



Topographic-dynamic reorganisation model of dreams (TRoD) – A spatiotemporal approach

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ABSTRACT

Dreams are one of the most bizarre and least understood states of consciousness. Bridging the gap between brain and phenomenology of (un)conscious experience, we propose the Topographic-dynamic Re-organization model of Dreams (TRoD). Topographically, dreams are characterized by a shift towards increased activity and connectivity in the default-mode network (DMN) while they are reduced in the central executive network, including the dorsolateral prefrontal cortex (except in lucid dreaming). This topographic re-organization is accompanied by dynamic changes; a shift towards slower frequencies and longer timescales. This puts dreams dynamically in an intermediate position between awake state and NREM 2/SWS sleep. TRoD proposes that the shift towards DMN and slower frequencies leads to an abnormal spatiotemporal framing of input processing including both internally- and externally-generated inputs (from body and environment). In dreams, a shift away from temporal segregation to temporal integration of inputs results in the often bizarre and highly self-centric mental contents as well as hallucinatory-like states. We conclude that topography and temporal dynamics are core features of the TroD, which may provide the connection of neural and mental activity, e.g., brain and experience during dreams as their “common currency”.

1. Introduction

1.1. Dreams: a special state of both consciousness and brain

Dreams are one of the most bizarre states of consciousness. They display a peculiar level of awareness as a hybrid state between awake consciousness and completely unconscious. At the same time, dreams (during REM sleep) exhibit bizarre mental contents which usually do not surface in our waking consciousness. While the dream contents are often strange or bizarre, they nevertheless are somewhat (i.e., indirectly) semantically associated with our own daytime experiences (Blagrove et al., 2011; Corsi-Cabrera et al., 1986; Koninck et al., 1990; Malinowski and Horton, 2014; Nielsen et al., 2004; Solomonova et al., 2015; Stickgold et al., 2001; Wamsley and Stickgold, 2011). Moreover, dream

contents mediate newly learned skills and individual differences in intellectual strengths and weaknesses (Blagrove and Pace-Schott, 2010; Butler and Watson, 1985; Fitch and Armitage, 1989; Fogel et al., 2018, 2022; Foulkes et al., 1990).

Dreams also reflect a special state of the brain. During phasic REM sleep, changes in key nodes of the Default-Mode Network (DMN) have been observed (Hong et al., 2021). There is not a simple decrease in functional brain communication, though, but rather, a topographic re-organization of higher-order areas like in the case of DMN & frontoparietal connectivity (relative to other regions like lower-order unimodal) (See below for details) (Houldin et al., 2021). A variety of changes in other brain's regions and networks has also been observed; these include the hippocampus and amygdala; the extent to which is correlated with emotional load, bizarreness, and the vividness of dreams

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(De Gennaro et al., 2011; see also Benedetti et al., 2015).

Changes in the brain's topography become even more complex in lucid dreaming. Subjects showing high frequency of lucid dreaming exhibit increased functional connectivity during the awake resting state between prefrontal and temporal-parietal cortex (Baird et al., 2018). The state of lucid dreaming itself is associated with increased activation of the precuneus, parietal, prefrontal and temporal cortex (Dresler et al., 2012) and sensorimotor areas (Dresler et al., 2011). These topographic features are accompanied by dynamic changes in the power and/or phase in beta, theta, alpha and gamma frequencies (Siclari et al., 2017, 2018, 2020; Ruby, 2020; Schreiner et al., 2018, 2021; Schreiner and Staudigl, 2020) and specific EEG microstates Bréchet and Michel (2022) during dreams.

Taken together, this renders dreams a special brain state and form of consciousness that remains challenging to investigate scientifically from both a neuronal and phenomenological perspective.

1.2. From brain to experience: neurophenomenal hypotheses

How do these topographic and dynamic changes in the brain during dreams yield the experience of bizarre contents and the peculiar level/state of consciousness? Various models have been suggested, including: predictive coding (Clark, 2013; Hobson, 2009; Hobson et al., 2021), activation input modulation (AIM, Hobson, 2009; Hobson et al., 2022), integrated information (Tononi et al., 2016), spatiotemporal framework (Windt, 2010, 2020), the activation-synthesis theory (Hobson and McCarley, 1977) and the scanning hypothesis of REM sleep (Leclair-Visonneau et al., 2010). These models focus mainly on the neural changes underlying dreams. In contrast, they more-or-less leave open how these neural changes lead to the abnormal experience of one's self and its bizarre mental contents during dreams. Bridging that yet open gap between neural and mental levels of dreams is the main goal of this paper. Therefore, our aim is to connect the experience in dreams to their neural substrates by developing so-called neuro-phenomenal hypotheses (Northoff 2014a and b, Northoff, 2015).

Here, we introduce the Topographic Dynamic Re-organization model of Dreams (TroD). In a nutshell, the TroD proposes that both topography and temporal dynamics are reorganized in the dreaming brain which, in turn, reorganizes the spatiotemporal coordinates of our experience, that is, *the structure of consciousness and its mental contents* (See Fig. 1). We introduce an explicitly spatiotemporal model of dreams which allows to bridge the gap between neuronal fluctuations and mental (or phenomenal) experience (Northoff et al., 2020a, 2020b). This remains one of the main challenges in the scientific study of dreaming and of consciousness in general (see Box 2).

The TroD relies on two key background assumptions. First, following the Temporo-spatial Theory of Consciousness (TTC) (Northoff and Huang, 2017; Northoff and Zilio, 2022a, 2022b), it assumes dream consciousness to be essentially based on the brain's spatiotemporal features, notably its topography and temporal dynamics (see Box 2 for comparing the TTC with other theories of consciousness). Secondly, TroD relies on the background assumption that the spatiotemporal features of the brain's neural activity, i.e., its neural topography and temporal dynamics, resurface in more-or-less corresponding spatiotemporal features of our experience, i.e., mental topography and temporal dynamics. Both topography and temporal dynamics are shared by neural and mental states as their "common currency" (Northoff et al., 2020a, 2020b; Northoff and Scalabrini, 2021). Finally, we do not claim to develop an overarching or complete theory of dreams. Instead, our aims are more modest. Here, we aim to describe a model of dreams elaborating the connection of neural and mental features, e.g., neuro-phenomenal hypotheses that can be tested experimentally Fig. 1.

2. Part I. Topographic re-organization during dreams

2.1. Default-mode network and lateral prefrontal cortex

One cannot conceive the brain's topographic changes in REM sleep without taking into consideration the other sleep stages. NREM 1 sleep is characterized by mostly activation in visual cortex and its various widespread regions. At the same time, it seems that the lateral prefrontal cortex and the Central Executive Network (CEN) tend to reduce their activity level at this stage (Tanabe et al., 2020). NREM 2 shows more diffuse changes which are not yet clearly identified, as the results are somewhat counterintuitive, if not contradictory (Fox et al., 2016; Tanabe et al., 2020), although event-related approaches have clarified brain areas that are specifically activated during NREM, in response to events such as spindles (Andrade et al., 2011; Caporro et al., 2012; Jegou et al., 2019; Laufs et al., 2007; Schabus et al., 2007; Tyvaert et al., 2008) and slow waves (Caporro et al., 2012; Dang-Vu et al., 2008) and their functional significance (Bergmann et al., 2012; Boutin et al., 2018; Dang-Vu et al., 2010; Fang et al., 2020, 2022; Fogel et al., 2017). Finally, slow-wave sleep (SWS) shows generally reduced activity levels in widespread regions of the brain with lower degrees of functional connectivity between all regions (Tanabe et al., 2020). Given the difficulty in acquiring simultaneous EEG and fMRI, in general, and especially during sleep, caution is warranted, as these results are based on a limited number of small studies, especially for REM sleep.

REM-sleep is characterized by a variety of changes in different regions. One key finding is increased activity and connectivity within the cortical midline regions of the DMN in especially medial prefrontal cortex (Fox et al., 2016; Houldin et al., 2021). At the same time, activity in lateral prefrontal cortex and CEN is reduced (Fox et al., 2016). However, recent work has found that all canonical resting state networks (Smith et al., 2019) are present in REM sleep, and that there are no unique resting state functional networks specific to REM sleep per se (Houldin et al., 2019). In addition, functional connectivity in REM sleep resembles that of the awake state (Houldin et al., 2021). Hence, the basic networks are all present during dreams as in the awake state. What is different in dreams compared to the awake state is the exact weighting or balancing among the different networks relative to each other, that is, their overall topographic organization. The REM-related changes in the reciprocal modulation of medial vs. lateral prefrontal cortex/DMN vs. CEN, with the shift towards the DMN at the expense of CEN need to be considered within the overall topographic context that puts REM-sleep within the continuum of the different sleep stages (Houldin et al., 2019, 2021).

MRI studies of lucid dreaming (LD) also suggest a key role of the DMN and CEN (see Dresler et al., 2015; Baird et al., 2019 for excellent overviews). LD is a state where one becomes aware that they are asleep and in a dream state. In a seminal study, Voss et al. (2009) observed increased activity in lateral prefrontal cortex as key region of the CEN; that was further supported by a subsequent combined fMRI-EEG study where lateral prefrontal activity was heightened together with the precuneus and inferior parietal lobule as typical regions of the CEN (Dresler et al., 2012). Subsequently, further support for elevated activity of the dorsolateral prefrontal cortex (Filevich et al., 2015) and its increased functional connectivity with temporo-parietal associations regions (Baird et al., 2018, 2019) were reported (See also Dresler et al., 2015) Fig. 2.

2.2. The hippocampus

During REM sleep, increased activation and connectivity of medial temporal regions, including the hippocampus are observed (Fox et al., 2016 for review). Given that the hippocampus is key in encoding and retrieving memory, this fits well with the observation that recent and remote memories are retrieved during dreams as well as. At the same time, memory consolidation is enhanced during dream-rich sleep.

Topographic-dynamic Reorganization model of dreams

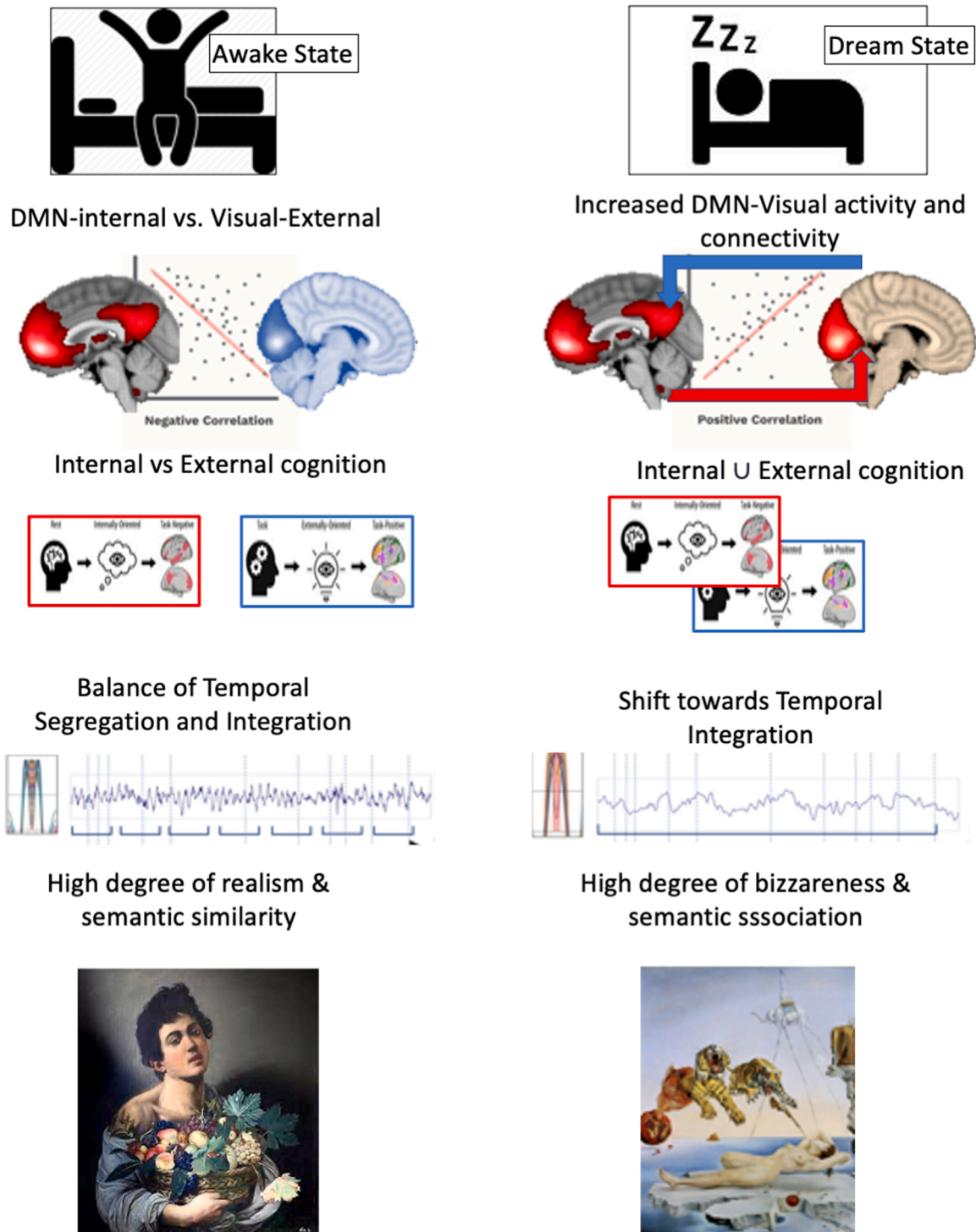
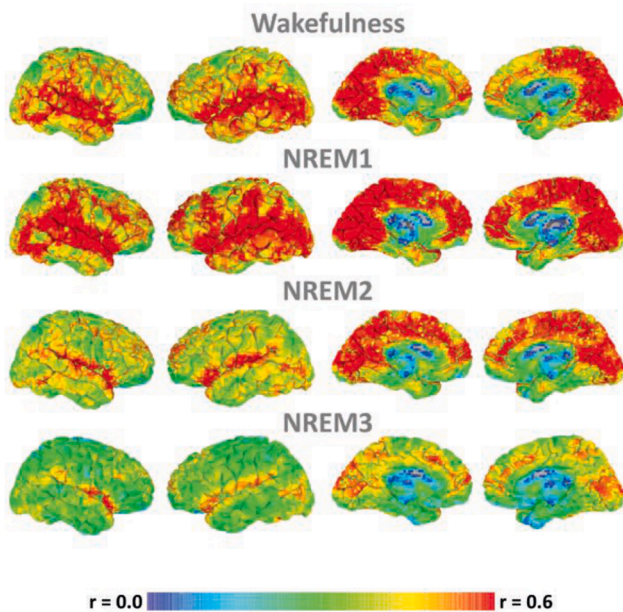


Fig. 1. Visual representation of “Awake state” vs “Dream state” according the Topographic-dynamic Reorganization model of dream (TRoD). The main hypotheses of topographical, internal-external cognition, dynamic and content levels are represented for both states.

