

Ongoing Brain Activity and Its Role in Cognition: Dual versus Baseline Models

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Georg Northoff¹, Deniz Vatansever², Andrea Scalabrini³, and Emmanuel A. Stamatakis⁴

Abstract

What is the role of the brain's ongoing activity for cognition? The predominant perspectives associate ongoing brain activity with resting state, the default-mode network (DMN), and internally oriented mentation. This triad is often contrasted with task states, non-DMN brain networks, and externally oriented mentation, together comprising a “dual model” of brain and cognition. In opposition to this duality, however, we propose that ongoing brain activity serves as a neuronal baseline; this builds upon Raichle's original search for the default mode of brain function that extended beyond the canonical default-mode brain regions. That entails what we refer to as the “baseline model.” Akin to an internal biological clock for the rest of the organism, the ongoing brain activity may serve as an internal point of reference or standard by providing a shared neural code for the brain's rest as well as task states, including their associated cognition. Such shared neural code is manifest in the spatiotemporal organization of the brain's ongoing activity, including its global signal topography and dynamics like intrinsic neural timescales. We conclude that recent empirical evidence supports a baseline model over the dual model; the ongoing activity provides a global shared neural code that allows integrating the brain's rest and task states, its DMN and non-DMN, and internally and externally oriented cognition.

Keywords

spontaneous activity, dual model, baseline model, spatial topography, temporal dynamic

Introduction

One pervasive feature of the brain and its mechanistic functioning is its ongoing physiological activity (Berger 1929; Northoff 2014a, 2014b; Raichle 2009; Raichle and others 2001). The ongoing activity's importance for the brain's processing is underlined by the fact that it consumes 80% to 90% of the overall energy budget of the brain, which, although representing only 2% of the total body mass, accounts for nearly 20% of the overall body's energy budget (Raichle 2006; Zhang and Raichle 2010). Such high energy consumption suggests that the ongoing activity must take on an important role or function for healthy mentation, including both internally and externally oriented cognition (Raichle 2015a).

The importance of the ongoing activity's role or function is further supported by its modulation of mental features like “self” (Davey and others 2016; Frewen and others 2020; Northoff 2016a, 2016b; Qin and Northoff 2011; Qin and others 2020) (see also Box 4) and consciousness (Luppi and others 2019; Northoff and Huang 2017; Northoff and Lamme 2020), as well as its changes in neurologic (Carhart-Harris 2018; Huang and others

2018b; Huang and others 2020; Owen 2019; Tanabe and others 2020; Zhang and others 2018) and psychiatric conditions (Damiani and others 2019; Martino and others 2020; Northoff and others 2021; Scalabrini and others 2020; Zhang and others 2019).

What is the exact role or function by which the ongoing activity mediates cognition and mental features? Building on and extending Marcus Raichle's earlier proposition of a default mode of brain function (Raichle 2010, 2015a, 2015b; Raichle and others 2001), we propose that the brain's ongoing activity serves as a neuronal baseline. This is made possible by a commonly shared neural code the ongoing activity provides across rest and task states, which, importantly, also mediates both internally and

¹University of Ottawa, Ottawa, ON, Canada

²Fudan University Shanghai, Shanghai, China

³University G. D'Annunzio of Chieti-Pescara, Chieti, Abruzzo, Italy

⁴University of Cambridge, Cambridge, Cambridgeshire, UK

Corresponding Author:

Georg Northoff, 1145 Carling Avenue, University of Ottawa, Ottawa, ON K1Z 7K4, Canada.

Emails: georg.northoff@theroyal.ca, www.georgnorthoff.com

externally oriented forms of cognition (see Yeshurun and others 2021 for the assumption of such neural code albeit in a more cognitive way).

A biological clock serves as internal reference or standard by providing a temporal code for the timing of the organism. In parallel, the ongoing brain activity may serve as an internal reference or standard by providing a globally shared spatial and temporal neural code for the brain's processing during both rest and task states, across both default-mode network (DMN) and non-DMN networks, and for both internally and externally oriented cognition.

We therefore speak of a “baseline model” of the brain's ongoing activity, which assumes that the spatiotemporal brain dynamics provide a globally shared neural code for rest and task states, DMN and non-DMN, and internally and externally oriented cognition. We assume that such globally shared neural code is manifest in the spatiotemporal organization of the ongoing activity, namely, its whole-brain topography and dynamics. Importantly, as the ongoing activity and its spatiotemporal dynamics spread across the whole brain, we do not limit the ongoing activity's role to the DMN (Buckner and DiNicola 2019; Yeshurun and others 2021). Rather, the baseline model includes the whole brain, namely, its topography within which the DMN as core occupies a prominent position relative to other networks at the periphery (see Margulies and others 2016).

The assumption of a baseline model stands in contrast to the currently more dominant and often tacitly presupposed “dual model.” The dual model associates the role or function of the ongoing activity with resting state,

DMN, and internally oriented cognition, which are supposed to stand in contrast or dual relation to a corresponding triad of task states, non-DMN, and externally oriented cognition. Together, this amounts to a duality on neuronal, network, and cognitive levels—hence the name *dual model*.

Unlike the baseline model, the dual model does not take into view the role of the ongoing activity as a globally shared neural code that can serve as a common unifying reference or standard for the dualities on all three levels. Thus, it is our aim to introduce and develop a more comprehensive and inclusive role of the brain's ongoing activity beyond internally oriented cognition. This is the key goal of our article, and the baseline model serves that purpose.

We first introduce the dual model (part 1). This is followed by a review of recent empirical evidence on how the spatial (part 2) and temporal (part 3) dynamics of the brain's ongoing activity are key and provide a commonly shared neural code in mediating both internally and externally oriented cognition (rather than exclusively mediating internally oriented cognition). We then introduce what we describe as the “baseline model” (part 4), which is compared with other related models like the metabolic-energetic (Raichle), inside-out (Buzsáki), and predictive coding (Friston) models (part 5). Related issues like historical predecessors (Box 1), methodological implications (Box 2), and outstanding issues (Box 3) are discussed in boxes. Last, we discussed how the baseline model at a neuronal level has implications for the concept of self at a psychological level (Box 4).

