

# As without, so within: How the brain’s temporospatial alignment to the environment shapes consciousness

Georg Northoff\* (1,2,3), Philipp Klar\* (4), Magnus Bein (5), Adam Safron (6,7,8)

\* equal contribution

1. Mind, Brain Imaging and Neuroethics Research Unit; The Royal's Institute of Mental Health Research, University of Ottawa; Ottawa, ON, Canada
2. Mental Health Centre, Zhejiang University School of Medicine, Hangzhou, China
3. Centre for Cognition and Brain Disorders, Hangzhou Normal University, Hangzhou, China
4. Medical Faculty, C. & O. Vogt-Institute for Brain Research, Heinrich Heine University of Düsseldorf, Düsseldorf, Germany
5. Department of Biology and Department of Psychiatry, McGill University
6. Center for Psychedelic and Consciousness Research, Department of Psychiatry & Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA
7. Cognitive Science Program, Indiana University, Bloomington, IN, USA
8. Institute for Advanced Consciousness Studies, Santa Monica, CA, USA

## Abstract: Long version

Consciousness is constituted by a structure that includes contents as foreground and the environment as background. This structural relation between the experiential foreground background presupposes a relationship between the brain and the environment, often neglected in theories of consciousness. The Temporo-spatial Theory of Consciousness (TTC) addresses the brain-environment relation by a concept labeled “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. (1) The background layer comprises longer and more powerful timescales mediating topographic-dynamic similarities between different subjects’ brains. (2) 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 (INT) and temporal receptive windows (TRW). (3) 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. (1) The inter-subjectively shared contextual background of consciousness. (2) An intermediate layer that mediates the relationship between different contents of consciousness. (3) 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.

### **Abstract: Short version**

Consciousness is characterized by a structure of foreground contents and an environmental background. This structure presupposes a relationship between the brain and the environment neglected in many neuroscientific theories of consciousness. One neuroscientific theory of consciousness that addresses the brain-environment relation is the Temporo-Spatial Theory of Consciousness (TTC). By the mechanism of “temporo-spatial alignment”, the TTC considers the symmetry and synchronization of the brain with the environment. Alignment is a mechanism by which the brain adapts to and coordinates its neuronal activity with various interoceptive bodily and exteroceptive environmental stimuli. Based on a synthesis between empirical data and theoretical considerations, we suggest a three-layer conceptual model of neuro-phenomenal mechanism for consciousness. The neuronal layers are constituted by various lengths of the brain’s intrinsic neuronal timescales that correspond to phenomenal layers of consciousness, such as the environmental background and specific contents in the foreground of consciousness. The suggested three layers are thus shared between the brain’s neuronal activity and consciousness, providing their “common currency” on dynamical grounds coupled to the environment. In establishing an intimate relationship between the environment and brain, temporo-spatial alignment can also be conceived in terms of basic physical-energetic processes, such as free energy, and the dynamical emergence of (a)symmetries.

## **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 (Northoff and Zilio 2022a and b). 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 Northoff and Lamme 2020, Seth and Bayne 2022). Based on the mechanism of temporo-spatial alignment (Northoff 2013; Northoff Zilio 2022a), 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 (IWMT) (Safron 2020, 2022)—that considers the relationship of the brain to the environment as a key feature of consciousness (Northoff and Huang 2017, Northoff and Zilio 2022a and b). 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 (Northoff 2018), processes and encodes extrinsic inputs (see Box 1 in Golesorkhi et al. 2021a 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 behaviorism explained the locomotor or movement behavior 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 (von Holst 1939). 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 (Bandettini, Wong, Hinks, Tikofsky, and Hyde 1992), the investigation of the brain's spontaneous activity nonetheless lagged many years behind. The first so-called resting-state fMRI study by Biswal and colleagues investigated functional connectivity at rest, which occurred in 1995 (Biswal et al. 1995). It nonetheless took another six years until 2001, when Raichle and colleagues published their discovery of the resting-state's default-mode network (Raichle et al. 2001), until the investigation of the brain's spontaneous activity via the so-called resting-state spread into a mainstream operational research paradigm in functional MRI. Consequently, the resting-state represents an operational term referring to the empirical investigation of the brain's intrinsic spontaneous activity, such as via functional MRI, without applying specific stimuli or tasks to the subjects. Conversely, the brain's spontaneous activity describes ongoing and everlasting 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 functional magnetic resonance imaging (fMRI), the TTC is obtaining empirical evidence in support of the alignment hypothesis (Klar et al. 2022; Wainio-Theberge et al. 2021; Wolff et al. 2019a; Zilio et al. 2021).

#### *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; Köhler 1967; Wagemans et al. 2012) 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 (f.ex. the time-series of music or fluctuations of other sensory stimuli), cognitive dynamics (via psychological and behavioral tests recording associated time-series data (Rostami et al. 2022; Hua et al. 2022), and neuronal dynamics

(via the neuroimaging modalities of EEG, MEG, and fMRI). Environmental, cognitive-behavioral, and neuronal time-series share dynamics, such as fractal pink noise (Gisiger 2001; Gilden et al. 1995; Halley and Inchausti 2004; Klar et al. 2022; Riley et al. 2011; Voss and Clarke 1975). These shared dynamics between environmental, cognitive-behavioral, and neuronal levels consequently provide a bridge principle that we call “common currency” allowing the scientific environment-brain linkage for consciousness and behavior (Northoff et al. 2020; Kolvoort et al. 2020).