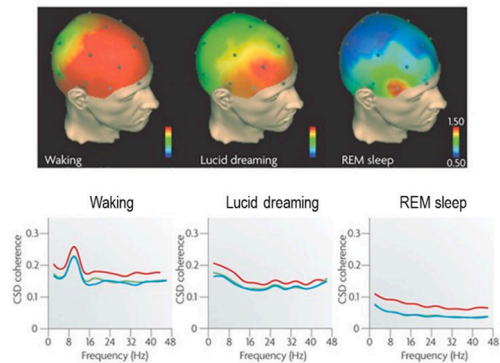
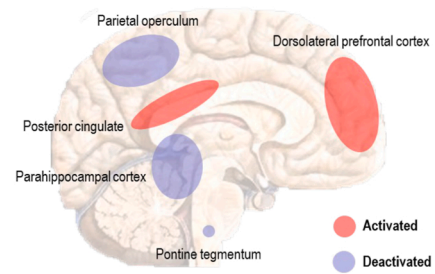
However, relatively little is known about replay during REM sleep, specifically. REM and NREM sleep are important for dissociable aspects of memory (for review see [Rasch and Born, 2013](#); [Fogel et al., 2022](#)), and reactivation has been observed in both REM ([Laureys et al., 2001](#); [Maquet, 2000](#)) and NREM ([Antony et al., 2018](#); [Bergmann et al., 2012](#); [Boutin et al., 2018](#); [Fogel et al., 2017](#); [Jegou et al., 2019](#)). Not only is reactivation observed during sleep, but there is also a replaying of the

spatial and temporal information of the encoded memory trace that repeatedly unfolds during subsequent sleep ([Buzsáki, 1989](#); [Girardeau et al., 2009](#); [Lansink et al., 2009](#); [Louie and Wilson, 2001](#); [Skaggs and McNaughton, 1996](#)).

Various studies show that the content of newly acquired memories is reflected in the content of our dreams ([Kussé et al., 2012](#); [Stickgold et al., 2000](#); [Wamsley et al., 2010a, 2010b](#); [Wamsley, 2014](#)), suggesting



Tanabe et al., 2020



Hobson, Gott, Friston, 2021

Fig. 2. Global signal correlation in human subjects in different stages of sleep (Tanabe et al., 2020 on the left side) and activated and deactivated regions of the brain during REM, relative to the wakefulness, as measured by Positron Emission Tomography (Hobson, Gott, Friston, 2021 on the right side).

that replay transcends the cellular, systems, behavioural and perceptual levels (Abel et al., 2013). While dream incorporation suggests that REM sleep might be principally responsible for replaying of newly acquired memories, hippocampal replay is primarily thought to occur during NREM sleep. During NREM sleep, the brain enters a burst state, characterized by sleep spindles and slow waves. Reactivation and replay are thought to occur during time-locked hippocampal ripples nested in the troughs of sleep spindles, temporally grouped by the excitatory phase of slow oscillations during NREM sleep (for review of the *Active Systems Consolidation hypothesis*, see Diekelmann and Born, 2010). This process is thought to underlie the hippocampal-neocortical transfer of the memory trace, as part of the memory consolidation process. While this might explain the role of NREM sleep in memory consolidation, the neural mechanisms and role of REM sleep (especially in humans, where dreaming can be confirmed) is less clear. However, recent studies suggest that REM sleep refines newly formed memory traces via selective pruning of synapses, and strengthening of remaining ones (Li et al., 2017).

Taken together, sleep is involved in the hippocampal-neocortical dialogue occurring during memory consolidation. This process, driven by the action of slow waves, spindles and hippocampal ripples, predominates during NREM sleep, and is reflected by reactivation an even neuronal replay of the memory trace. During subsequent REM sleep, the memory is processed further, and there is some limited evidence for replay, the intensity of which may be related to rapid eye movements and theta rhythms (Thompson et al., 2021). This process may be reflected in dream content (Wamsley and Stickgold, 2011).

We propose, albeit speculatively, that the changes in hippocampus and related memories need to be viewed within the context of the brain's overall change in topography and temporal dynamics. Specifically, the hippocampus-based retrieval of memories during dreams takes place within a DMN-centred topographic organization that dynamically is slower than in the awake state. That, we propose, will lead to an altered meaning of the retrieved events during dreams compared to the awake state (See below for details).

2.3. Visual cortex

What about sensorimotor regions? There is increased activity in widespread regions of the visual cortex during dreams, i.e., REM, compared to NREM sleep stages (Domhoff and Fox, 2015; Fox et al., 2013, 2016). This is even more remarkable given that the eyes are closed during sleep such that the subjects do not receive direct visual input from the external environment. The observed activity increase in visual cortex may consequently be related to *internally-generated* rather than external inputs from either within the visual cortex itself or other regions, that is, its own spontaneous activity. This is further supported by EEG studies that, during resting state in REM, show increased faster frequencies (gamma) in parietal and occipital electrodes, the so-called '*posterior hot zones*' of consciousness (Storm et al., 2017; Tononi et al., 2016), which also correlates with the phenomenologically reported dream content (Siclari et al., 2017, 2018; see also Br chet et al., 2020 for EEG-based occipital microstates related to dreams; see also Ruby, 2020 for a critical review).

Together, the visual cortex' resting state activity is elevated in dreams which can only be related to an increase in internally-generated visual inputs by the spontaneous activity itself. In contrast, task-evoked activity in the visual cortex is usually associated with externally-generated visual inputs. During sleep, this remains absent due to the lack of visual processing of external environmental inputs (the eyes are closed). Interestingly, the extent of visual cortex spontaneous activity during dreams reaches the same level as the awake state when processing external visual inputs (Houidin et al., 2021).

During dreams, subjects may thus take the increased internally-oriented visual inputs of their spontaneous visual cortex activity to be indicative of events occurring in the external environment (Northoff and Qin, 2011 for an analogous case in auditory cortex during auditory hallucination in schizophrenia). The internally-generated visual inputs are processed similar to as externally-generated visual inputs, for which reason they may be perceived as external visual events from the outer environment (rather than as internal visual imaginations of one's own inner self) (Hong et al., 2008, 2018, Hobson et al., 2022).

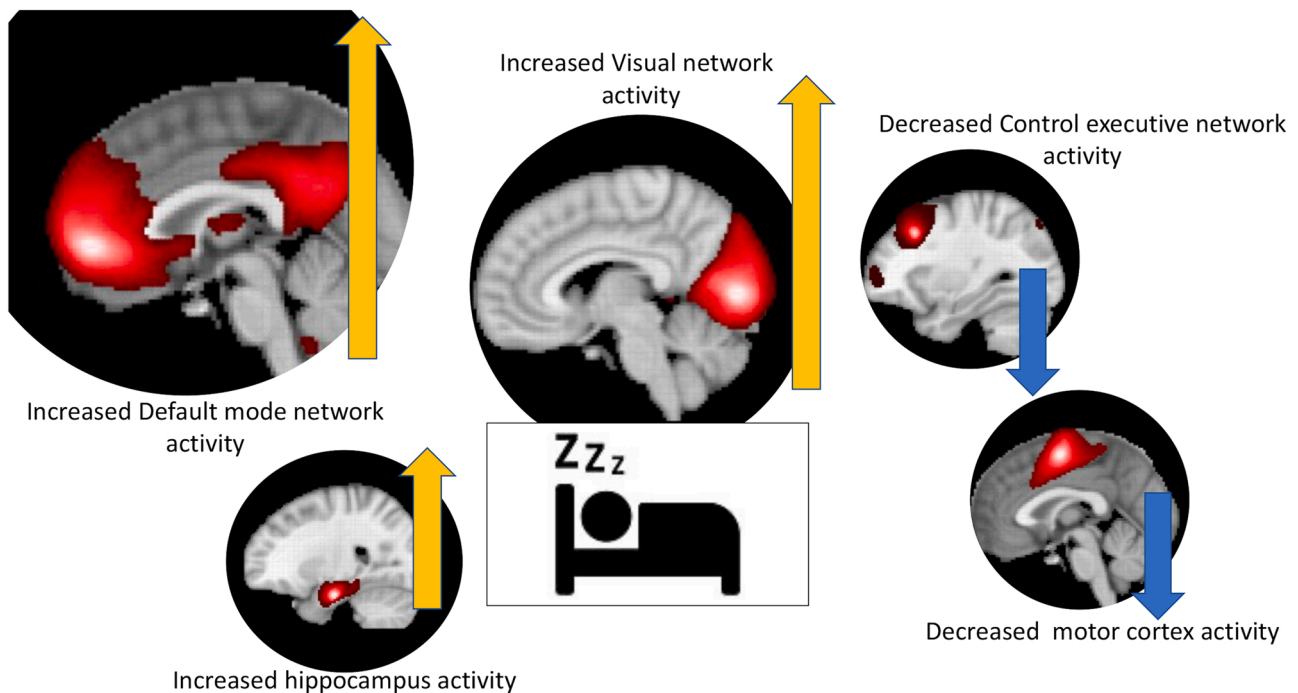


Fig. 3. Visual representation of increased and decreased activity in brain regions during dreams.

This is well in line with the observation that the visual cortex activity pattern and its contents during dreams resemble those during external perception in the awake state (Horikawa et al., 2013; see also Andrillon and Kouider, 2020 for review of partially preserved input processing in dreams). As in auditory hallucination (Northoff and Qin, 2011), one is therefore more or less certain that the ‘dream world’ reflects or, perhaps even is the ‘real world’ – except in Lucid dreaming where one is aware of the dream as dream and where the visual imagery is even more realistic than in the awake state (LaBerge et al., 2018; Siclari et al., 2017, 2018). Visual experiences during dreams may thus be conceived more or less analogous to visual hallucinations, i.e., hallucinoid dreaming (Hobson, 2009; Nelson et al., 1983; Siclari et al., 2017, 2018; Tononi, 2008; Walker and Stickgold, 2004; Windt, 2010, 2020).

Other primary regions beyond the visual cortex show similar patterns. For instance, the auditory cortex can show increased activation during dreams – this is manifest in auditory hallucination-like perception (Dresler et al., 2011, 2021; Fogel et al., 2022; Mainieri et al., 2019; Siclari et al., 2020). While the motor cortex is usually decreased in dreams except in sleepwalking (Dresler et al., 2011, 2021; Fogel et al., 2022; Mainieri et al., 2019; Siclari et al., 2020). Together, this suggests that the changes during dreams involve various unimodal regions and are not limited to the visual cortex.

2.4. Summary of cortical changes: topographic re-organisation

Together, these findings suggest that while REM-sleep is characterized by a remarkably wake-like functional state (Houlin et al., 2019, 2021), there is also a distinct cortical topography compared to both awake state and NREM-sleep (see also Qin et al., 2021): (i) the reciprocal DMN-CEN balance is shifted towards the DMN with reduced activity level in CEN; (ii) medial temporal regions including the hippocampus seem to show elevated activity; (iii) the visual cortex, despite the closed eyes with lack of external visual input, is elevated in its spontaneous activity; (iv) the motor-related areas show preserved activity in higher-order motor regions like supplementary area, but, generally decreased activity in motor cortex itself.

Accordingly, the dreaming brain (i.e., during REM) is characterized by a special topography (as distinct from both awake and non-REM

sleep) with an abnormal shift towards midline DMN, hippocampus, and visual cortex at the expense of CEN and other sensorimotor regions. The changes in the brain’s overall topography seem to go along with the preservation of the functional roles of the various regions like DMN, visual cortex, auditory cortex, or supplementary motor area by themselves in an awake-like way, that is, independent of their embedding in a unique dream-related topography Fig. 3.

3. Part II: from topographic re-organization to the spatial structure of dreams

3.1. From elevated visual cortex activity to immersive spatiotemporal hallucination (ISTH)

Why are the experiences in dreams so bizarre and, at the same time, familiar and seemingly real? We have the experience to navigate in some kind of external environment during dreams albeit in a distorted way. For instance, Windt (2010) proposes that there is still a spatiotemporal reference framework in place during dreams for the presence of self (see Box 1), full body illusions, and environmental experiences. She therefore proposes to characterize dreams as “immersive spatiotemporal hallucination” (ISTH). ISTH are described as amodal manifestations of hallucinations which, as in the awake state, include both internally- and externally-oriented cognition but operate within an abnormal spatiotemporal reference framework Box 2.