Box 1. Historical and Current Predecessors—From the Intrinsic Model of Brain to the Baseline Model.

The assumption of a more comprehensive role or function of the brain's ongoing activity has historical predecessors (see Northoff 2014a, 2014b, 2018a, 2018b; Raichle 2009, 2010). Thomas Graham Brown, a student of C. Sherrington, observed spontaneous activity discharges in the spinal cord, which, as they were independent of any movement, could only be generated internally (i.e., spontaneously). Hans Berger, the inventor of the electroencephalogram (EEG), also noticed the brain's spontaneous activity and its association with mental features, including what we now describe as externally oriented cognition (Berger 1929). Other neuroscientists in the first half of the 20th century followed this line, proposing a not yet fully defined key role for the brain's ongoing activity in externally oriented cognition (Bishop 1933; Goldstein 2000; Lashley 1950).

More recently, Raichle summarized these earlier views as an “intrinsic view” of the brain as they emphasize the intrinsic nature of the brain's ongoing activity as remaining prior to and independent of extrinsic modulation (Northoff 2012; Raichle 2009, 2010). This is also reflected in Buzsáki's notion of the “inside-out view” that, unlike the “outside-in view,” considers the brain's ongoing or inside activity as most fundamental and basic (Buzsáki 2019, 2020; see Northoff and others 2010a, 2010b; Northoff 2014a, 2014b for earlier versions of the inside-out model).

The intrinsic view of the brain emphasizes the fundamental nature of the brain's ongoing activity and especially its temporospatial dynamics (see below) for both task states, that is, rest-task interaction (Northoff 2012; Northoff, Qin, and others 2010; Northoff, Duncan, and others 2010), the brain's neural coding (Northoff 2014a), and mental features like consciousness (Northoff 2012, 2014b; Northoff and Huang 2017; Northoff, Wainio-Theberge and others 2019, 2020; Northoff and Lamme 2020).

(continued)

Box 1. (continued)

What is intrinsic to the brain? The intrinsic view emphasizes the spatial topography of the ongoing activity like its core-periphery organization (Huntenberg and others 2018; Margulies and others 2016), including its carryover from rest to task states (Golesorkhi and others 2021a, 2021b). Moreover, such intrinsic view is also exemplified by the brain's intrinsic temporal organization as in hierarchy of the intrinsic neural timescales as discussed above. Most interestingly, two recent studies in fMRI and magnetoencephalography (MEG) show that the spatial core-periphery organization converges with the temporal hierarchy of the intrinsic neural timescales during both rest and task states (Golesorkhi and others 2021a, 2021b; see also Ito and others 2020; Raut and others 2020). Together, these findings suggest convergence in the intrinsic spatial and temporal organization of the brain's ongoing activity.

How is such intrinsic model of the brain related to the here suggested baseline model? The baseline model of the ongoing activity strongly builds upon the brain's intrinsic spatiotemporal organization. Going beyond the merely intrinsically spatiotemporal hierarchical characterization of the brain's ongoing activity, the baseline model postulates a specific role or function of the brain's intrinsic spatiotemporal organization for cognition: that role or function consists of serving as a reference or standard for the brain's processing during all states (i.e., rest and task), in all networks (i.e., DMN and non-DMN), and any form of cognition, including internally and externally oriented cognition. The baseline model can thus be seen as extension of the intrinsic model of brain.

Box 2. Methodological Implications of the Baseline Model.

The assumption of a baseline carries important methodological implications for how to investigate the brain. The dual model takes the dichotomy of internally and externally oriented cognition as the starting point. From there it infers that both forms of cognition must also be mediated by a corresponding dichotomy on the neuronal level (i.e., DMN and non-DMN as well as rest and task). The cognitive dichotomy of internally and externally oriented cognition is complemented by a corresponding neuronal dichotomy of rest and task states. Conceived methodologically, the cognitive measures of internally and externally oriented cognition serve here as independent variables while the neuronal measures of rest and task states take on the role as dependent variables.

That is contested in the baseline model as it entails the reverse approach. It takes the brain's ongoing activity on the neuronal level as its starting point prior to and independent of the dichotomy of internally and externally oriented cognition on the cognitive level (see Northoff and others 2010a, 2010b). Rather than inferring from cognition to brain, as the dual model, it infers cognition, including the duality of internally and externally oriented cognition, from the brain itself, that is, from the intrinsic spatial and temporal organization of the brain (see Box 1 for the intrinsic model of brain). This methodological approach puts the baseline model in close vicinity to the inside-out (Buzsáki 2019, 2020) and brain-based (Northoff 2014a) approaches.

On the cognitive level, this means that measures of, for instance, internally oriented cognition may be strongly context dependent, that is, on the external context in which they occur (see Lyu and others 2021; Vatansever and others 2015, 2017). Methodologically, this means that, unlike in the dual model, neuronal measures of the ongoing activity, including rest and task states, serve as the independent variable while cognitive measures are dependent variables. Such "methodological reversal" makes first and foremost possible to take into view the possible role of the brain's ongoing activity as neuronal baseline, including its role or function to serve as internal reference or standard for cognition.

The baseline model postulates that cognition is structured and organized in a spatiotemporal way requiring spatiotemporal neuroscience (Northoff and others 2010a, 2010b). Specifically, one may want to investigate how our perception, emotion, actions, and cognition as well as mental features like self and consciousness are structured in spatial and temporal terms on the psychological level. Rather than focusing on the type of contents characterizing our cognition, one may then want to investigate the dynamics of contents, that is, the structure or pattern in the changes across different contents.