After briefly introducing the concept of alignment in connection to the three timescale layers we visualized 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 temporo-spatial alignment for other dynamic concepts, such as the free energy principle and symmetry/anti-symmetry.

**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 intrinsic neuronal timescales (INT) to environmental dynamics measurable by stimuli- or task-related temporal receptive windows (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: 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 (1) low-frequency high-amplitude timescales associated with the conscious background over a (2) intermediate layer bridging the first layer with (3) 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.

#### *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 (Fox and Raichle 2007; Mitra and Raichle 2016). 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 (Bijsterbosch et al. 2017). Spontaneous BOLD fluctuations are similar between individuals, reflecting the brain’s intrinsic functional architecture shared between populations.

*Intersubjective correlation (ISC) confirms similarity in topography and dynamics:* More recently, a novel method labeled inter-subject correlation (ISC) emerged. ISC aims to investigate shared functional states between the brain’s topography of the different subjects (Nastase et al. 2019; Yeshurun et al. 2021). 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. Functional MRI studies applying ISC measure responses to naturalistic stimuli, such as movies, stories, or auditory narratives (Simony et al. 2016), where the responses of one brain can even predict responses in other subjects’ brains that participated in the same naturalistic paradigm (Hasson et al. 2004; Hasson and Frith 2016). Hasson et al. (2004) 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 the others. Recent electrophysiological EEG and MEG recordings also show shared spatiotemporal

brain dynamics between different subjects (Chang et al. 2015; Chen and Farivar 2020; Hasson et al. 2012).

The inter-subject correlation 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 (1) fMRI (Tumati et al. unpublished) and (2) 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.

(1) *fMRI study*: The fMRI study (Tumati et al. unpublished) utilized 3 Tesla data from the Human Connectome Project S1200 release (Van Essen et al. 2013) of 974 healthy young subjects obtained from rest and task recordings (TR = 0.72 s). Functional scan acquisition comprised two 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 (MMP) atlas (Glasser et al. 2016) to obtain ROI-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 inter-subject correlation (ISC) by computing the BOLD's time-series standard deviation (SD) for each of the 360 regions.

Healthy physiological processes of the human body, such as heart-rate variability (Lipsitz and Goldberger 1992), blood flow (Bassingthwaight and van Beek 1988), volumes of breaths (Hoop, Kazemi and Liebovitch 1993), and fMRI recordings of human brain activity under conscious wakefulness (Huang et al. 2017; Klar et al. 2022) require a mixture between regularity and variability. The BOLD's standard deviation 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 SD across healthy subjects. Conversely, subjects with psychiatric disorders, such as schizophrenia, are expected to show a reduced degree of inter-subject correlation of the SD. It is expected that various psychiatric manifestations of schizophrenia on the level of experience and behavior correspond to the neurodiversity of temporo-spatial patterns of brain activity, therefore reducing the inter-subject correlation of the SD.

Tumati et al. (unpublished) hypothesized that (1) the resting-state intra-regional SD is topographically shared across the two scanning days recordings within- and between-subjects, and that (2) the relation between rest and task states SD topographies are similar, hence showing a rest-to-task carry-over effect of SD topography.

The findings yielded the following results. First, the resting-state SD topography showed high overlap across healthy subjects. The within-subject shared SD topography between days one and two yielded a high mean correlation across subjects ( $r = 0.84$ ), indicating similar intra-individual SD topography. The between-subject shared SD topography for day one ( $r = 0.74$ ) and day two ( $r = 0.74$ ) yielded high mean correlations across subjects. Second, the authors analyzed the SD topography in task states. As hypothesized, the SD 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 SD 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.

**Figure 2.** Inter-subject correlation (ISC) of the BOLD time-series standard deviation (SD) 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 SD between days one and two. **c)** Statistical comparison between regional differences into three groups: low, mid, and highly shared SD. The accompanying boxplots display the difference between the three group-based regions. **d)** SD topography at the single subject level. The mean SD correlation between days one and two across all subjects yielded a high

Pearson correlation ( $r = 0.84$ ). The correlation of each subject's SD 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:  $r = 0.55$ ).

(2) *EEG study*: the EEG study (Wainio-Theberge et al. unpublished) also utilized spatial inter-subject correlation (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 analyzed three EEG datasets. The first schizophrenia dataset comprised 34 subjects with schizophrenia (mean age/SD = 22.12/3.93) and 35 healthy controls (mean age/SD = 24.06/3.24) with a recording time of 5 min. The second schizophrenia dataset comprised 24 subjects with schizophrenia (mean age/SD = 45.5/8.91) and 25 healthy controls (mean age/SD = 45.88/15.79) with a recording time of 3 min. The third depression dataset comprised 44 depressed subjects (mean age/SD = 18.7/1.12) with high Beck Depression Inventory (BDI) scores and 74 healthy controls (mean age/SD = 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 intersubjective 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) (Minkowski 1927; Klar and Northoff 2021). Wainio-Theberge et al. (unpublished) hypothesized that subjects of the schizophrenia group exhibit a substantially lower inter-subject correlation (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 (Huang et al. 2017). (Other measurements included the log-transformed fractal and oscillatory power not reported by us here.) Conversely, the expectation for depressed patients was increased inter-subject correlation.

