, Thut G. 2019 A new unifying account of the roles of neuronal entrainment. *Curr. Biol.* **29**, R890–R905. (doi:10.1016/j.cub.2019.07.075)

79. Giraud AL, Poeppel D. 2012 Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.* **15**, 511–517. (doi:10.1038/nn.3063)
80. Nozaradan S, Peretz I, Mouraux A. 2012 Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *J. Neurosci.* **32**, 17 572–17 581. (doi:10.1523/jneurosci.3203-12.2012)
81. Doelling KB, Poeppel D. 2015 Cortical entrainment to music and its modulation by expertise. *Proc. Natl Acad. Sci. USA* **112**, E6233–E6242. (doi:10.1073/pnas.1508431112)
82. Lawrence ELA, Harper NS, Cooke JE, Schnupp WH. 2014 Temporal predictability enhances auditory detection. *J. Acoust. Soc. Am.* **135**, EL357–EL363. (doi:10.1121/1.4879667)
83. Cravo AM, Rohenkohl G, Wyart V, Nobre AC. 2013 Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *J. Neurosci.* **33**, 4002–4010. (doi:10.1523/jneurosci.4675-12.2013)
84. Buzsáki G, Draguhn A. 2004 Neuronal oscillations in cortical networks. *Science* **304**, 1926–1929. (doi:10.1126/science.1099745)
85. Schroeder CE, Lakatos P. 2009 The gamma oscillation: master or slave? *Brain Topogr.* **22**, 24–26. (doi:10.1007/s10548-009-0080-y)
86. Schroeder CE, Wilson DA, Radman T, Scharfman H, Lakatos P. 2010 Dynamics of active sensing and perceptual selection. *Curr. Opin. Neurobiol.* **20**, 172–176. (doi:10.1016/j.conb.2010.02.010)
87. Northoff G. 2014 *Unlocking the brain. Volume 2: consciousness*. New York, NY: Oxford University Press.
88. Lakatos P, Schroeder CE, Leitman DI, Javitt DC. 2013 Predictive suppression of cortical excitability and its deficit in schizophrenia. *J. Neurosci.* **33**, 11 692–116 702. (doi:10.1523/jneurosci.0010-13.2013)
89. Fried P, Reynolds JH, Rorie AE, Desimone R. 2001 Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**, 1560–1563. (doi:10.1126/science.1055465)
90. Golesorkhi M, Gomez-Pilar J, Catal Y, Tumati S, Yagoub MCE, Stamatakis EA, Northoff G. 2022 From temporal to spatial topography: hierarchy of neural dynamics in higher- and lower-order networks shapes their complexity. *Cereb. Cortex* **32**, 5637–5653. (doi:10.1093/cercor/bhac042)
91. Hasson U, Nastase SA, Goldstein A. 2020 Direct fit to nature: an evolutionary perspective on biological and artificial neural networks. *Neuron* **105**, 416–434. (doi:10.1016/j.neuron.2019.12.002)
92. Zahavi D. 2005 *Subjectivity and selfhood. Investing the first-person perspective*. Cambridge, MA: MIT Press.
93. Northoff G, Smith D. In press. The subjectivity of self and its ontology: from the world–brain relation to the point of view in the world. *Theory Psychol.* (doi:10.1177/09593543221080120)
94. Huang Z *et al.* 2016 Decoupled temporal variability and signal synchronization of spontaneous brain activity in loss of consciousness: an fMRI study in anesthesia. *Neuroimage* **124**, 693–703. (doi:10.1016/j.neuroimage.2015.08.062)
95. Tagliazucchi E, Chialvo DR, Siniatchkin M, Amico E, Brichant JF, Bonhomme V, Noirhomme Q, Laufs H, Laureys S. 2016 Large-scale signatures of unconsciousness are consistent with a departure from critical dynamics. *J. R. Soc. Interface* **13**, 20151027. (doi:10.1098/rsif.2015.1027)
96. Vanhaudenhuyse A *et al.* 2011 Two distinct neuronal networks mediate the awareness of environment and of self. *J. Cogn. Neurosci.* **23**, 570–578. (doi:10.1162/jocn.2010.21488)
97. Wengler K, Goldberg AT, Chahine G, Horga G. 2020 Distinct hierarchical alterations of intrinsic neural timescales account for different manifestations of psychosis. *eLife* **9**, e56151. (doi:10.7554/elife.56151)
98. Uscătescu LC *et al.* 2021 Reduced intrinsic neural timescales in schizophrenia along posterior parietal and occipital areas. *NPJ Schizophrenia* **7**, 55. (doi:10.1038/s41537-021-00184-x)
99. Northoff G, Sandsten KE, Nordgaard J, Kjaer TW, Parnas J. 2021 The self and its prolonged intrinsic neural timescale in schizophrenia. *Schizophr. Bull.* **47**, 170–179. (doi:10.1093/schbul/sbaa083)
100. Kent L, Wittmann M. 2021 Erratum to: Time consciousness: the missing link in theories of consciousness. *Neurosci. Conscious.* **2021**, niab015. (doi:10.1093/nc/niab011)
101. Singhal I, Srinivasan N. 2021 Time and time again: a multi-scale hierarchical framework for time-consciousness and timing of cognition. *Neurosci. Conscious.* **2021**, niab020. (doi:10.1093/nc/niab020)
102. Northoff G, Gomez-Pilar J. 2021 Overcoming rest–task divide—abnormal temporospatial dynamics and its cognition in schizophrenia. *Schizophr. Bull.* **47**, 751–765. (doi:10.1093/schbul/sbaa178)
103. Sengupta B, Tozzi A, Cooray GK, Douglas PK, Friston KJ. 2016 Towards a neuronal gauge theory. *PLoS Biol.* **14**, e1002400. (doi:10.1371/journal.pbio.1002400)
104. Northoff G. 2016 Is the self a higher-order or fundamental function of the brain? The ‘basis model of self-specificity’ and its encoding by the brain’s spontaneous activity. *Cogn. Neurosci.* **7**, 203–222. (doi:10.1080/17588928.2015.1111868)
105. De Jaegher H. 2013 Embodiment and sense-making in autism. *Front. Integr. Neurosci.* **7**, 15. (doi:10.3389/fnint.2013.00015)
106. Ciaunica A, Safron A, Delafield-Butt J. 2021 Back to square one: the bodily roots of conscious experiences in early life. *Neurosci. Conscious.* **2021**, niab037. (<https://academic.oup.com/nc/article/2021/2/niab037/6432320>)
107. Fagerholm ED, Foulkes WMC, Gallero-Salas Y, Helmchen F, Friston KJ, Moran RJ, Leech R. 2020 Conservation laws by virtue of scale symmetries in neural systems. *PLoS Comput. Biol.* **16**, e1007865. (doi:10.1371/journal.pcbi.1007865)
108. Sakthivadivel DAR. 2022 Towards a geometry and analysis for Bayesian mechanics. (<https://arxiv.org/abs/2204.11900>)