For instance, instead of detailing mind wandering by its contents like internal versus external as well as past, future, or present, one may want to investigate the change of contents: how often do the thought contents switch between internally and externally oriented contents, between past, future, and present, and how long do the contents last in their duration? Such thought dynamics may then be linked to the brain's dynamics, that is, the spatiotemporal dynamics of its ongoing activity (for first steps in this direction, see Luppi and others 2019; Rostami and others 2021; Vanhaudenhuyse and others 2011)—dynamics may thus be shared by both brain and thought as their "common currency" (Northoff and others 2020, 2021).

Box 3. Outstanding Issues of the Baseline Model.

Our proposal of the ongoing activity serving as neuronal baseline that, through its spatiotemporal dynamics (STD), structures and shapes rest and task states in a domain-general way, leaves open several issues. We left open how the ongoing activity's STD are related to its energetic metabolism, which, albeit tentatively, is supported on empirical grounds (Hyder and Rothman 2010; Hyder and others 2011; Shulman and others 2009). If our proposal of the STD as index of the ongoing activity's function as neuronal baseline holds, one would expect close convergence of STD features with metabolic-energetic features (for initial support, see He 2011). Future studies combining both neuronal STD and metabolic-energetic measurement are warranted (for first steps, see He 2011). If the presumed close link of metabolic-energetic features and STD holds, it would extend Raichle's original suggestion in that it connects high energetic metabolism to specific neuronal features (i.e., STD) in providing the default mode of brain function (Raichle and others 2001).

Yet another issue left open is our rather arbitrary selection of STD features and measures like global signal topography (i.e., global signal correlation [GSCOR] and coactivation pattern [CAP]) and intrinsic neural timescales (i.e., autocorrelation window [ACW] and power law exponent [PLE]/detrended fluctuation analysis [DFA]) as indexes of the neuronal baseline. Future studies are needed to include other STD measures like Lempel-Zev complexity (Golesorkhi and others 2021a, 2021b; Varley and others 2020; Wolff and others 2019a, 2019b) and median frequency (Golesorkhi and others 2021a, 2021b; Huang and others 2018a). Finally, we left open how both internally and externally oriented cognition are shaped and structured by the ongoing activity's STD. If the resting state's STD does indeed modulate task-related activity and associated perception/cognition, one would expect that both internally and externally oriented cognition are also shaped and structured in spatiotemporal topographic-dynamical ways. One would then assume that, despite their differences in content, internally and externally oriented cognition may nevertheless share some similarities, that is, "common currency" (Northoff and others 2020, 2021), in their underlying spatiotemporal dynamics, as both are based on the ongoing activity's STD.

This is, for instance, supported by the co-occurrence of both internally and externally oriented cognition contents in mental features like self (Northoff 2016a, 2016b, 2017; Qin and others 2020), consciousness (Northoff and Huang 2017; Northoff and Lamme 2020), mind wandering (Christoff and others 2016; Dixon and others 2014; Northoff 2018a, 2018b; Vanhaudenhuyse and others 2011), and various psychiatric disorders (Northoff 2016a, 2016b, 2017, 2018a, 2018b; Northoff and others 2021). STD may consequently provide a "common currency" of internally and externally oriented cognition and, even more radical, between neuronal and mental features, that is, brain and mind (Kolvoort and others 2020; Northoff and others 2020, 2021). That remains to be further investigated in the future. Cognitive neuroscience would then be complemented by what we described as "spatiotemporal neuroscience" (Northoff and others 2020, 2021).

Box 4. Spatiotemporal Nestedness and Its Relevance for the Self at a Psychological Level.

Spatiotemporal nestedness refers to a type of organization of different spatial and temporal scales of neural activity. Rather than operating in parallel, unconnected, or causally connected but separate, the different spatial and temporal scales of neural activity are contained or nested within each other. Nestedness accounts for self-similarity: just like the different sizes of the Russian dolls are nested within each other, the different temporal and spatial scales of the brain's neural activity are contained and nested within each other in a self-affine way (Northoff 2018a, 2018b). This means that they are organized in a scale-free way.

Such scale-free activity typically characterizes ubiquitous systems in nature, from the seismic earth waves to the stock market fluctuations (He 2014; He and others 2010). Scale-free activity with spatial nestedness also characterizes the brain. Spatially, regions are nested within networks, which, among the latter, constitute small-world topography (Zhang and others 2020). This is, for instance, manifest in a particular topography with different degrees of global spatial activity representation in particular regions/networks: the local activity of particular regions is spatially nested within the global activity of the whole brain.

At a psychological level, another example of nestedness can be the self, considered a key feature of our mental life that allows integrating various internal-external inputs (Northoff 2016a, 2016b; Sui and Humphreys 2015). A recent large-scale imaging/fMRI meta-analysis by Qin and others (2020) confirmed the key role of the right insula for the self (see also Scalabrini, Wolman, and others 2021). They observed especially the right insula, together with left insula, dorsal anterior cingulate cortex, thalamus, and parahippocampus, to be involved in mediating the interoceptive self, that is, the self that is recruited during tasks requiring interoceptive awareness like the awareness of one's own heartbeat.

They also observed the right insula, together with left insula, interior frontal gyrus, premotor cortex, temporoparietal junction (TPJ), and medial prefrontal cortex (MPFC), to be recruited in other studies of self like extero-proprioceptive self about the outer boundaries of the own body (see also Blanke and others 2015). Finally, the right insula was also observed in the typical studies on mental or cognitive self-reference using trait adjectives (and related paradigms) that strongly recruit the DMN (i.e., cortical midline structure). Together, this amounts to a three-layered spatially nested topography of the self with its distinct aspects like interoception, extero-proprioception, and cognition.