Since EEG lacks voxel-based time-series, the authors assessed the time-series of each of the 30 electrodes for inter-subject correlations. Wainio-Theberge et al. (unpublished) 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: (1) healthy-healthy correlation; (2) schizophrenia-schizophrenia correlation; (3) depression-depression correlation; and (4) 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 amongst 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 vs. depressed-healthy ( $p = 0.89$ ) and depressed vs. 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. (unpublished) 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 (Minkowski 1927) and contemporary views (Parnas and Sass 2001; Parnas 2012) on the psychopathology of schizophrenia, namely the disconnectedness to the social intersubjective life-world that healthy subjects share.

*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 (Friston 2011; Cole et al. 2010; Raichle 2015). 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 (Klar et al. 2022; Golesorkhi et al. 2021a; Zhang et al. 2018); a threefold topographic hierarchy of interoceptive, exteroceptive, and cognitive processing stages of the self (Qin et al. 2020); and the manifestation of different sensory input regions measured via the power-law exponent and Sample Entropy (Catal et al. 2022). 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 inter-subject correlations 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 vs. psychiatric groups. Notably, the schizophrenia group lost a shared inter-subject correlation 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 temporo-spatial 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 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, Scalabrini et al. 2021 for inter-subjective and cultural layers of the brain). Figure 3 visualizes the inter-subject correlation of the brain's neuronal dynamics across its topography for the environment-brain relation, namely temporo-spatial alignment on inter-subjective social grounds.

**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.

#### *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 “temporal receptive windows” (TRW) of electrophysiological and hemodynamic signals across subjects in response to the same environmental inputs.

*Temporal receptive windows (TRWs):* The temporal receptive window (TRW), initially suggested by Hasson et al. (2008), 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. (2008) 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 on TRWs (Lerner et al. 2014; Himberger et al. 2018; Jääskeläinen et al. 2021). Paradigmatically, Lerner et al. (2011) 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.

*From temporal receptive windows (TRWs) to intrinsic neuronal timescales (INT):* Inter-individually shared hierarchy of TRWs in the cerebral cortex raises the question to what extent TRWs are rooted in the brain’s intrinsic functional organization, as represented by spontaneous or resting state activity through intrinsic neuronal timescales (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. (2019b). The autocorrelation’s specification is sometimes labeled the autocorrelation window (ACW) in neuroimaging (Gao et al. 2020; Golesorkhi et al. 2021a and b; Wolff et al. 2022). 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 than fast and less powerful timescales, mirroring the properties of task-related TRWs.

Recordings of INT spanning from single-unit (Murray et al. 2014) over electrocorticography (ECoG) (Cavanagh et al. 2020; Honey et al. 2012) and MEG (Golesorkhi et al. 2021a; Demirtaş et al. 2019) to fMRI (Raut et al. 2020) demonstrated that intrinsic neuronal timescales, like TRWs, vary following an anatomical hierarchy. Furthermore, the fMRI study by Huang et al. (2018) 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. (2022) demonstrated that the brain’s power-law distribution, measured by the power-law exponent (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-square linear regression in the frequency-domain on a logarithmic scale increased.



*Theoretical inferences:* These observations of temporal receptive windows (TRWs) in response to extrinsic stimuli or task-related activity and intrinsic neuronal timescales (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 (Golesorkhi et al. 2021a; Wolff et al. 2022).

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 spatiotemporal 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 temporal receptive windows (Golesorkhi et al. 2021a; Hasson et al. 2015; Wolff et al. 2022). 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 (Safron et al. 2022). Given our findings of intersubjective similarity in topography and dynamics, we suppose that such temporal and spatial shaping of input processing is shared between subjects, i.e., inter-individually (see Figure 4).

**Figure 4.** The intermediate layer provides stochastic alignment by modulating a repertoire of the brain's intrinsic neuronal timescales (INT), measured in the resting-state, to a range of environmental dynamics resulting in temporal receptive windows (TRWs), measured in naturalistic stimuli paradigms.

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

The previous section introduced stimulus-related temporal receptive windows (TRWs) and intrinsic neuronal timescales (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.

*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) (Schirner et al. 2022; Waschke et al. 2021). 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 (Lakatos et al. 2019). In entrainment, intero- and exteroceptive stimuli force periodic delays in neuronal activity that locks their phase to that of the stimuli (Lakatos et al. 2019). 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 are rhythms between the nervous system's motor output, such as speech, and auditory perception of speech comprising shared frequencies (Giraud and Poeppel 2012). Neuronal entrainment supports perception and behavior such as music perception (Nozaradan et al. 2012; Doelling and Poeppel 2015), auditory detection (Lawrance et al. 2014), or visual contrast sensitivity (Cravo et al. 2013). 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 (Buzsáki and Draguhn 2004).

*Rhythmic vs. continuous mode:* To further unpack the environment-brain relation on the grounds of entrainment we elaborate two suggested mechanisms by Schroeder and Lakatos (2009a; 2009b): (1) a “rhythmic mode” of brain activity; and (2) a “continuous mode” of brain activity regarding the environment-brain interaction (see also Schroeder et al. 2010). The rhythmic and continuous modes of brain activity can represent two extreme endpoINT on a mutual and quantitative continuum (Northoff 2014) that, paradigmatically, is shifted to one of the poles such as in the neuropsychiatric disorder of schizophrenia (Lakatos et al. 2013).

(1) 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.