How does the topographic re-organization towards increased spontaneous activity of DMN and VC lead to the ISTH in the sense of Windt? For that, we need to distinguish between generation and cognition of inputs. Inputs to the brain can be either exogenous or endogenous: exogenous inputs originate externally from the outer environment – we call them externally-generated inputs. While endogenous inputs are generated internally within the organism itself, including the body (intero- and proprioceptive inputs) and the brain (neuronal inputs) – they can be described as internally-generated inputs (Northoff, 2014a). These inputs’ generation processing needs to be distinguished from our perception/cognition of the same input. Inputs, independently from the source of their generation (see below), may be cognized as either related to, or oriented towards the outer external environment, i.e.,

Box 1

Topographic re-organization of the self in dreams.

Dreams as a manifestation of self in psychoanalysis.

Freud considered dreams as the “*via regia to the unconscious*”, which was considered both as a source of instinctual energies pressing for discharge, and as a container of fantasies and memories banished and then repressed from consciousness (Freud, 1900). By contrast, Jung (1928–30) saw dreams as a spontaneously produced pictures of the current situation of the whole psyche, including unconscious aspects serving also to compensate the attitude of ego consciousness, and of a collective unconscious shared by society. For (Jung, 2013), dreams were considered as a manifestation of the self in the attempt to lead the individual towards wholeness, the balance of the various counterparts of the self and your place in the world around. Similarly in self psychology, Kohut (1977) proposed that the function of dreams is to heal and reintegrate the self and its intrinsic sense of continuity. These psychoanalytic theories, in line with our proposal of the Topographic-dynamic Reorganization model of dreams (TROD), suggest that dreams serve the purpose of a structural re-organization of the self and its psyche-brain (see also Northoff and Scalabrini, 2021; Scalabrini, Mucci, Northoff, 2022b; Scalabrini et al., 2021).

Imbalance of mental and proprio/exteroceptive self during dreams.

The awake state is characterized by a distinct topography featured by its integration of three layers of self (Qin et al., 2020). Briefly, the interoceptive self featuring the inner body is the lowest layer as being related to the insula and subcortical regions as well as by cortical regions of the salience network (like the dorsal anterior cingulate cortex). That is followed by the proprioceptive/exteroceptive self that extends to the outer body as mediated by additional regions like temporo-parietal junction and premotor cortex. Finally, the third most upper layer consists in the mental self that is mediated by the default mode network (DMN) and especially its midline structures like the pregenual anterior and posterior cingulate cortex (Qin et al., 2020). This amount to a hierarchical three layer of self with the right anterior insula representing the common denominator of the hierarchy (Scalabrini, Wolman and Northoff, 2021) [Figure Box 1.1](#).

How is this three-layer hierarchical structure of the self affected in dreams? Let us start with the upper layer of the mental self. The increase in DMN suggests an increase in the mental self. Psychologically, the increase of mental self may be related to what is described as the “felt presence” of self: this describes an increased presence of the own self in one’s mental states, i.e., mental self, during dreams (Windt, 2021).

The increased presence of the self in dreams (i.e., we are almost exclusively “the star of the show” in our dreams) is further supported by the accompanying dynamic changes. In the awake state, more powerful slow frequencies and longer time windows in DMN activity are known to mediate higher degrees of self-consciousness (Huang et al., 2016; Kolvoort et al., 2020; Wolff et al., 2019). The shift towards slower frequencies and longer timescales during dreams may thus translate into an increased presence of the mental self: the increased power of the slower frequencies may be manifest psychologically in the experience of a more powerful mental self that is increasingly present in and shapes more strongly one’s perceptions and cognitions.

The increase in mental self may go along with a relative decrease of the layer of the proprioceptive self as mediated by TPJ and other regions. In the awake state, the TPJ is well known to mediate out-of-body experiences (properly induced) even in healthy subjects (Blanke et al., 2015). Inferring again from the awake state, one would thus assume that the typical occurrence of partial or full body illusions (FBI) with, in the most bizarre instances, out-of-body experiences during dreams (Windt, 2021), may be related to the (relative) activity decrease of the TPJ and other regions constituting the middle layer of the proprioceptive self. Hence, the proprioceptive self and its neural correlates may be diminished (in at least a relative way) leading to a detachment from one’s own body with body illusions (a phenomenon that is accentuated in lucid dreaming) [Figure Box 1.2](#).

Relative increase of the interoceptive self during dreams.

Finally, these topographical changes on the cortical level may, in part, be driven by subcortical sources and their various transmitter systems. Subcortically located transmitter systems like serotonin, noradrenaline, acetylcholine, dopamine and others (Fox et al., 2013) systematically change during sleep, in general, and also in dreams where they seem to show peculiar shifts in their balances (see above; Hobson, 2009). Since subcortical regions in pons, brainstem, and forebrain like the raphe nucleus (serotonin) and the nucleus basalis (acetylcholine) mediate the cortical balance of DMN, CEN and other non-DMN networks (Conio et al., 2020; Martino et al., 2020), changes in the cortical topography may be related, in part, to these subcortical shifts in the balances of the different transmitter systems.

Do these subcortical changes translate into a relative increase in the interoceptive self and thus the bodily-based self during dreams? The bodily- or interoceptive self may be decoupled from and less nested within the mental self. This may be manifest in the decrease of voluntary control of the interoceptive self by the mental self: the interoceptive self may show increased spontaneity and involuntary automaticity with the increased occurrence of drives, primary processes and primary affects/emotions as it is typical for dreams (Panksepp and Biven, 2012).

Together, one would assume that the subcortical-cortical changes during dreams may be related to a relative increase of the interoceptive self with reactivation of seemingly lost or unconscious body-related memories; i.e., “embodied memories” (Fischmann, Leuzinger-Bohleber, 2018; Scalabrini et al., 2021). While, at the same time, the interoceptive self is increasingly detached from and less nested within the more upper layers of the proprioceptive and especially mental self.

Let us compare the situation to the Russian dolls. Dreams are like a state where one Russian doll takes on an abnormal shape (interoceptive self) due to the abnormal subcortical-cortical modulation. That Russian doll, in turn, can no longer be properly integrated with and contained by the other next larger Russian doll, the proprio/exteroceptive self nor be controlled by the largest one, the mental or cognitive self. The three Russian dolls of our hierarchically nested self can thus be characterized by dissociation of the largest (mental self) and the smallest (interoceptive self) dolls as their connecting link or glue, the middle doll as the proprio/exteroceptive self, becomes abnormally weak. Both the smallest and largest Russian doll develop consecutively a “life of their own” becoming more independent and thus less spatiotemporally nested within each other.

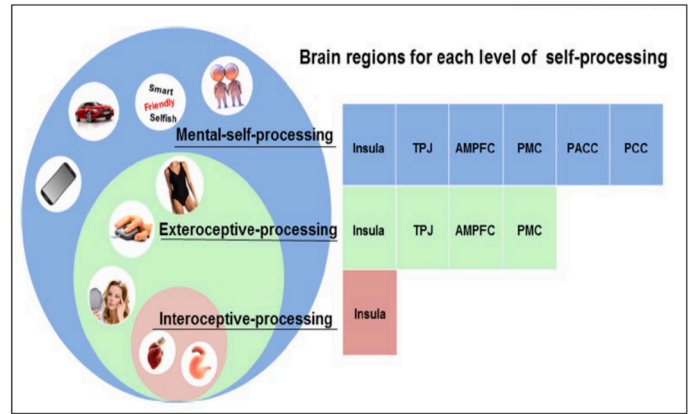
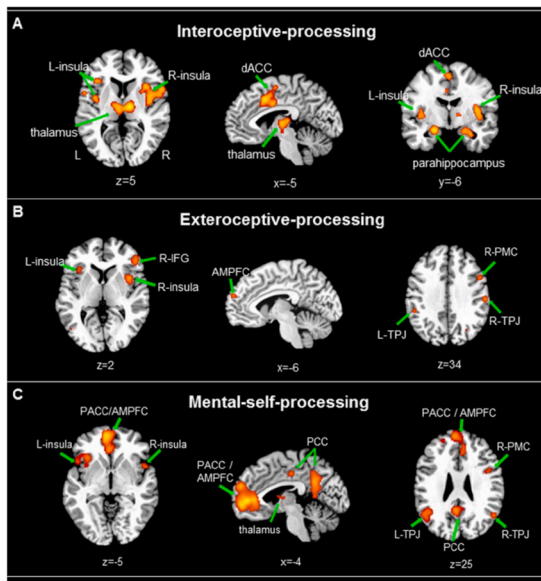


Figure Box 1.1. Abbreviations – L: left; R: right; dACC= dorsal anterior cingulate cortex; IFG= inferior frontal gyrus; TPJ= temporal parietal junction; AMPFC= anterior medial prefrontal cortex; PMC=premotor cortex; PACC= pregenual anterior cingulate cortex; PCC= posterior cingulate cortex. : Visual Representation of the topographical hierarchical model of the three layers of self, adapted from Qin, Wang and Northoff (2020).

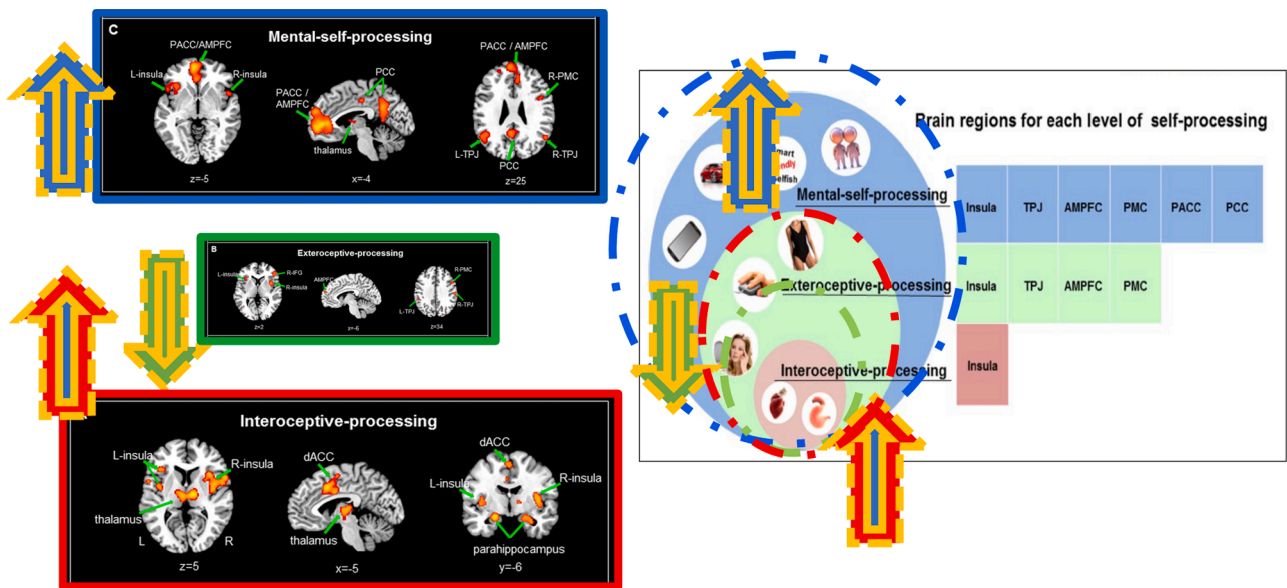


Figure Box 1.2. Topographic reorganization of the brain (left) and its self (right) with increases in the interoceptive and the mental self (upward arrow) and decreases in the exteroceptive self (downward arrow).

externally-oriented, or more related to our inner world of our mind and self, i.e., internally-oriented (Vanhaudenhuyse et al., 2011; Smallwood et al., 2021; Yeshurun et al., 2021; Northoff et al., 2022).

How is the generation of inputs related to our cognition? At first glance, one would assume a one-to-one relationship: internally-generated input should lead to internally-oriented cognition while externally-generated input should lead to externally-oriented cognition. This may usually hold for the awake state, but even then, we may sometimes perceive an internally-generated input in an externally-oriented way (and vice-versa). Such confusion between generation and perception of inputs may even be stronger so in dreams (and other mental states like in psychedelic states (Carhart-Harris and Friston, 2019; Friston, 2010) (Box 3) or hallucinations from psychiatric disorders

like schizophrenia (Northoff and Gomez-Pilar, 2021; Northoff et al., 2021).

We hypothesize such confusion to also occur in dreams, and perhaps, more consistently. For instance, the visual cortex shows increased activity during dreams (see above) which, as the eyes are closed, is only possible due to a higher proportion of internally-generated inputs (from within the visual cortex itself or other sources like DMN). These internally-generated inputs are nevertheless perceived to be related to an external environment, that is, as externally-oriented. One may also formulate the same scenario in terms of predictive coding: an internally-generated prediction is “matched” with an internally- rather than externally-generated input. This, in turn, yields a prediction error which, as in the awake state, is associated with external contents in the

Box 2

Dreams and consciousness.

What dreams can tell us about consciousness: Level/state, content, and form.

Dreams can inform us about the different dimensions of consciousness as level/state, content, and form (Northoff, 2013, 2014; Northoff and Heiss, 2015; Bayne and Laureys et al., 2016, 2005). They clearly show that the level/state of consciousness is related to subcortical-cortical biochemicals like acetylcholine, adrenaline/noradrenaline, serotonin, and dopamine including their respective subcortical nuclei. Thereby, the balance between the different transmitter systems including their ascending subcortical-cortical topography is key for determining the level/state of consciousness – this is in line with recent views on consciousness (Aru et al., 2019).

Yet another lessons dreams can teach us concerns the content of consciousness. The content of consciousness does not only depend upon the inputs themselves but also on the neuronal context within which the inputs are processed. That very same neuronal context like the brain's intrinsic slow-fast frequency balance and the long-short timescale balance seems to be abnormally shifted towards slower frequencies and longer timescales in dreams while, unlike in NREM 2/SWS, preserving faster frequencies and shorter timescales (to a certain degree).