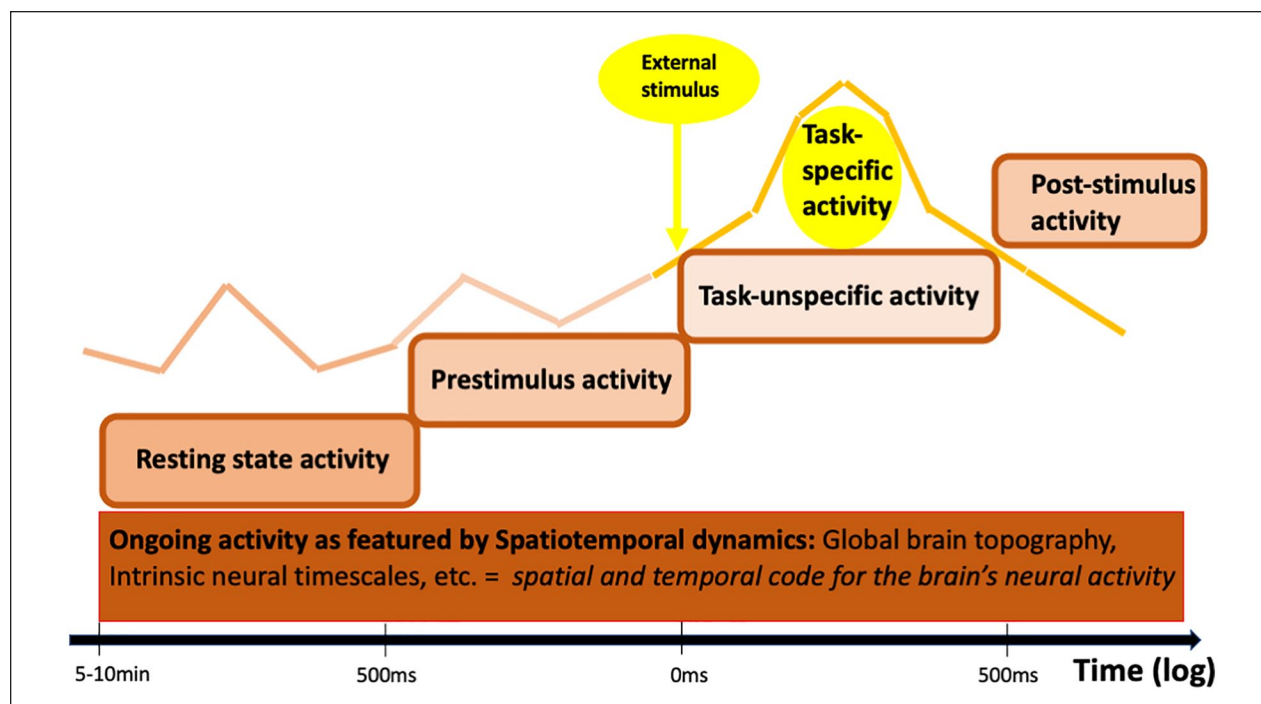


Figure 1. Different components of ongoing activity.

Part I: Dual Model—Dualities of Rest versus Task, DMN versus Non-DMN, and Internally versus Externally Oriented Cognition

Ongoing Activity—Rest, Prestimulus, and Task States as Distinct Components

Prior to retabulating existing assumptions and proposing novel perspectives, we need to first clarify the concept of an “ongoing brain activity.” Here we use the term *ongoing activity* to describe an amalgam that includes distinct neural activity components like resting state, prestimulus, and task-related activity. The first component of ongoing activity concerns what operationally is described as resting state that is usually measured during the absence of specific stimuli or tasks (i.e., eyes closed or open), for longer stretches of time (i.e., minutes) (Logothetis and others 2009). Resting state activity is often also described as intrinsic activity, which refers to the component of neural activity that is ongoing and not modulated by extrinsic tasks or stimuli and therefore present during both rest and task states (Cole and others 2012, 2014, 2016; Ito and others 2020).

Cognitively, resting state activity has been associated with various forms of internally oriented cognition (see below for details). Given such association of the ongoing activity with cognition, one may consider resting state or intrinsic activity as just another task state: it features covert, not yet fully known internal stimuli or tasks rather

than overt external tasks or stimuli as in what is typically described as task states (Cole and others 2014, 2016; Ito and others 2020; Tavor and others 2016).

A second component of ongoing activity can be found in prestimulus activity, that is, the neural activity immediately preceding the onset of a specific stimulus or task (i.e., the 100–1000 ms preceding stimulus onset) (Bai and others 2015; He 2013; Huang and others 2017; Wainio-Theberge and others 2021; Wolff and others 2019a, 2019b). Finally, a third component of ongoing activity can be found during task-related activity where it is present in what is also coined “background activity”: it may represent that component of task-related activity that, operating in the background, reflects the carryover and continuation of the ongoing activity during task states (Barnes and others 2009; Cole and others 2012, 2013, 2016; Di and Biswal 2019; Di and others 2013a, 2013b; Di and others 2020; Fair and others 2007; Ito and others 2020; Northoff and others 2010a, 2010b; Smith and others 2009) (see Fig. 1).

Are Resting State and Prestimulus Activity Two Sides of a Coin?

In the operationalization of fMRI acquisition, resting state activity and prestimulus activity are considered two different moments albeit operating on different timescales (5–10 minutes, 100–1000 ms). However, in brain dynamics, even if referring to two different moments in time, they might also be considered conceptually as two

sides of a coin, namely, the ongoing activity as characterized by its multiple timescales (see below). Despite their temporal differences, resting state and prestimulus activity may show a high degree of similarities as traced to their common basis in the ongoing activity.