(2) The continuous mode of neuronal activity comes into play when environmental stimuli show high degrees of randomness with lack 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 (Fries et al. 2001). 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.

**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.

#### *Neuronal aspects of the three-layer organization:*

Summarizing the three subsections above, we suggest a three-layers of the brain’s temporo-spatial alignment with the environment. Layer one introduced an inter-individually shared cortical topography of neuronal dynamics. Inter-subject correlation (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 temporal receptive windows (TRWs) related to stimulus- or task-evoked activity and subsequently on intrinsic neuronal timescales (INT) of the brain’s ongoing spontaneous activity as operationally measured via 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 spatiotemporal 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 (Nastase et al. 2019; Yeshurun et al. 2021). 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 spatiotemporal 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 (Catal et al. 2022; Golesorkhi et al. 2022). Figure 6 provides an overview of the three-layer organization.

**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.

### **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.

*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 (Golesorkhi et al. 2021a; Hasson et al. 2020). 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 (Zahavi 2005; Northoff and Smith 2022). This, in turn, provides the background of consciousness, paradigmatically termed "vital contact with reality" by psychiatrist Minkowski (1927).

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.

*fMRI 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 Northoff and Huang 2017, Northoff and Zilio 2022a and b). Zhang et al. (2018) 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 (Huang et al. 2016; Tagliazucchi et al. 2016) 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 color and long-range temporal correlations, under propofol- and sevoflurane-induced unconsciousness.

The awake subjects in Zhang et al. (2018) showed a statistically significant shared voxel-based topography of the SD and the PLE under conscious wakefulness. Conversely, the loss of these inter-individually shared topographies was accompanied by the loss of consciousness in anesthesia which, as we assume, is related to the loss of shared input processing capacities based on the loss of shared resting-state topographic dynamics.

*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 (Minkowski 1927), indicating the loss of their 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.

*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 times scales and is relatively more stable, the intermediate layer is more flexible and can be associated with the changing contents of consciousness. A repertoire of intrinsic timescales (INT) that can form temporal receptive windows (TRWs) under stimulus- or task-related activity allows temporal integration and segregation balances of environmental inputs (Wolff et al. 2022; Golesorkhi et al. 2021a). Temporal integration (Himberger et al. 2018) allows connecting several inputs into one coherent content, while temporal segregation differentiates input clusters from each other, distinguishing contents of consciousness (Northoff and Zilio 2022b). 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- vs externally-oriented thoughts operate on timescales around 10-30 s (Vanhaudenhuyse et al. 2011, Rostami et al. 2022). 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 (Wengler et al. 2020, Uscatescu et al. 2021, Northoff et al. 2021) 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 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.

*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 ms range (Kent and Wittmann 2021; Northoff and Zilio 2021; Singhal and Srinivasan 2021). 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 (Northoff and Lamme 2020; Lakatos et al. 2019). 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 (Hua et al. 2022). 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 (Hua et al. 2022). 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 (Lakatos et al. 2019; Northoff and Zilio 2022b).

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 (Lakatos et al. 2013, Wolff et al. 2022). 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 Northoff and Gomez-Pilar 2021). This is supported by the fact that the ITPC deficits strongly correlate with positive symptoms (Lakatos et al. 2013, Wolff et al. 2022). 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 temporo alignment between environment and brain (Northoff et al. 2020). We summarize the suggested three-layer concept as follows: (1) the background layer is relatively stable on long-range and global spatiotemporal scales; this layer manifests itself in the experience of a shared and stable contextual background of the environment; (2) 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; (3) 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 fast frequencies is related to specific foreground contents of consciousness at specific pINT in time.

## Discussion - Temporo-spatial alignment, free energy and symmetry

### *Further inquiry in the three-layer model of consciousness*

#### *“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 modeled 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 egocentric perspective, or the preservation of enduring self-processes—could be thought of as “force fields” over conjoined neural and environmental dynamics (Sengupta et al. 2016).

More specifically, the ability to create aligned inner and outer (wave)forms can be understood as a kind of predictive modeling, where these symmetries may be understood as establishing a 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 (Northoff 2016; Northoff and Smith 2022). 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.

#### *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 (De Jaegher 2013). These may not only be enhanced by integrative world models, but in many ways may be required for such modeling processes to be successfully bootstrapped in an intersubjective fashion (Ciaunica, Safron, and Delafield-Butt 2021). That is, with respect to schizophrenia, disrupted temporo-spatial alignment and integrated world modeling 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 (Sengupta et al. 2016; Fagerholm et al., 2020; Sakthivadivel, 2022) that preserve essential symmetries of brain and environment through their various sources of temporal and spatial coherence (Northoff et al., 2020; Safron, 2022).

(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 neurophenomenal mechanisms of point of view and consciousness (iii-v) are detailed in Northoff and Smith (2022).

#### **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 Northoff and Zilio 2022b, Singhal and Srinivasan 2021, Kent and Wittmann 2021). 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" (Northoff et al. 2020a and b). Going beyond the brain, that makes 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.

### **Acknowledgment**

We herewith provide our gratitude to Shankar Tumati (figure and data on resting state variability) and Soeren Wainio-Theberge (schizophrenia data and figure) for providing and sharing their unpublished data for our manuscript.