The abnormally slow neuronal context featured by longer timescales predisposes for increased temporal integration of different inputs (Wolff et al., 2022) which, usually in the awake state, are temporally segregated from each other. Such temporal re-structuring of inputs through their increased temporal integration and decreased segregation contributes to our understanding of the bizarre nature of contents in dreams. More generally, it also unravels the deep temporal basis of the contents of consciousness as it is for instance postulated by the Temporo-spatial theory of consciousness (TTC) (Northoff and Huang, 2017; Northoff and Zilio, 2022a, 2022b).

Finally, the abnormal neuronal context in dreams, e.g., the slow-fast frequency shift and long-short timescales shift, organizes and structures the brain's input (and also output) processing in an altered way. It provides the form (or structure) of consciousness as third dimension besides level/state and content (Northoff, 2013, 2014; Northoff and Heiss, 2015). The abnormal form of consciousness in dreams is constituted by both spatial and temporal changes as manifest in an altered topography and dynamic. Dreams can thus be considered a paradigmatic example of the importance of the form as third dimension of consciousness as highlighted in especially the TTC (Northoff and Huang, 2017; Northoff and Zilio, 2022a).

Theories of consciousness – IIT, GNWT, and TTC.

One of the main theories of consciousness, the Integrated Information Theory (IIT) (Tononi et al., 2016) postulates that integration is a key feature of consciousness. Dreams support that notion and specify it: it is temporo-spatial integration of the neural activity itself, the brain's inner time and space (Northoff and Huang, 2017; Northoff 2018) that structures and shapes the contents of consciousness. Temporal integration is related to especially the balance of long-short timescales (Wolff et al., 2022; Golesorkhi et al., 2021a). While spatial integration is constituted by synchronization between different regions as measured by phase-based functional connectivity (fMRI) and coherence (EEG).

We can see that both temporal and spatial integration of neural activity is abnormal in dreams as measured by longer autocorrelation window (ACW) (temporal integration) and increased theta phase locking value between electrodes/regions (theta PLV). That shapes the processing of both internally- and externally-generated inputs including their integration and linkage in an abnormal way during dreams. Hence, IIT reflects integration that is key for consciousness which, though, can be specified in terms of spatial and temporal integration on the purely neural activity level. This makes it also necessary to extend beyond the rather limited short timescales in IIT to include a variety of different and longer timescales as postulated in TTC (Northoff and Zilio, 2022b).

Dreams can also contribute to the Global Neuronal Workspace Theory (GNWT) (Mashour et al., 2020; Dehaene et al., 2014, 2017). One major claim of the GNWT is that the dorsolateral prefrontal cortex (DLPFC) is key in providing access to the global neuronal workspace. The distinction lucid vs non-lucid dreams as distinguished by high vs low DLPFC activity (and connected regions) clearly illustrate the role of DLPFC for providing access of consciousness as manifest the awareness that one is dreaming (Dresler et al., 2012, Hobson et al., 2022) (see also above).

Finally, dreams lend further support to the TTC (Northoff and Huang, 2017; Northoff and Zilio, 2022a, 2022b). One key assumption of the TTC is that spatial topography and temporal dynamic are shared by both neuronal and mental features as their “common currency” (Northoff et al., 2020a and b). The topographic and dynamic abnormalities on the neuronal level may thus resurface in corresponding spatiotemporal changes on the mental level: inner time and space may be abnormally perceived and experienced in dreams. For instance, due to the increased slowness in the frequency, subjects may experience their consciousness in a slower mode during dreams than in the awake state. Moreover, the topographic changes with increased DMN and visual cortex activity may abnormally centre and/or also shrink the perceived space around the self while the environment is experienced in a more distant way. Future studies focusing on inner time and space experience in dreams are thus warranted – they may provide the link of neuronal and mental topography/dynamic, i.e., their “common currency”.

environment, that is, an externally-oriented perception (rather than an internally-oriented perception featured by internal contents) (Hobson, 2009; Hobson et al., 2022; Hong et al., 2008, 2018).

Taken together, despite receiving almost exclusively internally-generated input (and less externally-generated inputs) during dreams, the elevated spontaneous activity in visual cortex “treats” the internally-generated input “as if” it were an externally-generated input: “*the brain isolated from the outside world, treats its endogenous stimulation as if it were exogenous*” (Hobson, 2009, p.809). This, according to Hobson (2009, p.808), leads the dreamer to make “*built-in predictions about external time and space*” (see also Hobson et al., 2022) which, in truth, are predictions about the subject's own internal time and space. Due to the constitution and prediction of such externally-oriented time and space, the

internally-generated input is perceived as an external (rather than internal) stimulus from the environment (rather than within the own mind). There is thus a discrepancy between the generation of the input, e.g., internal within the brain itself, and its cognition as being ‘located’ in the external environment. We thus hypothesize hallucinations in dreams to ultimately stem from a confusion of inner and outer time-space – one can therefore speak of “*as if external perception*” and “*as if external contents*” during dreams (Northoff, 2011; p.196).

3.2. From increased DMN activity to elevated internally-oriented cognition

Dreams are characterized by topographic functional re-organisation

Box 3

Other states of consciousness - Dreams vs meditation and psychedelics.

Dreams vs meditation.

Dreams can be compared to other altered states of consciousness like meditation and drug-induced psychosis. Let us start with meditation.

Meditation is characterized by the decrease of DMN activity and connectivity with a positive relationship of DMN and CEN (Bauer et al., 2019; Cooper et al., 2022). This results phenomenologically in decreased self-focus allowing for integration of internal self and external environment into one homogenous experience, i.e., non-dual awareness (Cooper et al., 2022). The opposite can be observed in dreams. Here DMN activity and connectivity are abnormally strong compared to CEN – the internal self-focus is increased and its dual or dichotomous relationship with the external environment is further emphasized.

Combine this with dynamic changes. Both meditation and dreams show a slowing down of their dynamic compared to the non-meditative awake state (Irrmischer et al., 2018; Cooper et al., 2022). This means a higher propensity to integrate internally- and externally-generated inputs into more homogenous contents as it can be observed indeed in both states, dreams and meditation. However, unlike in dreams, the contents in meditation are not as bizarre. Instead, as based on the topographic changes, there is a stronger tendency to overcome the distinction of internally- and externally-generated/oriented contents in meditation when perceiving them as non-distinct and integrated (Cooper et al., 2022).

This is different in dreams. Due to the decrease in externally-generated inputs, temporal integration focuses mainly on integrating the different internally-generated inputs from within the brain/body and its distinct regions. The shift from integrating internal-external inputs to predominant internal-internal input integration may explain the main difference in the contents of consciousness in meditation and dreams while, at the same time, displaying somewhat similar dynamic changes in frequency and timescales. Accordingly, it may be the case that the same dynamic changes, i.e., slowing down with longer INT, are “used” in different ways: meditation shows high degree of self-environment integration while dreams exhibit self-environment segregation. This, as we suppose, may be based on their different topographies with an increased (dreams) or decreased (meditation) DMN.

Dreams vs psychedelics.

Yet another interesting state of consciousness are drug-induced psychosis (DIP) with psychedelics like psilocybin and LSD (Carhart-Harris and Friston, 2019 for overview). As in meditation, the negative relationship and differences of DMN and CEN are somewhat resolved and replaced by their positive relation in psychedelics – this leads to somewhat similar experience of connectedness and integration of the internal self within the external environment (Carhart-Harris and Friston, 2019). This obviously is different in dreams where there is stronger connectedness to and centredness on the own self which is experienced as moving within and distinct from a spatiotemporally altered environmental context.

Psychedelics induce higher levels of entropy of the contents of consciousness including increased subjective uncertainty as providing major support for the entropy hypothesis of consciousness (Carhart-Harris et al., 2014; Carhart-Harris, 2018). Applying active inference and predictive coding, this led Carhart-Harris and Friston (2019) to postulate the relaxed beliefs under psychedelics (REBUS) hypothesis. This hypothesis postulates that higher-order associative regions’ priors confer a broad summarization of the mind and world, effectively suppressing away (potential) content. It therefore follows that if this suppression is relaxed, as it is under psychedelics, content will necessarily be released. For example, psychedelics may lead the emergence of previously unconscious psychological material into conscious awareness.

One may be inclined to also assume somewhat analogous relaxed beliefs in dreams with a key difference, though. The mental self seems to exert decreased top-down modulation and cognitive control with empirical priors, over specifically, the prediction error of the interoceptive self in dreams (see Box 1). This releases emotions and unconscious drives associated with the neural processing of the subcortical-cortical bottom-layer of the interoceptive self. Instead of relaxed beliefs under psychedelics (REBUS), one may therefore better speak of “Released Emotions under Dreams” (REUD). That would converge with the recent predictive coding approach to dreams by Allan Hobson (see Hobson et al., 2022).

of the cortex (and its subcortical modulation). One key feature of this reorganization is that the balance of DMN-CEN shifts towards the DMN. The CEN and especially the lateral prefrontal cortex are related to cognitive control and goal-orientation (Christoff et al., 2016). As one might expect, these are strongly diminished in dreams where rational and voluntary control are lost while spontaneity and automatic involuntary dynamic of affect/emotion and cognition/thought are strongly increased (Solms, 2011). Following Panksepp’s primary emotion description (Panksepp and Biven, 2012; Solms, 2020), affects/emotions and their related contents are characterized by very strong degrees of spontaneity during dreams resulting in free-floating and unconstrained affects and thoughts with strongly diminished rationality. We hypothesize that the loss of rational voluntary control and goal-orientation with respect to emotions and cognition are related to the relative decrease of CEN activity in dreams (Hobson, 2009; Hobson et al., 2021). In contrast, CEN increases during lucid dreaming may reflect increased voluntary control with the awareness that one is in a dream state rather than an awake state (Baird et al., 2018, 2019; Dresler et al., 2012; Hobson et al., 2022; Voss et al., 2009) (see above for more details on lucid dreaming).

What about the role of the DMN in dreams? The DMN is well known to mediate internally-oriented and self-generated cognition like mental time travel (Northoff, 2017; Schacter et al., 2012), autobiographical

memory (Schacter et al., 2012), and mind-wandering (Christoff et al., 2016; Fox et al., 2016; see also Buckner, DiNicola, 2019; Northoff et al., 2022; Scalabrini et al., 2022a; Smallwood et al., 2021; Yeshurun et al., 2021). Given that DMN activity and connectivity are increased during dreams, we hypothesize that all three forms of internally-oriented cognition are increased and/or altered in dreams: there is indeed increased mental time travel with abnormal shifts towards either the past or future accompanied by detachment from the present, i.e., the actual point in time (Hobson et al., 2022; Schacter et al., 2012; Windt, 2010; Baird et al., 2022). Autobiographical memories are also increasingly retrieved during dreams. This memory retrieval may be especially related to increased hippocampal activity (Barry et al., 2021). Finally, there is increased mind-wandering with freely floating unconstrained thoughts in dreams (Christoff et al., 2016; Smallwood and Schooler, 2015; Smallwood et al., 2021).

Together, albeit tentatively, we hypothesize that the increase in internally-oriented cognition like mind-wandering, autobiographical memory, and mental time travel during dreams may, in part, be related to the abnormal increase in DMN activity including the hippocampus (as related to autobiographical memory retrieval). Due to the decreased externally-generated input, internally-oriented cognition of the relatively increased internally-generated inputs becomes more central in

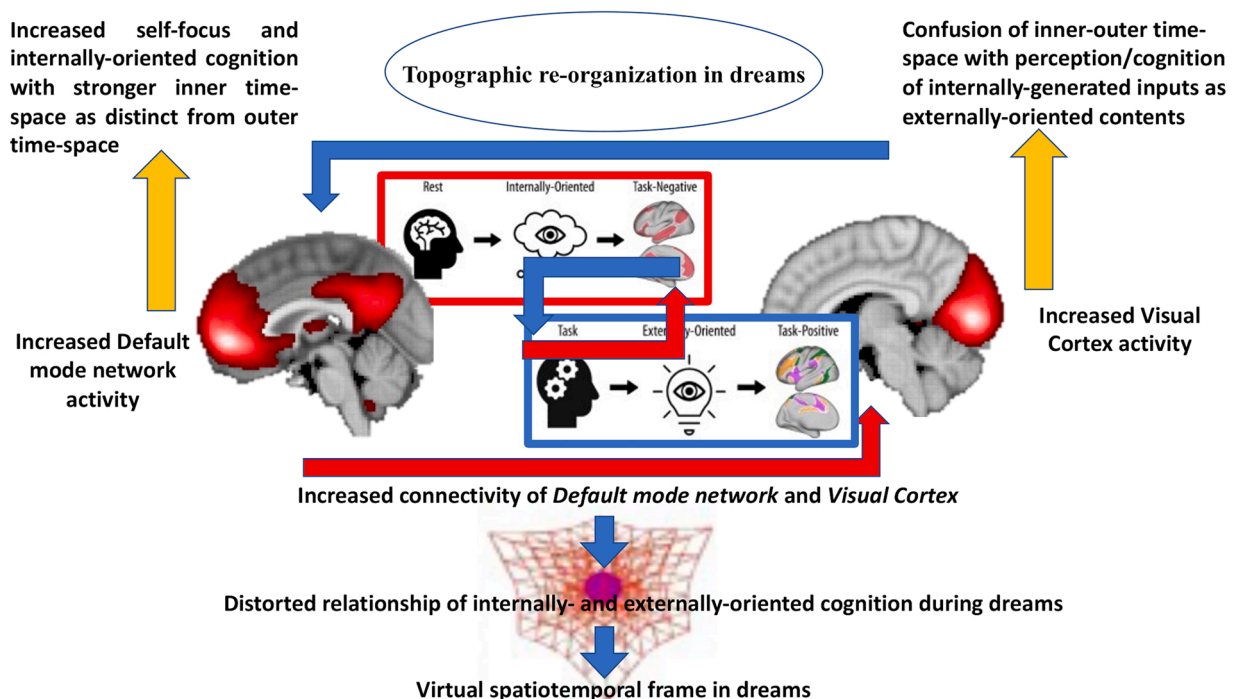


Fig. 4. Summary of topographical reorganization in dreams. The increased activity of the Default Mode Network and Visual cortex, together with their increased connectivity lead to the distorted relationship of internally and externally oriented cognition during dreams, i.e. a virtual spatiotemporal frame in dreams.

dreams than the awake state. The topographic shift towards DMN may thus be accompanied by a cognitive shift towards internally-oriented cognition in its various facets (self-referential, mind-wandering, autobiographical memory, mental time travel).