This is further supported by the observation that both resting state and prestimulus activity affect stimulus-related activity. Various research focused on how the impact of the external stimulus on the brain during stimulus-related activity depends upon the brain's prestimulus variability (Huang and others 2018b; Wolff and others 2019a, 2019b). Analogously, the spontaneous activity's shapes task-evoked activity through its degree of scale-freeness (as measured with PLE), which is related to distinct aspects of self-consciousness (Huang and others 2016; Wolff and others 2019a, 2019b; Kolvoort and others 2020; Scalabrini and others 2017), animate social interaction through active touch (Scalabrini and others 2019), multisensory perception (Ferri and others 2015, 2017), and even complex learning chemistry formulae (Bongers and others 2020). Moreover, two recent studies using fMRI and MEG demonstrated that the spontaneous activity's dynamics (e.g., its power law exponent, delta/alpha power, and oscillatory/fractal components) correlate with the degree of nonadditivity during pre/poststimulus interaction (Aru and others 2019; Huang and others 2017; Wainio-Theberge and others 2020; Wolff and others 2020).

Taken together, these studies show similarity between prestimulus activity and resting state activity in their relationship with stimulus-related activity. These findings, albeit indirectly, suggest that prestimulus activity, just as resting state activity, is part of the ongoing activity (Northoff and Lamme 2020). Their divided terminology may thus be somewhat artificial and more influenced by operational constraints than truly reflecting the brain's spatiotemporal dynamics itself independent of methodological issues (Northoff 2014a, 2014b, 2018a, 2018b).

Dual Model I—Rest versus Task, DMN versus Non-DMN, and Internally versus Externally Oriented Cognition

Raichle and others (2001) identified higher levels of resting state metabolism in various cortical midline regions and parietal cortex. These regions show predominant task-induced deactivation during externally oriented cognition—they are coined as “task negative” (Binder and others 1999; Fransson 2005, 2006; Northoff and others 2000, 2004; Raichle and others 2001; Shulman and others 1997). Employing resting state functional connectivity, these regions were later subsumed under the umbrella of “default-mode network” (DMN) (Beckmann and others 2005; Fox and others 2005;

Greicius and others 2003). At the same time, externally oriented cognition is associated with activation in various non-DMN regions like frontoparietal, dorsal attention, and salience network regions (and sensory regions)—they are therefore described as “task positive” (Binder and others 1999; Fransson 2005, 2006; Northoff and others 2000, 2004; Raichle and others 2001; Shulman and others 1997). Together, these findings suggest a duality of task-negative and task-positive brain regions.

Subsequent studies associated task-negative features (i.e., deactivation) with resting state activity and DMN regions, while task-positive features (i.e., activation) were related with task-related activity and non-DMN regions like the frontoparietal network (Beckmann and others 2005; Fox and others 2005; Fransson 2005, 2006; McKiernan and others 2003). This prepared the ground for the mostly tacit assumption that resting state activity is predominantly centered on the regions of the DMN while task-related activity involves non-DMN regions and networks. Hence, the duality of task-negative and task-positive activity is now extended further to the duality of rest versus task and the duality of DMN versus non-DMN.

Finally, the duality further extends to the cognitive level as manifested in the duality of internally and externally oriented cognition. Internally oriented cognition is present in the resting state and strongly recruits the DMN. This has been demonstrated for various forms of internally oriented cognition, including self-referential processing (Andrews-Hanna and others 2010, 2014; Davey and others 2016; Huang and others 2016; Qin and Northoff 2011; Qin and others 2020; Whitfield-Gabrieli and others 2011; Wolff and others 2019a, 2019b), mental time travel (Northoff 2017; Østby and others 2012; Schacter 2012; see also Box 4), mind wandering (Christoff and others 2016; Northoff 2018a, 2018b; Smallwood and Schooler 2015; Smallwood and others 2021), and social cognition (Scalabrini and others 2017, 2019; Schilbach and others 2012, 2013; see also Andrews-Hanna and others 2014; Axelrod and others 2017; Braga and Leech 2015; Buckner and DiNicola 2019; Leech and others 2011, 2012; Spreng and others 2013, 2014). The dualities therefore, extend from the 1) neuronal level of rest versus task over the 2) network level of DMN versus non-DMN to the 3) cognitive level of internally versus externally oriented cognition.

Picking up Raichle's original search for the default mode of brain function (Raichle and others 2001), this triad of neuronal, network, and cognitive features extends his original metabolic-energetic characterization of the resting state to the cognitive level: associating resting state activity with the task-negative regions and subsequently the DMN, the role or function of ongoing activity is determined by resting state, DMN,

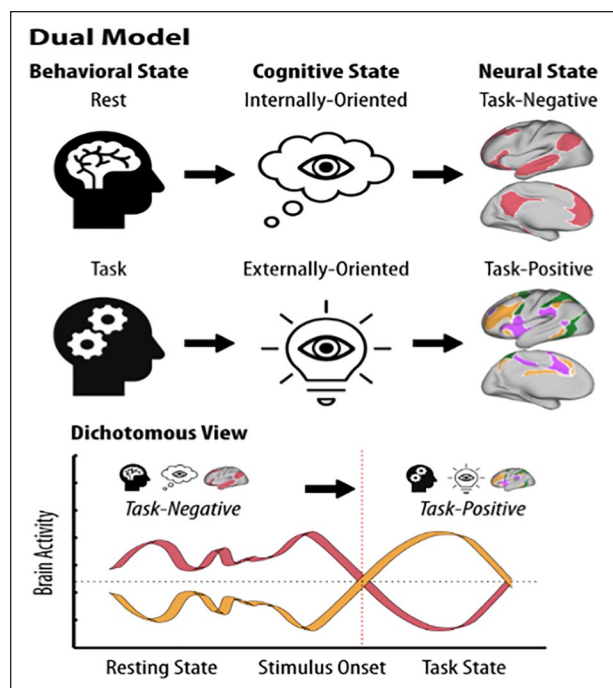


Figure 2. The dual model of brain and cognition. The existing presumptions in the literature assume related dualities across behavioral, cognitive, and neural states. While a “task-negative” resting state is associated largely with internally oriented cognition and suggested solely to recruit regions within the default-mode network (DMN), a “task-positive” task state is often linked to externally oriented cognition that engages regions across the frontoparietal, dorsal attention, and salience networks. In a dichotomous view of brain and cognition, these two states are assumed to play opposing actions that are alternated by the onset and offset of task stimulus.