### **Author contributions**

Georg Northoff and Philipp Klar wrote the main draft of the paper while Adam Safron and Magnus Bein expanded and revised subsequent drafts. The discussed data are from the group of Georg Northoff contributed by Shankar Tumati (variability) and Soeren Wainio-Theberge (schizophrenia).

### **Funding Statement**

G.N. is grateful for funding provided by UMRF, uOBMRI, Canada Institute of Health Research (CIHR) and Physicians Incorporated Services (PSI).

### **Data Accessibility Statement**

The data are available upon request.

### **References**

- Bandettini, P. A., Wong, E. C., Hinks, R. S., Tikofsky, R. S., & Hyde, J. S. (1992). Time course EPI of human brain function during task activation. *Magnetic Resonance in Medicine*, 25(2), 390-397.  
<https://doi.org/10.1002/mrm.1910250220>
- Bassingthwaighe JB, Liebovitch LS, West BJ. 1994. *Fractal Physiology*. New York: Oxford University Press.
- Bassingthwaighe, J.B., van Beek, J. H. G. M. Lightning and the Heart: Fractal Behavior in Cardiac Function. *Proc IEEE Inst. Electr. Electron. Eng.* **76(6)**, 693-699 (1988).
- Biswal, B., Yetkin, F. Z., Haughton, V. M. & Hyde, J. S. (1995). Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magnetic Resonance in Medicine*, 34(4), 537-541.  
<https://doi.org/10.1002/mrm.1910340409>
- Bijsterbosch J, Smith S, Beckmann C. 2007. *Introduction to Resting State fMRI Functional Connectivity*. Oxford: Oxford University Press.
- Buzsáki G, Draguhn A. 2004. Neuronal oscillations in cortical networks. *Science*. 304(5679): 1926-1929.  
<https://doi.org/10.1126/science.1099745>

- Catal Y, Gomez-Pilar J, Northoff G. 2022. Intrinsic Dynamics and Topography of Sensory Input Systems. *Cereb. Cortex*. 32(20):4592-4604. <https://doi.org/10.1093/cercor/bhab504>
- Cavanagh SE, Hunt LT, Kennerley SW. 2020. A Diversity of Intrinsic Timescales Underlie Neural Computations. *Front. Neural Circuits*. 14:615626. <https://doi.org/10.3389/fncir.2020.615626>
- Chang WT, Jääskeläinen IP, Belliveau JW, Huang S, Hung AY, Rossi S, Ahvenien J. 2015. *NeuroImage*. 114:49-56. <https://doi.org/10.1016/j.neuroimage.2015.03.066>
- Chen Y, Farivar R. 2020. Natural scene representations in the gamma band are prototypical across subjects. *NeuroImage*. 221:117010. <https://doi.org/10.1016/j.neuroimage.2020.117010>
- Ciaunica, A., Safron, A., & Delafield-Butt, J. (2021, November). Back to Square One: from Embodied Experiences in Utero to Theories of Consciousness. *Neuroscience of Consciousness*, 2021(2).
- 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. <https://doi.org/10.3389/fnsys.2010.00008>
- 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(9):4002-4010. <https://doi.org/10.1523/jneurosci.4675-12.2013>
- Demirtaş M, Burt JB, Helmer M, Ji JL, Adkinson BD, Glasser MF, Van Essen DC, Sotiropoulos SN, Anticevic A, Murray JD. 2019. Hierarchical Heterogeneity across Human Cortex Shapes Large-Scale Neural Dynamics. *Neuron*. 101(6):1181-1194. <https://doi.org/10.1016/j.neuron.2019.01.017>
- Doelling KB, Poeppel D. 2015. Cortical entrainment to music and its modulation by expertise. *Proc. Natl. Acad. Sci. U. S. A*. 112(45):E6233-6242. <https://doi.org/10.1073/pnas.1508431112>
- Fagerholm, E. D., Foulkes, W. M. C., Gallero-Salas, Y., Helmchen, F., Friston, K. J., Moran, R. J., & Leech, R. (2020). Conservation laws by virtue of scale symmetries in neural systems. *PLOS Computational Biology*, 16(5), e1007865. <https://doi.org/10.1371/journal.pcbi.1007865>
- Fox MD, Raichle ME. 2007. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat. Rev. Neurosci*. 8(9):700-711. <https://doi.org/10.1038/nrn2201>
- Freeman WJ, Rogers LJ, Holmes MD, Silbergeld DL. 2000. Spatial spectral analysis of human electrocorticograms including the alpha and gamma bands. *J. Neurosci. Methods*. 95(2):111-121. [https://doi.org/10.1016/S0165-0270\(99\)00160-0](https://doi.org/10.1016/S0165-0270(99)00160-0)
- Fried P, Reynolds JH, Rorie AE, Desimone R. 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*. 291(5508):1560-1563. <https://doi.org/10.1126/science.1055465>
- Friston KJ. 2011. Functional and effective connectivity: a review. *Brain Connect*. 1(1):13-36. <https://doi.org/10.1089/brain.2011.0008>
- Gao R, van den Brink RL, Pfeffer T, Voytek B. Neuronal timescales are functionally dynamic and shaped by cortical microarchitecture. *Elife*. 9:e61277. <https://doi.org/10.7554/elife.61277>
- Gilden DL, Thornton T, Mallon MW. 1995. 1/f noise in human cognition. *Science*. 267(5205):1837-1839 <https://doi.org/10.1126/science.7892611>
- Giraud AL, Poeppel D. 2012. Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci*. 15(4):511-517. <https://doi.org/10.1038/nn.3063>