3.3. From DMN-VC topography over abnormal spatiotemporal weighting of inputs to bizarre dream contents

The awake state is characterized by a more or less equal balance and fluctuation of internally- and externally-oriented cognition (Vanhaudenhuyse et al., 2011). Neuronally, these cognitive fluctuations are related to neuronal fluctuations of DMN and CEN-sensory activity (Northoff et al., 2022; Vanhaudenhuyse et al., 2011). This means that our experience of our own self/mind's inner time-space are converged and integrated with our perception and cognition of events in the outer time-space of the environment with both being more or less balanced in their fluctuations (Northoff et al., 2022).

That seems to be altered in dreams. Here the balance is shifted towards an abnormally strong DMN while CEN is decreased during dreams (see above). Internally-oriented cognition including the mind/self's inner time-space may consequently predominate over externally-oriented cognition in the outer time-space of the environment. Accordingly, dreams can be characterized by a shift of the subjects' spatiotemporal framework towards inner time-space at the expense of outer time-space.

This carries major implications for any kind of input processing including both internally- and externally-generated inputs. Any input may then be processed within such abnormally shifted spatiotemporal framework. The inputs may be more strongly weighted by (and thus associated with) the subject's inner time-space rather than the outer time-space of the external environment. Increased weighting of both internally- and externally-generated inputs by the subject's own inner time-space (rather than the outer time-space), in turn, may distort the spatial (and temporal) features of the perceived/cognized contents (which result from the temporal and spatial integration of the inputs; Wolff et al., 2022). Such spatial and temporal distortion of dream contents can most prototypically be seen in the paintings by Salvador Dali

who relied on his dreams when painting.

Together, the topographic re-organization of the DMN-VC connection creates a novel spatiotemporal framework in the brain's neural activity featured by: (i) increased spontaneous VC activity that, as we hypothesize, leads to the hallucinatory confusion of inner-outer time-space with perception/cognition of internally-generated inputs as externally-oriented contents; (ii) increased DMN activity that, as we hypothesize, entails increased self-focus and internally-oriented cognition with stronger inner time-space as distinct from outer time-space; (iii) increased DMN-VC connectivity in dreams that, as we hypothesize, leads to the predominance of the self/mind's inner time-space over the environment's outer time-space; (iv) and entails, as we hypothesize, abnormal spatial (and temporal) weighting for any input processing including both internally- and externally-generated inputs; which (v) results in the often bizarre spatially (and temporally) distorted dream contents Fig. 4.

4. Part III: dynamic re-organization during dreams

4.1. Power and phase-related changes in different frequency bands

EEG is ideal for understanding the temporal dynamics of the power spectrum and various related electrophysiological changes during both the awake state and sleep. NREM 1 sleep is typically characterized by the decrease of alpha (8–13 Hz) combined with the strengthening of power and occurrence of theta rhythms (5–8 Hz). NREM 2 features high frequency spindles (11–16 Hz) and large-amplitude, slow, K-complexes, as well as isolated slow waves. Finally, SWS shows highly synchronized slow waves (0.5–4 Hz). Compared to NREM 2 and SWS, REM sleep shows desynchronized low amplitude activity in EEG in mainly theta (5–8 Hz) and beta (13–30 Hz) which resemble the awake state; the difference being that REM-sleep lacks the highly synchronized alpha power that characterizes the awake state (eyes closed). The alpha power is typically decreased while theta power is relatively increased during dreams (Ruby, 2020; Siclari et al., 2017, 2018). Moreover, gamma power in specifically occipital cortex electrodes, the "posterior hot zones" (Storm et al., 2017; Tononi et al., 2016), is increased during

dreams relative to NREM-sleep (Ruby, 2020; Siclari et al., 2017, 2018).

Results about power changes in relation to dreaming in the standard EEG frequencies are somewhat inconsistent though. Ruby (2020) provides an overview of the literature comparing EEG power changes during dream report vs no-report in both REM and NREM sleep. When a dream report is produced about REM sleep is associated with power increases in theta, alpha and gamma, although decreases have also been reported (Ruby, 2020; Siclari et al., 2017, 2018). Several studies do not report a difference in power between the presence or absence of dreams for REM-sleep (Ruby, 2020). For NREM sleep, decreases in delta power are reported in some studies, with most studies showing no power difference between presence and absence of dream report produced for NREM sleep (Ruby, 2020). However, one of the major methodological challenges in relying on dreams reports to signal the presence/absence of dreams, is whether dream recall is reliable (i.e., do 'no reports' indicate the absence of dreams, or, simply failure to recall dream content?).

Nonetheless, these findings do raise the question whether power changes in general as well as in single frequencies like delta are the most relevant measure to distinguish consciousness and unconsciousness and, specifically, dream-related activity from non-dreams (Frohlich et al., 2021). Recent studies also report phase-related changes during dreams and, specifically, replay (Findlay et al., 2020 and Schreiner et al., 2020 for recent reviews). Schreiner et al., (2018, 2021, 2020) demonstrate that phase-related changes especially in the theta band are key for memory reactivation: they show high phase similarity in 5 Hz for remembered words in both awake and NREM-sleep while controlling for power in the same frequency range (Schreiner et al., 2018). These were related to fluctuations in slow waves around 1 Hz. Analogous phase-related coupling of 1 Hz Slow waves is also observed for spindles, where again, they may drive memory reactivation (Antony et al., 2018; Bergmann et al., 2012; Boutin et al., 2018; Fogel et al., 2017; Jegou et al., 2019) and replay (Schreiner et al., 2020, 2021). Although not specifically related to dream contents, these findings suggest that phase-related processes may be key for memory reactivation or replay during sleep.

4.2. Slow-fast frequency power and Long-short timescales

The general shift towards slower frequencies in dreams is also reflected in the power law exponent (PLE). PLE can be used to measure the balance of slow and fast frequencies, which is lower in REM compared to NREM but still higher than in the awake state (Zilio et al., 2021). This suggests that a peculiar balance of slow and fast frequencies during dreams: slower frequencies are stronger than in awake state but not as strong as in NREM 2 and SWS while faster frequencies are stronger in dreams than in NREM 2 and SWS but not yet as strong as in awake state.

The intermediate position of REM sleep between awake and deep sleep (SWS) is also reflected in its intrinsic neural timescales (INT). The INT reflect the temporal window of the brain's neural activity which can be measured by the autocorrelation window (ACW) (Golesorkhi et al., 2021a, 2021b; Wolff et al., 2022). The awake brain's spontaneous activity shows a hierarchy of INT with longer timescales in higher-order transmodal regions like DMN and shorter timescales in unimodal lower-order regions like primary sensory cortex (Golesorkhi et al., 2021a, 2021b; Hasson et al., 2015; Ito et al., 2020; Raut et al., 2020; Wolff et al., 2022; Yeshurun et al., 2021). REM sleep is characterized by shorter intrinsic neural timescales than NREM 2/SWS as measured by the ACW: the ACW in dreams/REM is shorter than in NREM 2 and SWS but still longer than in the awake state (Zilio et al., 2021). This suggests that the dynamic hierarchy of short-long INT is shifted towards longer INT in dreams compared to the awake state while not yet being as long as in NREM 2/SWS. Accordingly, as in the case of frequency, the dreaming state is an intermediate state when it comes to the INT. These studies provide a useful foundation to further investigate the spatial and temporal features of neuronal activity that occur during sleep and which

relate to the content of dreams. This may provide a useful test of the TRoD model, in particular Fig. 5.

5. Part IV: from dynamic re-organization to the temporal structure of dreams

5.1. Awake brain and its "normal" contents: balance of temporal integration and segregation of inputs

What do the data on the abnormal INT in dreams mean for their input processing? For that, we need to make a brief detour into the role of INT in the awake brain.

INT provide the brain with a dynamic repertoire of different timescales including shorter and longer timescales in neural activity (Golesorkhi et al., 2021a, 2021b; Wolff et al., 2022). Depending on the length of their temporal windows, the different timescales sum up and thus temporally integrate and smooth different inputs at their distinct points in time, or, alternatively, segregate them in a temporally precise way. Longer time windows mediate predominant temporal integration of the different inputs across their distinct time points – they provide high degree of temporal smoothing (Golesorkhi et al., 2021a; Wolff et al., 2022). Shorter timescales, in contrast, rather segregate the various inputs according to their distinct points in time – there is high degree of temporal precision (i.e., enabling greater differentiation over time).

The balance of short and long timescales with a wide dynamic repertoire between the two extremes of temporal integration and segregation provides the awake brain with a balance of temporal integration and segregation. This for instance makes possible to separate internally- and externally-generated inputs on the basis of their distinct timescales: externally-generated inputs from the environment usually operate on faster frequencies and longer timescales than the slower and longer internally-generated inputs from brain and body (Deco and Kringelbach, 2017; Golesorkhi et al., 2021b; Wolff et al., 2022). Accordingly, relying on their different temporal features, the distinction of internally- and externally-oriented cognition can follow more or less the one of internally- and externally-generated inputs. There is strong correspondence of input generation and input cognition in the awake state.

5.2. Dreaming brain and its "strange" contents: shifts towards increased temporal integration of inputs

The situation is slightly different in sleep, in general, and dreams in particular. Due to the shift towards slower frequencies and longer INT, the balance of temporal integration and segregation is shifted towards temporal integration: the inputs at different timepoints are now all summed and lumped together independent of whether they are internally- or externally-generated. Subjects in deep sleep like NREM 2/SWS are consequently no longer able to perceive and experience any differentiation of internally- and externally-oriented cognition and, more generally, between self and environment (Northoff and Zilio, 2022a, 2022b). Subjects in NREM 2/SWS may thus not perceive anything; their consciousness is lost almost completely, similar to deep anesthesia (Zilio et al., 2021).

We hypothesize that is not the case in dreams, though. Unlike in NREM 2/SWS, the shorter timescales are still somehow preserved though counter-balanced by stronger longer timescales (when compared to the awake state). The dreaming state (REM) takes on an intermediate position: there is higher degree of temporal integration and smoothing than in the awake state but still higher degrees of temporal segregation and precision compared to NREM 2/SWS. This does not mean that subjects do not perceive anything or nothing in NREM 2/SWS but only that they may perceive a less differentiated and more homogenous percept as the different contents are more integrated and unified with each other through the longer timescales with higher temporal integration (Stickgold et al., 2001b; Nielsen et al., 2022) (See also Northoff and Zilio, 2022a, 2022b).

We hypothesize that this peculiar balance of temporal integration-segregation shifts the balance of internally- and externally-oriented cognition: increased temporal integration (due to the longer INT) means that externally-generated inputs are more likely to be integrated with internally-generated inputs rather than being segregated from them. This means that externally-oriented cognition contents do not only include externally-generated inputs but an additional strong dose of internally-oriented inputs (compared to the awake state). The externally-oriented cognition is consequently infused by internally-generated inputs. This, in turn, leads to the perception/cognition of the subject's own inner mental contents as the contents of the outer environment in their externally-oriented cognition. We propose that such confusion of internally- and externally-generated inputs in our cognition (internally- and externally-oriented) is key for generating the often bizarre dream content. At the neuronal level, we propose that this is based on the dream-specific dynamic shift towards slower frequencies and longer timescales Fig. 6.

5.3. Increased temporal integration on the cognitive level: semantic association rather than semantic similarity/identity

At a cognitive level, increased temporal integration may for instance be manifest in increased semantic association. Fogel et al. (2018) developed a particular objective experimental method to investigate the degree of semantic association during dreams in relation to reports of wake mental contents. They let subjects, during the awake state, mentally rehearse either playing tennis (after a practice session where they were engaged in a virtual tennis game), or mental rehearsal for navigating through a virtual maze (after a training session where they explored a virtual maze environment) and obtained detailed verbal reports of their mental rehearsal conceptions.

Participants subsequently took short naps (containing sleep

onset periods only), from which they were woken up and asked to report their dreams (i.e., during hypnagogic reverie/hallucinations; a state not unlike REM sleep). The dream reports were then entered into a machine learning-based algorithm for detecting semantic relations to tennis playing (and spatial navigation). This made possible to objectively quantify the degree to which semantic contents associated with tennis were incorporated into the contents experienced during dreams (a process that is conventionally/typically through subjective dream content analysis, with no direct comparison to reported wake experiences).

The results show that there is semantic relationship of the dream contents with tennis playing. For instance, the subjects dreamt about playing ball on a green lane in a park but did not experience tennis playing itself. This suggests semantic association but not semantic similarity/identity: the contents during the awake state (tennis) were incorporated into the dream contents (soccer playing in a park) but were not replayed in an identical, or even similar way. Hence, there is semantic association but not semantic similarity or identity. This is different from episodic recall of a past event, that one might engage in while awake. Rather, during dreams, distantly related semantic elements from the daytime experience are interwoven into a new narrative. This speaks for higher degrees of integration of semantically more distant events within the current events.