and internally oriented cognition as distinguished from externally oriented cognition. Given such primarily cognitive characterization of the DMN, several authors spoke of a “cognitive baseline” (Andrews-Hanna and others 2010, 2014), “default cognitive process” (Horn and others 2014), “psychological baseline” (Northoff and Bermpohl 2004), or “behavioral baseline” (Raichle 2015a, footnote 2 on p. 8). Importantly, such “cognitive baseline,” as we say in the following, must be distinguished from the more operational notion of baseline as it is often used in imaging studies when subtracting the target condition from a control condition (with the latter serving as baseline for the former) (Morcom and Fletcher 2007).

What do these findings entail for the role of the ongoing activity? Although often not explicated, these studies tacitly presuppose a certain model of the ongoing activity’s function that is associated with the resting state, the DMN, and internally oriented cognition. Together, that

amounts to dualities on neuronal, network, and cognitive levels, which contrast rest versus task, DMN versus non-DMN, and internally versus externally oriented cognition (see Fig. 2).

Dual Model II—Doubts on the Dualities of Rest versus Task and DMN versus Non-DMN

Even though the dual model seems to be the dominant background assumption in current studies on cognition, it shows some inconsistencies with the empirical data. Various imaging studies using fMRI and EEG/MEG demonstrate that, on the purely neuronal level, spontaneous activity is present in all three: resting state (i.e., the absence of any overt task stimulus), prestimulus activity, and task-related activity (Bolt and others 2017; Cheng and others 2018; Cole and others 2012, 2014, 2016; He 2011; Huang and others 2017; Ito and others 2020; Mennes and others 2010, 2011; Wainio-Theberge and others 2020; Wolff and others 2019a, 2019b, 2020).

In addition, fMRI and EEG/MEG data demonstrate nonadditive rather than merely additive modulation of task-related activity by prestimulus and/or resting state activity (Hesselmann and others 2008; He 2013; Huang and others 2017; Sadaghiani and others 2010 2015; Wainio-Theberge and others 2020). Finally, recent studies demonstrate that alterations (i.e., decreases or increases) in rest/prestimulus task interaction may lead to major cognitive abnormalities as in schizophrenia (Northoff and others 2021; Northoff and Gomez-Pilar 2021) and anxiety disorders (Lucherini and others 2021). Together, these results shed serious doubt upon the presumed neuronal duality of rest and task states, including their presumed independence of each other.

The supposed network duality of DMN versus non-DMN also needs to undergo intense scrutiny. Recent evidence shows that the DMN does not only exhibit deactivation during task states but also activation (Chen and others 2017; Simony and others 2016; Spreng and Schacter; Vatansever and others 2015, 2017; Yeshurun and others 2021)—this puts into doubt the DMN’s characterization as task-negative as opposed to task-positive non-DMN regions like executive control network (Chen and others 2017; Simony and others 2016; Spreng and Schacter 2012; Vatansever and others 2015, 2017; Yeshurun and others 2021), while non-DMN regions like the visual cortex can also exhibit deactivation (i.e., task-negative responses) (Golesorkhi and others 2021a, 2021b; Vatansever and others 2017). Finally, the DMN is active not only during internally oriented cognition but also during high loads of externally oriented cognition (Chen and others 2017; Hasson and others 2015; Lyu and others 2021; Vatansever and others 2015, 2017;

Yeshurun and others 2021). Conversely, non-DMN regions are also implicated in internally oriented cognition (Christoff and others 2009a, 2009b; Dixon and others 2014). Together, these findings shed strong doubt upon the dualities of task-negative versus task-positive activity and DMN versus non-DMN.

Dual Model III—Doubts on the Duality of Internally versus Externally Oriented Cognition

How about the duality of internally and externally oriented cognition—does it conform to the dualities of rest versus task and DMN versus non-DMN? The data are not fully consistent with such cognitive duality either (see also Dixon and others 2014 for a comprehensive review). The resting state has been associated not only with internally oriented cognition but also externally oriented cognition (Bai and others 2015; Ferri and others 2015, 2017; Sadaghiani and others 2009, 2010, 2015; Scalabrini and others 2017, 2019). For instance, interindividual differences during either resting state (fMRI) or prestimulus (EEG) correlate with interindividual differences in both externally oriented perception (Bai and others 2015; Ferri and others 2015, 2017; Hesselmann and others 2010; Sadaghiani and others 2009, 2010, 2015; Scalabrini and others 2017, 2019) and internally oriented cognition (Andrews-Hanna and others 2014; Buckner and DiNicola 2019; Davey and others 2016; Huang and others 2016; Kolvoort and others 2020; Murray and others 2015; Northoff 2017; Østby and others 2012; Qin and Northoff 2011; Schilbach and others 2012, 2013; Spreng and Schacter 2012; Spreng and others 2014; Wolff and others 2019a, 2019b).

Yet another example of the blurry lines between internally and externally oriented cognition is mind wandering. Following the dual model, one would expect that mind wandering could only include internally oriented cognition contents and is exclusively associated with the DMN while externally oriented cognition contents should be excluded and be related to non-DMN. That is not the case, though. Mind wandering can include both internally and externally oriented cognition contents like self-referential and sensory-imagery contents and extends beyond the DMN by including non-DMN regions (Christoff and others 2009b; Christoff and others 2016; Dixon and others 2014; Rostami and others 2021; Smallwood and Schooler 2015; Sormaz and others 2018; Turnbull and others 2019; Vanhauzenhuysen and others 2011; Vatansever and others 2019; Yeshurun and others 2021).