- Gisiger T. 2001. Scale invariance in biology: coincidence or footprint of a universal mechanism? *Biol. Rev. Camb. Philos. Soc.* 76(2):161-209. <https://doi.org/10.1017/s1464793101005607>
- Glasser MF, Coalson TS, Robinson EC, Hacker CD, Harwell J, Yacoub E, Ugurbil K, Andersson J, Beckmann CF, Jenkinson M, Smith SM, Van Essen DC. 2016. A multi-modal parcellation of human cerebral cortex. *Nature.* 536(7615):171-178. <https://doi.org/10.1038/nature18933>
- 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.* <https://doi.org/10.1093/cercor/bhac042>
- Golesorkhi M, Gomez-Pilar J, Tumati S, Fraser M, Northoff G. 2021a. Temporal hierarchy of intrinsic neural timescales converges with spatial core-periphery organization. *Commun. Biol.* 4(1):277. <https://doi.org/10.1038/s42003-021-01785-z>
- Golesorkhi, M, Gomez-Pilar J, Zilio F, Berberian N, Wolff A, Yagoub MCE, Northoff G. (2021b). The brain and its time: intrinsic neural timescales are key for input processing. *Communications Biology*, 4(1), 1-16. <https://doi.org/10.1038/s42003-021-02483-6>
- Halley JM, Inchausti P. 2004. The increasing importance of 1/f-noises as models of ecological variability. *Fluctuation and Noise Letters.* 04(02):R1-R26. <https://doi.org/10.1142/S0219477504001884>
- Hasson U, Chen J, Honey CJ. 2015. Hierarchical process memory: memory as an integral component of information processing. *Trends Cogn. Sci.* 19(6):304-313. <https://doi.org/10.1016/j.tics.2015.04.006>
- Hasson U, Frith CD. 2016. Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371(1693):20150366. <https://doi.org/10.1098/rstb.2015.0366>
- 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(2):114-121. <https://doi.org/10.1016/j.tics.2011.12.007>
- Hasson U, Nastase SA, Goldstein A. 2020. Direct Fit to Nature: An Evolutionary Perspective on Biological and Artificial Neural Networks. *Neuron.* 105(3):416-434. <https://doi.org/10.1016/j.neuron.2019.12.002>
- Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R. 2004. Intersubject synchronization of cortical activity during natural vision. *Science.* 303(5664). 1634-1640. <https://doi.org/10.1126/science.1089506>
- Hasson U, Yang E, Vallines I, Heeger DJ, Rubin N. 2008. A Hierarchy of Temporal Receptive Windows in Human Cortex. *J. Neurosci.* 28(10):2539-2550. <https://doi.org/10.1523/jneurosci.5487-07.2008>
- Himberger KD, Chien HY, Honey CJ. 2018. Principles of Temporal Processing Across the Cortical Hierarchy. *Neuroscience.* 389:161-174. <https://doi.org/10.1016/j.neuroscience.2018.04.030>
- Honey CJ, Thesen T, Donner TH, Silbert LJ, Carlson CE, Devinsky O, Doyle WK, Rubin N, Heeger DJ, Hasson U. 2012. Slow Cortical Dynamics and the Accumulation of Information over Long Timescales. *Neuron.* 76(2):423-434. <https://doi.org/10.1016%2Fj.neuron.2012.08.011>
- Hoop, B., Kazemi, H., Liebovitch, L. S. Rescaled range analysis of resting respiration. *Chaos.* 3(1), 27-29 (1993).
- 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(1):209. <https://doi.org/10.1038/s42003-022-03146-w>
- 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(9):2304-2317. <https://doi.org/10.1523/jneurosci.2545-17.2018>