This notion is compatible with the overfitting hypothesis of dreams (Hoel, 2021; Deperrois et al., 2022). In a nutshell, this hypothesis assumes increased generalization during dreams in order to avoid overfitting to one particular content, event or concept during daily learning. Overfitting is, for instance, avoided by integrating existing concepts, events and contents from the awake state into a new context by linking them to new and other concepts, events and contents during the dreaming state. Hence, the constitution of semantic association rather than semantic similarity/identity reduces the danger of overfitting by generalizing the awake concepts, events, and contents through

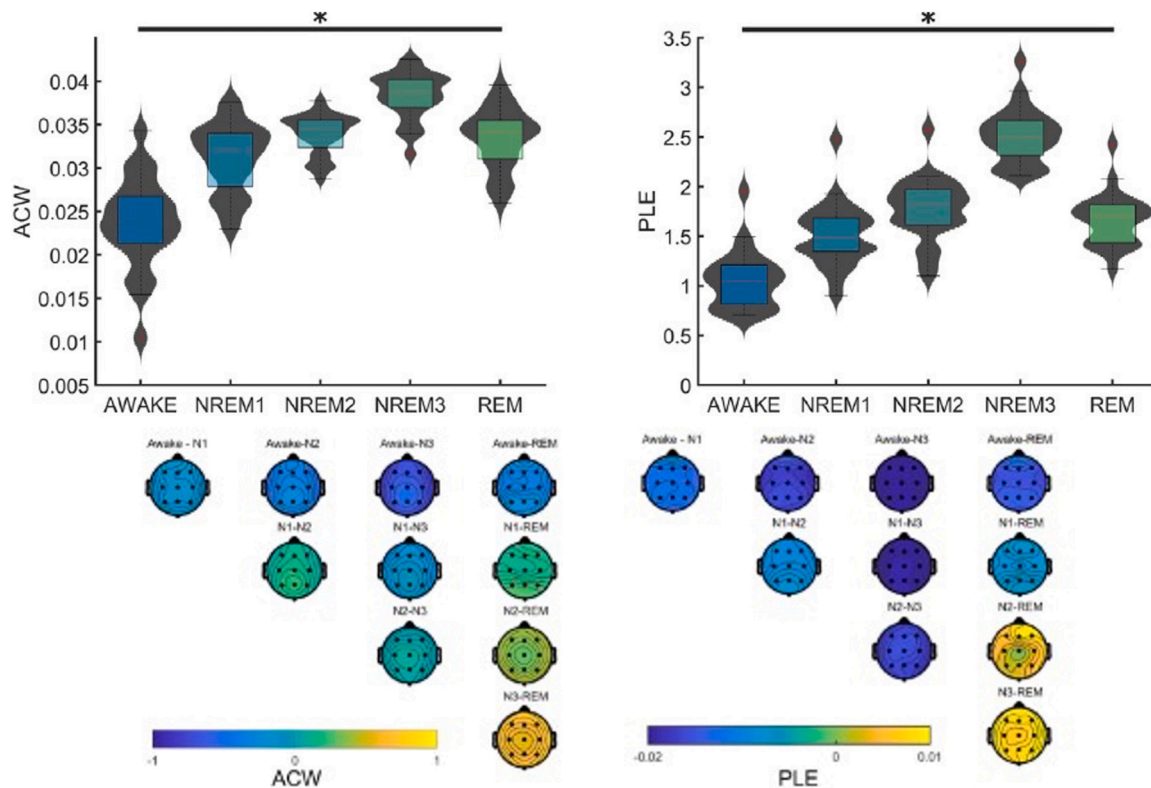


Fig. 5. Autocorrelation window (ACW) and Power Law exponent (PLE) - upper part - and topographical maps in the different sleep stages including dream (REM) - lower part.

Adapted from Zilio et al. (2021).

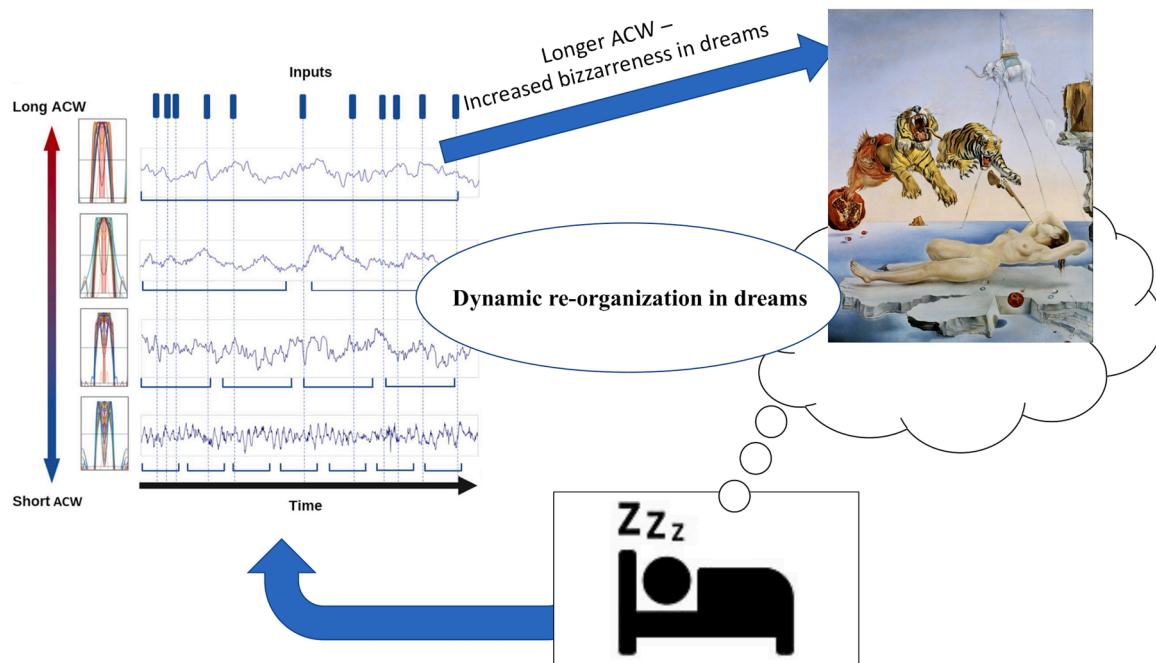


Fig. 6. Visual representation of dynamic reorganization in dreams.

integrating them in a new context during the dreaming state.

Taken together, we hypothesize that the externally-generated input (i.e., tennis or spatial navigation) in this study is processed in an abnormally prolonged temporal context, the brain's longer INT during dreams. This favours high degrees of temporal integration over temporal segregation: the single externally-generated inputs related to tennis or spatial navigation at their specific discrete time points are integrated and synthesized with incoming internally-generated inputs. Such high degree of temporal integration distorts the original contents (i.e., tennis, spatial navigation). This allows for semantic association rather than semantic similarity. At the same time, the temporal windows are not yet as long as in NREM 2/SWS so that, unlike in the latter, temporal segregation and thereby distinction of different semantic contents is still possible in dreams (Northoff and Zilio, 2022a, 2022b). In other words, there is still some semantic association, rather than no semantics at all as in SWS. Thus, given that the hypnagogic state is similar to both REM sleep and NREM sleep in terms of its phenomenology, we would hypothesize that, accordingly, the spatiotemporal features associated with hypnagogia would be REM-like, but may have some similarities to NREM sleep as well.

5.4. From enhanced neuronal synchronization to bizarre dream contents

The dynamic findings clearly show the importance of phase-related processes. This can be seen in EEG synchronization of neural activity with memory contents (Schreiner et al., 2018, 2021, 2020). Synchronization also plays a key role in fMRI. fMRI data show increased resting state functional connectivity within DMN as well as of DMN with visual cortex (see above). Functional connectivity itself is based on phase-related processes, that is, how different regions' neural activity synchronize with each other time (Huang et al., 2015, 2017). Together, these findings show the key role of increased neuronal synchronization during dreams with respect to the processing of inputs.

How do the increased degrees of synchronization contribute to the dream phenomenology? Our neuro-phenomenal assumption is two-fold concerning both the content and spatiotemporal context of dreams. Schreiner et al. (2018) show that similar theta phase-related mechanisms of memory reactivation operate in both awake and sleep states. Theta phase is aligned and thus entrained (see Lakatos et al., 2019 for

review) to the memory content that is reactivated during both dream and awake states. The importance of phase-related mechanisms for our cognitive thought contents is further supported by a recent observation that on- and off-thoughts, i.e., thoughts unrelated or related to a particular external task content, mediated by alpha- and theta peak frequency respectively (but not their respective power) (Hua et al., 2022).

Albeit tentatively, we hypothesize that the often bizarre dream contents are closely related to increased phase-based synchronization as measured by phase-based measures like peak frequency, phase locking value, phase shifting/coherence (in EEG), and functional connectivity (in fMRI). The increased synchronization means that the discrete time points of different inputs (including both internally- and externally-generated inputs) have a higher likelihood of being processed together. Thus, they are synthesized with each other: inputs from both body/brain (internally-generated) and environment (externally-generated) are supposedly synchronized with each other. As we hypothesize, this may result in abnormal dream contents. For instance, from our earlier example, if externally-oriented inputs like tennis playing are synchronized with internally-oriented inputs related to past memories of playing soccer on a green lane, one may experience the tennis playing (from the awake state) in terms of playing soccer on a green lane during dreams – the increased synchronization thus creates novel semantic associations and a unique narrative that often characterizes REM dreams, which are not present in the awake state. Increased synchronization may thus be one mechanism by means of which the brain avoids overfitting (Hoel, 2021; Deperois et al., 2022) during the dreaming state by generalizing the awake concepts, contents, and events in a novel context Fig. 7.

6. Conclusion – topographic-dynamic Reorganization model of dreams (TRoD)

Dreams are bizarre states as they display unusual contents, a strongly self-centric perspective, and a peculiar level/state of consciousness. Reviewing the various neuronal changes in both topography and temporal dynamics, here, we propose the Topographic-dynamic Reorganization model of dreams (TRoD) which aims to relate neuronal and mental levels, that is, between brain and experience. TRoD complements

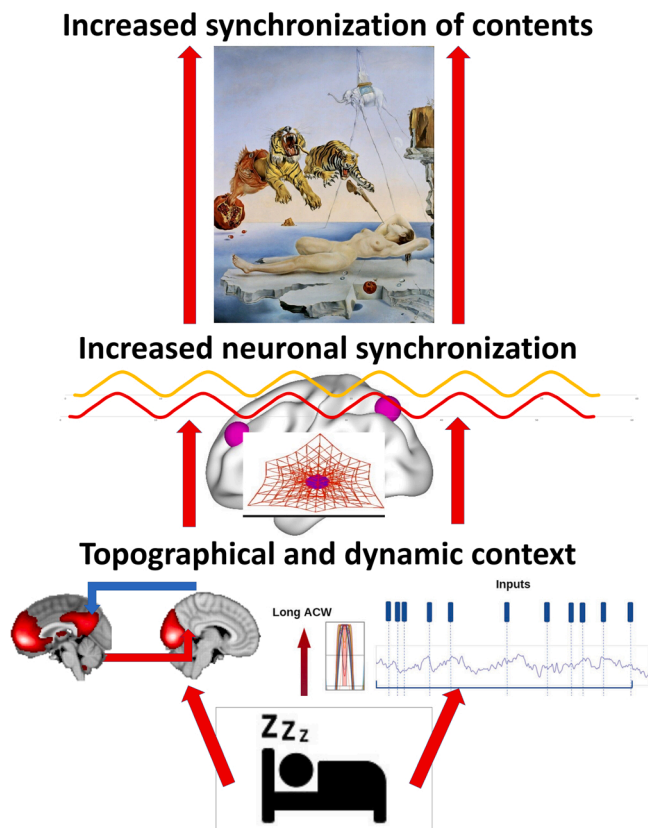


Fig. 7. Summary of Topographic-dynamic Reorganization model of dreams (TRoD).

and extends other models of dreams (see above and below) by providing a more comprehensive framework; a spatiotemporal framework with specific predictions and testable hypotheses.

Topographically, the brain's neural activity is re-organized with a shift towards the DMN at the expense of the CEN. This leads to higher likelihood of linking and integrating externally-generated inputs within internally-generated inputs. This results in a strongly ego- or self-centric perspective with high degrees of semantic association that typically characterizes dreams. The topographic changes are accompanied by dynamic re-organization with a shift towards slower frequencies and longer timescales compared to the awake state. At the same time, faster frequencies and shorter timescales are still somehow present as distinguished from the deeper sleep stages (NREM 2/SWS). This dynamic shift favors temporal integration of inputs over their temporal segregation. This may lead to an abnormal synthesis of externally-generated inputs within the ongoing internally-generated inputs, which may be manifest in the bizarre mental contents.

In sum, the TRoD proposes that the experience of dreams is intimately related to the manifestation of the topographic and dynamic re-organization in the brain's neural activity. The brain's topographic and temporal reorganization constitutes an altered spatiotemporal structure of consciousness leading to often bizarre dream experiences. Temporal dynamic and spatial topography are thus shared by neural and mental levels as the "common currency" of brain and experience. Such spatiotemporal approach to dreams is well in accordance with approaches to consciousness, e.g., Integrated Information Theory (IIT) (Tononi et al., 2016) and especially the Temporo-spatial theory of consciousness (Northoff and Huang, 2017; Northoff and Zilio, 2022a, 2022b) (Box 2), our sense of self (Box 1), and altered states of consciousness like meditation and psychedelics (Box 3).