More indirect support for the blurring between internally and externally oriented cognition comes from pathological conditions. Psychiatric disorders like schizophrenia that exhibit changes in the brain's ongoing activity (i.e., resting state) show changes in both internally and externally

oriented cognition (Ebisch and others 2018; Northoff and Duncan 2016; Northoff and Gomez-Pilar 2021). This would not be possible if externally oriented cognition was not modulated or related in some yet unclear way to the resting state itself.

Together, the cognitive duality of internally and externally oriented cognition is undermined by results suggesting their interaction and interdependence. That converges with the general data demonstrating a close relationship and direct interaction of rest and task as well as of DMN and non-DMN. This sheds strong doubt upon the dualities or dichotomies of rest versus task, DMN versus non-DMN, and internally versus externally oriented cognition as presupposed in the dual model. The need to go beyond the dual model necessitates a reformulation of the current assumptions to devise a new model that can incorporate existing evidence. This is the goal of the baseline model. How can the ongoing activity shape our various forms of cognition? We propose that the ongoing activity's spatial and temporal dynamical features are key in providing a neuronal baseline that, through a global temporal and spatial neural code, mediates both internally and externally oriented cognition. That shall be demonstrated in the following.

Part II: Spatial Dynamics of Ongoing Activity—Global Brain Activity and Its Topography

Global Brain Activity and Its Infralow Frequencies I—Candidate Feature for Neuronal Baseline?

One key feature of the ongoing activity is that it extends beyond the DMN by including the whole brain. The neural activity of the whole brain, including DMN and non-DMN, is supposed to serve as an internal reference or standard for rest and task states. The involvement of the whole brain leads us to the brain's global activity. We here postulate that such global activity provides a spatial neural code that is key in mediating the ongoing activity's role as neuronal baseline for rest and task states, DMN and non-DMN, and internally and externally oriented cognition.

One way to measure ongoing brain activity is the global signal (GS) in fMRI (Liu and others 2017b, 2018; Power and others 2017; Zhang and others 2020). However, when speaking of GS, fMRI researchers are first confronted with a controversy as to whether to remove GS or not from their signal of interest (Liu and others 2015, 2018; Murphy and Fox 2017). Many studies suggest to regress the global signal from rest and task data in fMRI

(Chai and others 2012; Liu and others 2017b; Nalci and others 2017; Power and others 2017; Wong and others 2012) as GS has been associated with mere noise stemming from extra-neuronal sources like respiration (Birn and others 2006, 2008; Liu and others 2017b; Power and others 2017, 2019). Recent evidence, as described below, points out that GS is not mere nonneuronal noise and thus mere artifact but carries important physiological and possibly cognitive function (see Li and others 2019; Murphy and Fox 2017; Orban and others 2020; Uddin 2017, 2020; Zhang and others 2020). Hence, GS seem to be physiological and reflect “real” neuronal activity that, as we postulate, may mediate the ongoing activity’s role as neuronal baseline.

Several studies combined GS in fMRI with electrophysiological measurements in mainly monkeys (Chang and others 2016; Leopold and others 2003; Liu and others 2013, 2018; Scholvenick and others 2010, 2015; Turchi and others 2018; Wen and Liu 2016) and humans (Wen and Liu 2016). One key electrophysiological feature of GS is that it is related to the bandpower of different frequency ranges in different ways. For instance, infraslow frequency ranges (IFS) (<0.1 Hz) show a much higher relationship, that is, correlation with GS than faster frequencies like those in the slower (0.1–1 Hz) and faster ranges (1–100 Hz) (Leopold and others 2003; Scholvenick and others 2010, 2015).

Together, these studies document that GS is not mere nonneuronal noise (i.e., an artifact) but is based on “real” neuronal activity. Specifically, these results show that GS is strongly driven by the long cycle durations of the very slow (i.e., infraslow frequencies; <0.1 Hz) and less so by the faster frequencies. The differential contributions of slow and fast frequencies to GS seem to be a function of both frequency range and cortical distance. Several studies showed that delta/theta (1–8 Hz) and faster frequencies (40–80 Hz) contribute strongly to the extension of neural activity on the cortical level, that is, GS (Liu and others 2018; Scholvenick and others 2010, 2015; Wen and Liu 2016). In contrast, the faster alpha/beta range (10–30 Hz) is not related to such global extension but remains rather local as in visual cortex and thalamus (Chang and others 2016; Liu and others 2018; Scholvenick and others 2010; Wen and Liu 2016).

Accordingly, the slower the frequency range, the more and stronger its contributions to the global extension of neural activity across longer cortical distances as measured by GS (Chang and others 2016; Liu and others 2018; Scholvenick and others 2010; Wen and Liu 2016). The global spatial extension through infraslow frequencies makes GS an ideal neuronal candidate feature to serve as a spatial correlate of the brain’s neuronal baseline on neuronal, network, and cognitive levels.

Global Signal and Its Infraslow Frequencies II—They Meet Raichle’s Criteria of a Baseline

Given these findings, we propose that global brain activity as measured by GS and mediated by especially the infraslow frequency ranges may be one candidate for providing the physiological basis of the brain’s neuronal baseline. This is further supported by recent findings showing that GS in most regions of the brain remains either unchanged or decreases during the transition from rest to task (Zhang and others 2020) (Fig. 3A).

As this holds for a variety of different task states (Zhang and others 2020), GS seems to meet Raichle’s original criteria for a baseline (Raichle and others 2001). His three criteria include high levels at rest (Raichle and others 2001; Raichle and Mintun 2006), comparative reduction in activity level in task states (also called deactivation in fMRI) relative to the global activity as average across all regions (Gollo and others 2015, 2017; Raichle and others 2001), and its occurrence across different tasks in a domain-general way (i.e., relative activity reduction in different domains of cognition like memory, affect, etc. amounting to domain-general activity reductions) (Anticevic and others 2012; Binder 2012; Binder and others 1999; Mazoyer and others 2001; McKiernan and others 2003, 2006; Shulman and others 1997; Walter and others 2009) (see Fig. 3B).