- Huang Z, Zhang J, Longtin A, Dumont G, Duncan NW, Pokorný J, Qin P, Dai R, Ferri F, Weng X, Northoff G. 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. <https://doi.org/10.1093/cercor/bhv288>
- Huang Z, Zhang J, Wu J, Qin P, Wu X, Wang Z, Dai R, Li Y, Liang W, Mao Y, Yang Z, Zhang J, Wolff A, Northoff G. 2016. Decoupled temporal variability and signal synchronization of spontaneous brain activity in loss of consciousness: An fMRI study in anesthesia. *NeuroImage.* 124:693-703. <https://doi.org/10.1016/j.neuroimage.2015.08.062>
- Jääskeläinen IP, Sams M, Glerean E, Ahveninen J. 2021. Movies and narratives as naturalistic stimuli in neuroimaging. *NeuroImage.* 224:117445. <https://doi.org/10.1016/j.neuroimage.2020.117445>
- Kent L, Wittmann M. 2021. Erratum to: Time consciousness: the missing link in theories of consciousness. *Neurosci. Conscious.* 2021(2). <https://doi.org/10.1093/nc/niab011>
- Klar, P., Çatal, Y., Langner, R., Huang, Z., Northoff, G. 2022. Scale-free dynamics of the core-periphery topography. *Hum. Brain Mapp.* 1-21. <https://doi.org/10.1002/hbm.26187>.
- Köhler W. 1967. Gestalt psychology. *Psychol. Forsch.* 31(1):18-30. <https://doi.org/10.1007/bf00422382>
- 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(15):4355-4374. <https://doi.org/10.1002/hbm.25129>
- Lakatos P, Gross J, Thut G. 2019. A New Unifying Account of the Roles of Neuronal Entrainment. *Curr. Biol.* 29(18):R890-R905. <https://doi.org/10.1016/j.cub.2019.07.075>
- Lakatos P, Schroeder CE, Leitman DI, Javitt DC. 2013. Predictive suppression of cortical excitability and its deficit in schizophrenia. *J. Neurosci.* 33(28):11692-116702. <https://doi.org/10.1523/jneurosci.0010-13.2013>
- Lawrance ELA, Harper NS, Cooke JE, Schnupp WH. 2014. Temporal predictability enhances auditory detection. *J. Acoust. Soc. Am.* 135(6):EL357-363. <https://doi.org/10.1121/1.4879667>
- Lerner Y, Honey CJ, Katkov M, Hasson U. 2014. Temporal scaling of neural responses to compressed and dilated natural speech. *J. Neurophysiol.* 111(12):2433-2444. <https://doi.org/10.1152/jn.00497.2013>
- 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(8):2906-2915. <https://doi.org/10.1523/jneurosci.3684-10.2011>
- Lipsitz L. A., Goldberger, A. L. 1992. Loss of 'complexity' and aging. Potential applications of fractals and chaos theory to senescence. *IAMA.* 267(13), 1806-1809.
- Minkowski E. 1927. La schizophrénie. Psychopathologie des schizoïdes et des schizophrènes. Paris: Payot.
- Mitra A, Raichle ME. 2016. How networks communicate: propagation patterns in spontaneous brain activity. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 371(1705):20150546. <https://doi.org/10.1098/rstb.2015.0546>
- Murray JD, Bernacchia A, Freedman DJ, Romo R, Wallis JD, Cai X, Padoa-Schioppa C, Pasternak T, Seo H, Lee D, Wang XJ. 2014. A hierarchy of intrinsic timescales across primate cortex. *Nat. Neurosci.* 17(12):1661-1663. <https://doi.org/10.1038%2Fnn.3862>
- Nastase SA, Gazzola V, Hasson U, Keysers C. 2019. Measuring shared responses across subjects using intersubject correlation. *Soc. Cogn. Affect. Neurosci.* 14(6):668-685. <https://doi.org/10.1093/scan/nsz037>

- 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. <https://doi.org/10.1016/j.neubiorev.2017.07.013>
- 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. <https://doi.org/10.1016/j.neubiorev.2020.07.019>
- Northoff G, Smith D. 2022. The subjectivity of self and its ontology: From the world-brain relation to the point of view in the world. *Theory and Psychology*. 1-30. <https://doi.org/10.1177/09593543221080120>
- 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. <https://doi.org/10.1016/j.plrev.2019.05.002>
- Northoff G, Zilio F. 2022a. Temporo-spatial Theory of Consciousness (TTC) - Bridging the gap of neuronal activity and phenomenal states. *Behav. Brain Res.* 424:113788. <https://doi.org/10.1016/j.bbr.2022.113788>
- Northoff G, Zilio F. 2022b. From Shorter to Longer Timescales: Converging Integrated Information Theory (IIT) with the Temporo-Spatial Theory of Consciousness (TTC). *Entropy*. 24(2):270. <https://doi.org/10.3390/e24020270>
- Northoff G. 2014. *Unlocking the Brain. Volume 2: Consciousness*. New York: Oxford University Press.
- Nozaradan S, Peretz I, Mouraux A. Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *J. Neurosci.* 32(49):17572-17581. <https://doi.org/10.1523/jneurosci.3203-12.2012>
- Parnas J, LA Sass. 2001. Self, Solipsism, and Schizophrenic Delusions. *Philosophy, Psychiatry & Psychology*. 8(2):101-120. <http://dx.doi.org/10.1353/ppp.2001.0014>
- Parnas J. 2012. The core gestalt of schizophrenia. *World Psychiatry*. 11(2):67-69. <https://doi.org/10.1016%2Fj.wpsyc.2012.05.002>
- 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. <https://doi.org/10.1016/j.neubiorev.2020.05.004>
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(2), 676-682. <https://doi.org/10.1073/pnas.98.2.676>
- Raichle ME. 2015. The brain's default mode network. *Annu. Rev. Neurosci.* 38:433-447. <https://doi.org/10.1146/annurev-neuro-071013-014030>
- Raut RV, Snyder AZ, Raichle ME. 2020. Hierarchical dynamics as a macroscopic organizing principle of the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 117(34):20890-20897. <https://doi.org/10.1073/pnas.2003383117>
- Riley MA, Shockley K, van Orden G. 2011. Learning from the body about the mind. *Top. Cogn. Sci.* 4(1):21-34. <https://doi.org/10.1111/j.1756-8765.2011.01163.x>
- 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(5):258-272. <https://doi.org/10.1159/000523944>
- Safron, 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. *Frontiers in Artificial Intelligence*, 3(30). doi: 10.3389/frai.2020.00030
- Safron A (2022) Integrated World Modeling Theory expanded: Implications for the future of consciousness. *Frontiers in Computational Neuroscience* 16:642397. doi: 10.3389/fncom.2022.642397
- Sakthivadivel, D. A. R. (2022). *Towards a Geometry and Analysis for Bayesian Mechanics* (arXiv:2204.11900). arXiv. <https://doi.org/10.48550/arXiv.2204.11900>
- 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(2), 37-45. <https://doi.org/10.1111/pcn.13185>
- Schirner M, Kong X, Yeo BTT, Deco G, Ritter P. 2022. Dynamic primitives of brain network interaction. *NeuroImage*. 250:118928. <https://doi.org/10.1016/j.neuroimage.2022.118928>
- Schroeder CE, Lakatos P. 2009a. The gamma oscillation: master or slave? *Brain Topogr.* 22(1):24-26. <https://doi.org/10.1007/s10548-009-0080-y>
- Schroeder CE, Lakatos P. 2009b. Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci.* 32(1):9-18. <https://doi.org/10.1016/j.tins.2008.09.012>
- Schroeder CE, Wilson DA, Radman T, Scharfman H, Lakatos P. 2010. Dynamics of Active Sensing and perceptual selection. *Curr. Opin. Neurobiol.* 20(2):172-176. <https://doi.org/10.1016/j.conb.2010.02.010>
- Sengupta, B., Tozzi, A., Cooray, G. K., Douglas, P. K., & Friston, K. J. (2016). Towards a Neuronal Gauge Theory. *PLOS Biology*, 14(3), e1002400. <https://doi.org/10.1371/journal.pbio.1002400>
- Shulman RG, Hyder F, Rothmann DL. 2009. Baseline brain energy supports the state of consciousness. *Proc. Natl. Acad. Sci. U. S. A.* 106(27):11096-11101. <https://doi.org/10.1073/pnas.0903941106>
- Shulman RG, Rothman DL, Behar KL, Hyder F. 2004. Energetic basis of brain activity: implications for neuroimaging. *Trends Neurosci.* 27(8):489-495. <https://doi.org/10.1016/j.tins.2004.06.005>
- 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. <https://doi.org/10.1038/ncomms12141>
- Singhal I, Srinivasan N. 2021. Time and time again: a multi-scale hierarchical framework for time-consciousness and timing of cognition. *Neurosci. Conscious.* 2021(2). <https://doi.org/10.1093/nc/niab020>
- Sokoloff L, Mangold R, Wechsler RL, Kenney C, Kety SS. 1955. The effect of mental arithmetic on cerebral circulation and metabolism. *J. Clin. Invest.* 34:1101-1108. <http://dx.doi.org/10.1172/JCI103159>
- 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(114):20151027. <https://doi.org/10.1098/rsif.2015.1027>
- 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. <https://doi.org/10.1016/j.neuroimage.2013.05.041>
- von Holst, E. 1939. Über die nervöse Funktionsstruktur des rhythmisch tätigen Fischrückensmarks. *Pflügers Arch.* 241, 569-611. <https://doi.org/10.1007/BF01766126>
- Voss RF, Clarke J. 1975. 1/f Noise in Music and Speech. *Nature*. 258:317-318.
- 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(6):1172-1217. <https://doi.org/10.1037/a0029333>