References

- Abel, T., Havekes, R., Saletin, J.M., Walker, M., 2013. Sleep, plasticity and memory from molecules to whole-brain networks. *Curr. Biol.* 23 (17), R774–R788. <https://doi.org/10.1016/j.cub.2013.07.025>.
- Andrade, K.C., Spoomaker, V.I., Dresler, M., Wehrle, R., Holsboer, F., Sämann, P.G., Czigic, M., 2011. Sleep spindles and hippocampal functional connectivity in human NREM sleep. *J. Neurosci.* 31 (28), 10331–10339. <https://doi.org/10.1523/JNEUROSCI.5660-10.2011>.
- Andrillon, T., Kouider, S., 2020. The vigilant sleeper: neural mechanisms of sensory (de) coupling during sleep. *Curr. Opin. Physiol.* 15, 47–59. <https://doi.org/10.1016/j.cophys.2019.12.002>.
- Antony, J.W., Piloto, L., Wang, M., Pacheco, P., Norman, K.A., Paller, K.A., 2018. Sleep spindle refractoriness segregates periods of memory reactivation. *Curr. Biol.* 28 (11), 1736–1743. <https://doi.org/10.1016/j.cub.2018.04.020>.
- Aru, J., Suzuki, M., Rutiku, R., Larkum, M.E., Bachmann, T., 2019 30. Coupling the state and contents of consciousness. *Front Syst. Neurosci.* 13, 43. <https://doi.org/10.3389/fnsys.2019.00043>.
- Baird, B., Castelnovo, A., Gossesies, O., Tononi, G., 2018. Frequent lucid dreaming associated with increased functional connectivity between frontopolar cortex and temporoparietal association areas. *Sci. Rep.* 8 (1), 17798. <https://doi.org/10.1038/s41598-018-36190-w>.
- Baird, B., Riedner, B.A., Boly, M., Davidson, R.J., Tononi, G., 2019. Increased lucid dream frequency in long-term meditators but not following MBSR training. *Psychol. Conscious. (Wash. D. C.)* 6 (1), 40–54. <https://doi.org/10.1037/cns0000176>.
- Baird, B., Aparico, M.K., Allaudin, T., Riedner, B., Boly, M., Tononi, G., 2022. Episodic thought distinguishes spontaneous cognition in waking from REM NREM sleep. *Conscious. Cogn.* 97, 103247.
- Barry, D.N., Clark, I.A., Maguire, E.A., 2021. The relationship between hippocampal subfield volumes and autobiographical memory persistence. *Hippocampus* 31 (4), 362–374. <https://doi.org/10.1002/hipo.23293>.
- Bauer, C.C.C., Whitfield-Gabrieli, S., Díaz, J.L., Pasaye, E.H., Barrios, F.A., 2019. From State-to-Trait Meditation: Reconfiguration of Central Executive and Default Mode Networks. *eNeuro* 4 (6). <https://doi.org/10.1523/ENEURO.0335-18.2019>.
- Bayne, T., Hohwy, J., Owen, A.M., 2016. Are there levels of consciousness. *Trends Cogn. Sci.* 20 (6), 405–413. <https://doi.org/10.1016/j.tics.2016.03.009>.
- Benedetti, F., Poletti, S., Radaelli, D., Ranieri, R., Genduso, V., Cavallotti, S., Castelnovo, A., Smeraldi, E., Scarone, S., D'Agostino, A., 2015. Right hemisphere neural activations in the recall of waking fantasies and of dreams. *J. Sleep. Res.* 24 (5), 576–582. <https://doi.org/10.1111/jsr.12299>.
- Bergmann, T.O., Mölle, M., Diedrichs, J., Born, J., Siebner, H.R., 2012. Sleep spindle-related reactivation of category-specific cortical regions after learning face-scene associations. *Neuroimage* 59 (3), 2733–2742. <https://doi.org/10.1016/j.neuroimage.2011.10.036>.
- Blagrove, M., Pace-Schott, E.F., 2010. Trait and neurobiological correlates of individual differences in dream recall and dream content. *Int. Rev. Neurobiol.* 92 (10), 155–180. [https://doi.org/10.1016/S0074-7742\(10\)92008-4](https://doi.org/10.1016/S0074-7742(10)92008-4).
- Blagrove, M., Fouquet, N.C., Henley-Einion, J.A., Pace-Schott, E.F., Davies, A.C., Neuschaffer, J.L., Turnbull, O.H., 2011. PLoS ONE 6 (10). <https://doi.org/10.1371/journal.pone.0026708>.
- Blanke, O., Slater, M., Serino, A., 2015. Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron* 88 (1), 145–166. <https://doi.org/10.1016/j.neuron.2015.09.029>.
- Boutin, A., Pinsard, B., Boré, A., Carrier, J., Fogel, S.M., Doyon, J., 2018. Transient synchronization of hippocampo-striato-thalamo-cortical networks during sleep spindle oscillations induces motor memory consolidation. *Neuroimage* 169, 419–430. <https://doi.org/10.1016/j.neuroimage.2017.12.066>.
- Bréchet, L., Michel, C.M., 2022. EEG microstates in altered states of consciousness. *Front. Psychol.* 13. <https://doi.org/10.3389/fpsyg.2022.856697>.
- Bréchet, L., Brunet, D., Perogamvros, L., Tononi, G., Michel, C.M., 2020. EEG microstates of dreams. *Sci. Rep.* 10 (1), 1–9. <https://doi.org/10.1038/s41598-020-74075-z>.
- Buckner, R.L., DiNicola, L.M., 2019. The brain's default network: updated anatomy, physiology and evolving insights. *Nat. Rev. Neurosci.* 20 (10), 593–608. <https://doi.org/10.1038/s41583-019-0212-7>.
- Butler, S.F., Watson, R., 1985. Individual differences in memory for dreams: the role of cognitive skills. *Percept. Mot. Skills* 61 (3), 823–828. <https://doi.org/10.2466/pms.1985.61.3.823>.
- Buzsáki, G., 1989. Two-stage model of memory trace formation: a role for "noisy" brain states. *Neuroscience* 31 (3), 551–570. [https://doi.org/10.1016/0306-4522\(89\)90423-5](https://doi.org/10.1016/0306-4522(89)90423-5).
- Caporro, M., Haneef, Z., Yeh, H.J., Lenartowicz, A., Buttinelli, C., Parvizi, J., Stern, J.M., 2012. Functional MRI of sleep spindles and K-complexes. *Clin. Neurophysiol.* 123 (2), 303–309. <https://doi.org/10.1016/j.clinph.2011.06.018>.
- Carhart-Harris, R.L., 2018. The entropic brain - revisited. *Neuropharmacology* 142, 167–178. <https://doi.org/10.1016/j.neuropharm.2018.03.010>.
- Carhart-Harris, R.L., Friston, K., 2019. REBUS and the anarchic brain: toward a unified model of the brain action of psychedelics. *Pharmacol. Rev.* 71 (3), 316–344. <https://doi.org/10.1124/pr.118.017160>.
- Carhart-Harris, R.L., Leech, R., Hellyer, P.J., Shanahan, M., Feilding, A., Tagliazucchi, E., Chialvo, D.R., Nutt, D., 2014. The entropic brain: a theory of conscious states informed by neuroimaging research with psychedelic drugs. *Front Hum. Neurosci.* 8, 20. <https://doi.org/10.3389/fnhum.2014.00020>.
- Christoff, K., Irving, Z.C., Fox, K.C., Spreng, R.N., Andrews-Hanna, J.R., 2016. Mind-wandering as spontaneous thought: a dynamic framework. *Nat. Rev. Neurosci.* 17 (11), 718–731. <https://doi.org/10.1038/nrn.2016.113>.

- Jung, C.G., 2013. *Dream Analysis 1: Notes of the Seminar Given in 1928–30*. Routledge, London.
- Kohut, H. (1977). *The restoration of the self*. International Universities Press, Inc.
- Kolvoort, I.R., 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>.
- Kussé, C., Shaffii-LE Bourdieu, A., Schrouff, J., Matarazzo, L., Maquet, P., 2012. Experience-dependent induction of hypnagogic images during daytime naps: A combined behavioural and EEG study. *J. Sleep. Res.* 21 (1), 10–20. <https://doi.org/10.1111/j.1365-2869.2011.00939.x>.
- LaBerge, Stephen, Benjamin Baird, Philip G. Zimbardo, 2018. Smooth tracking of visual targets distinguishes lucid REM sleep dreaming and waking perception from imagination. *Nat. Commun.* 9 (1), 1–8.
- 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>.
- Lansink, C.S., Goltstein, P.M., Lankelma, J.V., McNaughton, B.L., Pennartz, C.M., 2009. Hippocampus leads ventral striatum in replay of place-reward information. *PLoS Biol.* 7 (8), e1000173 <https://doi.org/10.1371/journal.pbio.1000173>.
- Laufs, H., Hamandi, K., Salek-Haddadi, A., Kleinschmidt, A.K., Duncan, J.S., Lemieux, L., 2007. Temporal lobe interictal epileptic discharges affect cerebral activity in “default mode” brain regions. *Hum. Brain Mapp.* 28 (10), 1023–1032. <https://doi.org/10.1002/hbm.20323>.
- Laureys, S., 2005. The neural correlate of (un)awareness: lessons from the vegetative state. *Trends Cogn. Sci.* 9 (12), 556–559. <https://doi.org/10.1016/j.tics.2005.10.010>.
- Laureys, S., Peigneux, P., Phillips, C., Fuchs, S., Degueldre, C., Aerts, J., et al., 2001. Experience-dependent changes in cerebral functional connectivity during human rapid eye movement sleep. *Neuroscience* 105 (3), 521–525. [https://doi.org/10.1016/s0306-4522\(01\)00269-x](https://doi.org/10.1016/s0306-4522(01)00269-x).
- Leclair-Visonneau, L., Oudiette, D., Gaymard, B., Leu-Semenescu, S., Arnulf, I., 2010. Do the eyes scan dream images during rapid eye movement sleep? Evidence from the rapid eye movement sleep behaviour disorder model. *Brain* 133 (6), 1737–1746. <https://doi.org/10.1093/brain/awq110>.
- Li, W., Ma, L., Yang, G., Gan, W.B., 2017. REM sleep selectively prunes and maintains new synapses in development and learning. *Nat. Neurosci.* 20 (3), 427–437. <https://doi.org/10.1038/nn.4479>.
- Louie, K., Wilson, M.A., 2001. Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep. *Neuron* 29 (1), 145–156. [https://doi.org/10.1016/s0896-6273\(01\)00186-6](https://doi.org/10.1016/s0896-6273(01)00186-6).
- Mainieri, G., Maranci, J.B., Cousyn, L., Arnulf, I., 2019. Overt replay during REM sleep of the UPDRS finger taps sequence in a patient with REM sleep behavior disorder. *Sleep. Med.* 63, 38–40. <https://doi.org/10.1016/j.sleep.2019.05.018>.
- Malinowski, J., Horton, C.L., 2014. Evidence for the preferential incorporation of emotional waking-life experiences into dreams. *Dreaming* 24 (1), 18. <https://doi.org/10.1037/a0036017>.
- Maquet, P., 2000. Functional neuroimaging of normal human sleep by positron emission tomography. *J. Sleep. Res.* 9 (3), 207–232. <https://doi.org/10.1046/j.1365-2869.2000.00214.x>.
- Martino, M., Magioncalda, P., Conio, B., Capobianco, L., Russo, D., Adavastro, G., et al., 2020. Abnormal functional relationship of sensorimotor network with neurotransmitter-related nuclei via subcortical-cortical loops in manic and depressive phases of bipolar disorder. *Schizophr. Bull.* 46 (1), 163–174. <https://doi.org/10.1093/schbul/sbz035>.
- Mashour, G.A., Roelfsema, P., Changeux, J.P., Dehaene, S., 2020. Conscious Processing and the Global Neuronal Workspace Hypothesis. *Mar 4 Neuron* 105 (5), 776–798. <https://doi.org/10.1016/j.neuron.2020.01.026>.
- Nelson, J.P., McCarley, R.W., Hobson, J.A., 1983. REM sleep burst neurons, PGO waves, and eye movement information. *J. Neurophysiol.* 50 (4), 784–797. <https://doi.org/10.1152/jn.1983.50.4.784>.
- Nielsen, T.A., Kuiken, D., Alain, G., Stenstrom, P., Powell, R.A., 2004. Immediate and delayed incorporations of events into dreams: further replication and implications for dream function. *J. Sleep. Res.* 13 (4), 327–336. <https://doi.org/10.1111/j.1365-2869.2004.00421.x>.
- Nilsen, A., Juel, B.E., Thürer, B., Aamodt, A., Storm, J.F., 2022. Are we really unconscious in “unconscious” states? Common assumptions revisited. *Oct 5 Front Hum. Neurosci.* 16, 987051. <https://doi.org/10.3389/fnhum.2022.987051>.
- Northoff, G., 2011. *Neuropsychanalysis in Practice: Brain, Self and Objects*. OUP, Oxford.
- Northoff, G., 2013. What the brain’s intrinsic activity can tell us about consciousness? A tri-dimensional view (May). *Neurosci. Biobehav. Rev.* 37 (4), 726–738. <https://doi.org/10.1016/j.neubiorev.2012.12.004>.
- Northoff, G., 2014a. Do cortical midline variability and low frequency fluctuations mediate William James’ “Stream of Consciousness”? “Neurophenomenal Balance Hypothesis” of “Inner Time Consciousness”. *Conscious Cogn.* 30, 184–200. <https://doi.org/10.1016/j.concog.2014.09.004>.
- Northoff, G., 2014b. Are auditory hallucinations related to the brain’s resting state activity? A ‘neurophenomenal resting state hypothesis’. *Clin. Psychopharmacol. Neurosci.* 12 (3), 189. <https://doi.org/10.9758/cpn.2014.12.3.189>.
- Northoff, G., 2017. Personal identity and cortical midline structure (CMS): do temporal features of CMS neural activity transform into “self-continuity”? *Psychol. Inq.* 28 (2–3), 122–131. <https://doi.org/10.1080/1047840X.2017.1337396>.
- Northoff, G., Qin, P., 2011. How can the brain’s resting state activity generate hallucinations? A ‘resting state hypothesis’ of auditory verbal hallucinations. *Schizophr. Res.* 127 (1–3), 202–214. <https://doi.org/10.1016/j.schres.2010.11.009>.
- Northoff, G., Heiss, W.D., 2015. Why is the distinction between neural predispositions, prerequisites, and correlates of the level of consciousness clinically relevant? Functional brain imaging in coma and vegetative state. *Stroke* 46 (4), 1147–1151. <https://doi.org/10.1161/STROKEAHA.114.007969>.
- 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., Scalabrini, A., 2021. “Project for a Spatiotemporal Neuroscience”—Brain and Psyche Share Their Topography and Dynamic. *Front Psychol.* 12, 717402 <https://doi.org/10.3389/fpsyg.2021.717402>.
- Northoff, G., Gomez-Pilar, J., 2021. Overcoming rest–task divide—abnormal temporospatial dynamics and its cognition in schizophrenia. *Schizophr. Bull.* 47 (3), 751–765. <https://doi.org/10.1093/schbul/sbaa178>.
- 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., Wainio-Theberge, S., Evers, K., 2020a. 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., Wainio-Theberge, S., Evers, K., 2020b. Spatiotemporal neuroscience—what is it and why we need it. *Phys. Life Rev.* 33, 78–87. <https://doi.org/10.1016/j.plrev.2020.06.005>.
- Northoff, G., Vatansever, D., Scalabrini, A., Stamatakis, E.A., 2022. Ongoing Brain Activity and Its Role in Cognition: Dual versus Baseline Models, 10738584221081752 *Neuroscientist*. <https://doi.org/10.1177/10738584221081752>.
- Panksepp, J., Biven, L., 2012. *The archaeology of mind: neuroevolutionary origins of human emotions* (Norton series on interpersonal neurobiology). WW Norton & Company.
- 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>.
- Qin, P., Wu, X., Wu, C., Wu, H., Zhang, J., Huang, Z., et al., 2021. Higher-order sensorimotor circuit of the brain’s global network supports human consciousness. *Neuroimage* 231, 117850. <https://doi.org/10.1016/j.neuroimage.2021.117850>.
- Rasch, B., Born, J., 2013. About sleep’s role in memory. *Physiol. Rev.* 93 (2), 681–766. <https://doi.org/10.1152/physrev.00032.2012>.
- Raut, R.V., Snyder, A.Z., Raichle, M.E., 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>.
- Ruby, P.M., 2020. The neural correlates of dreaming have not been identified yet. Commentary on “The Neural Correlates of Dreaming. *Nat. Neurosci.* 2017”. *Front. Neurosci.* 14, 585470 <https://doi.org/10.3389/fnins.2020.585470>.
- Scalabrini, A., Wolman, A., Northoff, G., 2021. The self and its right insula—Differential topography and dynamic of right vs. left insula. *Brain Sci.* 11 (10), 1312. <https://doi.org/10.3390/brainsci11101312>.
- Scalabrini, A., Esposito, R., Mucci, C., 2021. Dreaming the unrepressed unconscious and beyond: repression vs dissociation in the oneiric functioning of severe patients. *Res. Psychother.: Psychopathol. Process Outcome* 24 (2). <https://doi.org/10.4081/rpippo.2021.545>.
- Scalabrini, A., Mucci, C., Northoff, G., 2022b. The nested hierarchy of self and its trauma: In search for a synchronic dynamic and topographical re-organization. *Sep 2 Front Hum. Neurosci.* 16, 980353. <https://doi.org/10.3389/fnhum.2022.980353>.
- Scalabrini, A., Schimmenti, A., De Amicis, M., Porcelli, P., Benedetti, F., Mucci, C., Northoff, G., 2022a. The self and its internal thought: In search for a psychological baseline (Jan). *Conscious Cogn.* 97, 103244. <https://doi.org/10.1016/j.concog.2021.103244>.
- Schabus, M., Dang-Vu, T.T., Albouy, G., Balteau, E., Boly, M., Carrier, J., et al., 2007. Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep. *Proc. Natl. Acad. Sci. U. S. A.* 104 (32), 13164–13169. <https://doi.org/10.1073/pnas.0703084104>.
- Schacter, D.L., Addis, D.R., Hassabis, D., Martin, V.C., Spreng, R.N., Szpunar, K.K., 2012. The future of memory: remembering, imagining, and the brain. *Neuron* 76 (4), 677–694. <https://doi.org/10.1016/j.neuron.2012.11.001>.
- Schreiner, S.J., Imbach, L.L., Valko, P.O., Maric, A., Maqkaj, R., Werth, E., et al., 2021. Reduced Regional NREM Sleep Slow-Wave Activity Is Associated With Cognitive Impairment in Parkinson Disease. *Front. Neurol.* 12, 618101 <https://doi.org/10.3389/fneur.2021.618101>.
- Schreiner, T., Staudigl, T., 2020. Electrophysiological signatures of memory reactivation in humans. *Philos. Trans. R. Soc. B* 375 (1799), 20190293. <https://doi.org/10.1098/rstb.2019.0293>.
- Schreiner, T., Doeller, C.F., Jensen, O., Rasch, B., Staudigl, T., 2018. Theta phase-coordinated memory reactivation reoccurs in a slow-oscillatory rhythm during NREM sleep. *Cell Rep.* 25 (2), 296–301. <https://doi.org/10.1016/j.celrep.2018.09.037>.
- Seth, A.K., 2013. Interoceptive inference, emotion, and the embodied self. *Trends Cogn. Sci.* 17 (11), 565–573. <https://doi.org/10.1016/j.tics.2013.09.007>.
- Siclari, F., Valli, K., Arnulf, I., 2020. Dreams and nightmares in healthy adults and in patients with sleep and neurological disorders. *Lancet Neurol.* 19 (10), 849–859. [https://doi.org/10.1016/S1474-4422\(20\)30275-1](https://doi.org/10.1016/S1474-4422(20)30275-1).