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 <https://doi.org/10.1016/j.neuroimage.2022.119245>

Wainio-Theberge S, Wolff A, Northoff G. 2021. Dynamic relationships between spontaneous and evoked electrophysiological activity. *Commun. Biol.* 4(1):741. <https://doi.org/10.1038/s42003-021-02240-9>

Waschke L, Kloosterman NA, Obleser J, Garrett DD. 2021. Behavior needs neural variability. *Neuron*. 109(5):751-766. <https://doi.org/10.1016/j.neuron.2021.01.023>

Wolff A, Yao L, Gomez-Pilar J, Shoaran M, Jiang N, Northoff G. 2019a. Neural variability quenching during decision-making: Neural individuality and its prestimulus complexity. *NeuroImage*. 192:1-14. <https://doi.org/10.1016/j.neuroimage.2019.02.070>

Wolff A, Di Giovanni DA, Gomez-Pilar J, Nakao T, Huang Z, Longtin A, Northoff G. 2019b. The temporal signature of self: Temporal measures of resting-state EEG predict self-consciousness. *Hum. Brain Mapp.* 40(3), 789-803. <https://doi.org/10.1002/hbm.24412>

Yeshurun Y, Nguyen M, Hasson U. 2021. The default mode network: where the idiosyncratic self meets the shared social world. *Nat. Rev. Neurosci.* 22(3):181-192. <https://doi.org/10.1038/s41583-020-00420-w>

Zahavi D. 2005. Subjectivity and Selfhood. Investing the first-person perspective. Cambridge: MIT Press.

Zhang J, Huang Z, Chen Y, Zhang J, Ghinda D, Nikolova Y, Wu J, Xu J, Bai W, Mao Y, Yang Z, Duncan N, Qin P, Wang H, Chen B, Weng X, Northoff G. 2018. Breakdown in the temporal and spatial organization of spontaneous brain activity during general anesthesia. *Hum. Brain Mapp.* 39(5):2035-2046. <https://doi.org/10.1002/hbm.23984>

Zilio F, Gomez-Pilar J, Cao S, Zhang J, Zang D, Qi Z, Tan J, Hiromi T, Wu, X, Fogel S, Huang Z, Hohmann MR, Fomina T, Synofziki M, Grosse-Wentrup M, Owen AM, Northoff G. 2021. Are intrinsic neural timescales related to sensory processing? Evidence from abnormal behavioral states. *NeuroImage*. 226:117579. <https://doi.org/10.1016/j.neuroimage.2020.117579>