- Siclari, F., Bernardi, G., Cataldi, J., Tononi, G., 2018. Dreaming in NREM sleep: a high-density EEG study of slow waves and spindles. *J. Neurosci.* 38 (43), 9175–9185. <https://doi.org/10.1523/JNEUROSCI.0855-18.2018>.
- Siclari, F., Baird, B., Perogamvros, L., Bernardi, G., LaRocque, J.J., Riedner, B., et al., 2017. The neural correlates of dreaming. *Nat. Neurosci.* 20 (6), 872–878. <https://doi.org/10.1038/nn.4545>.
- Skaggs, W.E., McNaughton, B.L., 1996. Replay of neuronal firing sequences in rat hippocampus during sleep following spatial experience. *Science* 271 (5257), 1870–1873. <https://doi.org/10.1126/science.271.5257.1870>.
- Smallwood, J., Schooler, J.W., 2015. The science of mind wandering: empirically navigating the stream of consciousness. *Annu. Rev. Psychol.* 487–518. <https://doi.org/10.1146/annurev-psych-010814-015331>.
- Smallwood, J., Bernhardt, B.C., Leech, R., Bzdok, D., Jefferies, E., Margulies, D.S., 2021. The default mode network in cognition: a topographical perspective. *Nat. Rev. Neurosci.* 22 (8), 503–513. <https://doi.org/10.1038/s41583-021-00474-4>.
- Smith, R., Lane, R.D., Parr, T., Friston, K.J., 2019. Neurocomputational mechanisms underlying emotional awareness: Insights afforded by deep active inference and their potential clinical relevance. *Neurosci. Biobehav. Rev.* 107, 473–491. <https://doi.org/10.1016/j.neubiorev.2019.09.002>.
- Solms, M., 2011. Neurobiology and the neurological basis of dreaming. *Handb. Clin. Neurol.* 98, 519–544. <https://doi.org/10.1016/B978-0-444-52006-7.00034-4>.
- Solms, M., 2020. New project for a scientific psychology: General scheme. *Neuropsychanalysis* 22 (1–2), 5–35. <https://doi.org/10.1080/15294145.2020.1833361>.
- Solomonova, E., Stenstrom, P., Paquette, T., Nielsen, T., 2015. Different temporal patterns of memory incorporations into dreams for laboratory and virtual reality experiences: relation to dreamed locus of control. *Int. J. Dream. Res.* 10–26. <https://doi.org/10.11588/ijodr.2015.1.16611>.
- Stickgold, R., James, L., Hobson, J.A., 2000. Visual discrimination learning requires sleep after training. *Nat. Neurosci.* 3 (12), 1237–1238. <https://doi.org/10.1038/81756>.
- Stickgold, R., Hobson, J.A., Fosse, R., Fosse, M., 2001a. Science 294 (5544), 1052–1057. <https://doi.org/10.1126/science.106353>.
- Stickgold, R., Malia, A., Fosse, R., Propper, R., Hobson, J.A., 2001b. Brain-mind states: I. Longitudinal field study of sleep/wake factors influencing mentation report length. *Mar 15 Sleep* 24 (2), 171–179. <https://doi.org/10.1093/sleep/24.2.171>.
- Storm, J.F., Boly, M., Casali, A.G., Massimini, M., Olcese, U., Pennartz, C.M., Wilke, M., 2017. Consciousness regained: disentangling mechanisms, brain systems, and behavioral responses. *J. Neurosci.* 37 (45), 10882–10893. <https://doi.org/10.1523/JNEUROSCI.1838-17.2017>.
- Tanabe, S., Huang, Z., Zhang, J., Chen, Y., Fogel, S., Doyon, J., et al., 2020. Altered global brain signal during physiologic, pharmacologic, and pathologic states of unconsciousness in humans and rats. *Anesthesiology* 132 (6), 1392–1406. <https://doi.org/10.1097/ALN.0000000000003197>.
- Thompson, K., Gibbings, A., Shaw, J., Ray, L., Hébert, G., De Koninck, J., Fogel, S., 2021. Sleep and Second-Language Acquisition Revisited: The Role of Sleep Spindles and Rapid Eye Movements. *Nat. Sci. Sleep.* 13, 1887–1902. <https://doi.org/10.2147/NSS.S326151>.
- Tononi, G., 2008. Consciousness as integrated information: a provisional manifesto. *Biol. Bull.* 215 (3), 216–242. <https://doi.org/10.2307/25470707>.
- Tononi, G., Boly, M., Massimini, M., Koch, C., 2016. Integrated information theory: from consciousness to its physical substrate. *Nat. Rev. Neurosci.* 17 (7), 450–461. <https://doi.org/10.1038/nrn.2016.44>.
- Tyvaert, L., LeVan, P., Grova, C., Dubeau, F., Gotman, J., 2008. Effects of fluctuating physiological rhythms during prolonged EEG-fMRI studies. *Clin. Neurophysiol.* 119 (12), 2762–2774. <https://doi.org/10.1016/j.clinph.2008.07.284>.
- Vanhaudenhuyse, A., Demertzi, A., Schabus, M., Noirhomme, Q., Bredart, S., Boly, M., et al., 2011. Two distinct neuronal networks mediate the awareness of environment and of self. *J. Cogn. Neurosci.* 23 (3), 570–578. <https://doi.org/10.1162/jocn.2010.21488>.
- Voss, U., Holzmann, R., Tuin, I., Hobson, J.A., 2009. Lucid dreaming: a state of consciousness with features of both waking and non-lucid dreaming. *Sleep* 32 (9), 1191–1200. <https://doi.org/10.1093/sleep/32.9.1191>.
- Walker, M.P., Stickgold, R., 2004. Sleep-dependent learning and memory consolidation. *Neuron* 44 (1), 121–133. <https://doi.org/10.1016/j.neuron.2004.08.031>.
- Wamsley, E.J., 2014. Dreaming and offline memory consolidation. *Curr. Neurol. Neurosci. Rep.* 14 (3), 1–7. <https://doi.org/10.1007/s11910-013-0433-5>.
- Wamsley, E.J., Stickgold, R., 2011. Memory, sleep, and dreaming: experiencing consolidation. *Sleep. Med. Clin.* 6, 97–108. <https://doi.org/10.1016/j.jsmc.2010.12.008>.
- Wamsley, E.J., Tucker, M., Payne, J.D., Benavides, J.A., Stickgold, R., 2010a. Dreaming of a learning task is associated with enhanced sleep-dependent memory consolidation. *Curr. Biol.* 20 (9), 850–855. <https://doi.org/10.1016/j.cub.2010.03.027>.
- Wamsley, E.J., Perry, K., Djonlagic, I., Reaven, L.B., Stickgold, R., 2010b. Cognitive replay of visuomotor learning at sleep onset: temporal dynamics and relationship to task performance. *Sleep* 33 (1), 59–68. <https://doi.org/10.1093/sleep/33.1.59>.
- Windt, J.M., 2010. The immersive spatiotemporal hallucination model of dreaming. *Phenomenol. Cogn. Sci.* 9 (2), 295–316. <https://doi.org/10.1007/s11097-010-9163-1>.
- Windt, J.M., 2020. Consciousness in sleep: How findings from sleep and dream research challenge our understanding of sleep, waking, and consciousness. *Philos. Compass* 15 (4), e12661. <https://doi.org/10.1111/phc3.12661>.
- 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 (2), 159–173. <https://doi.org/10.1016/j.tics.2021.11.007>.
- Wolff, A., Di Giovanni, D.A., Gómez-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 (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>.
- Zilio, F., Gomez-Pilar, J., Cao, S., Zhang, J., Zang, D., Qi, Z., et al., 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>.