GS appears to meet the three criteria of high levels in rest, reduction during task, and domain-general changes (Zhang and others 2020). We therefore tentatively propose that global brain activity as measured by GS in infraslow frequencies may provide a physiological substrate of the brains’ neuronal baseline (which is also well in line with the proposal of slow frequencies providing the brain’s default; Sanchez-Vivez and Mattia 2014; Sanchez-Vivez and others 2017). However, we need to specify the role of GS as neuronal baseline in more detail; that shall be the focus in the following.

Global Brain Activity and Its Topography I—Connecting Rest and Task as Well as DMN and Non-DMN

We so far assumed that the physiological substrates of GS, the infraslow/slow frequencies, may be an ideal candidate feature to serve as neuronal baseline. However, that needs to be demonstrated on all three levels: neuronal, network, and cognitive levels. The GS mediates important neuronal functions like the transition from rest to task states (Zhang and others 2020), circadian rhythm (Orban and others 2020), and psychological trait features (Li and others 2019). One would therefore assume that GS also mediates task states as it is supported by a recent

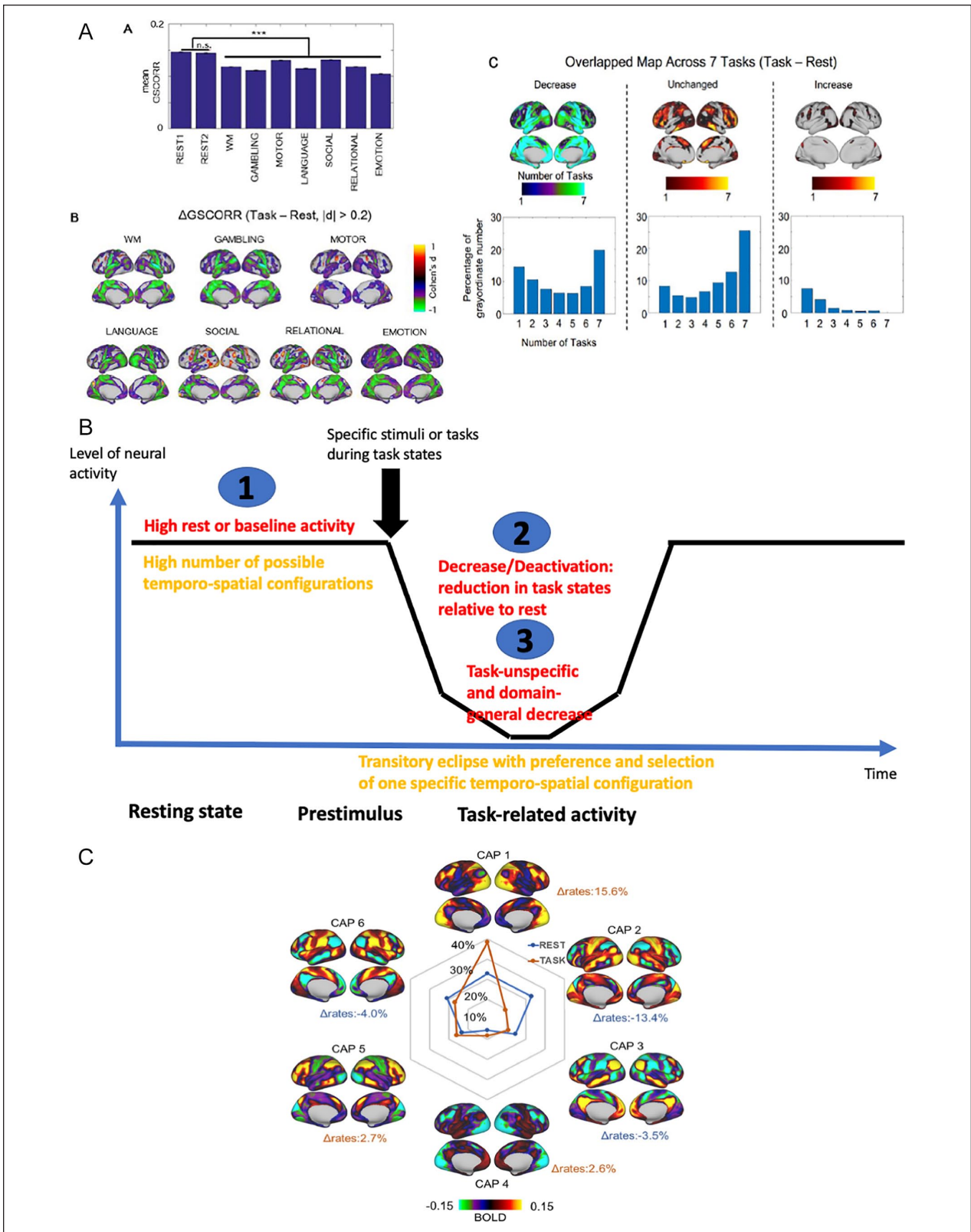


Figure 3. (A) Global signal topography during rest and task states with rest-task change (left) and overlapping regions/maps (right) (see Zhang and others 2020). (B) Three criteria for measures operating as indices of the brain's neuronal baseline (following and extending Raichle and others 2001). (C) Dynamic coactivation pattern and the frequency of their occurrence during rest and task states (see Zhang and others 2020).

study that shows the dynamic nature of GS rest-task transition through the coactivation pattern (CAP) (Zhang and others 2020).

Recent studies showed that during the highest amplitudes or peaks of the global signal, different CAPs between different networks can be found during resting state (Liu and others 2018; Zhang and others 2020). Zhang and others (2020) extended this observation from rest to task states. They observed six CAPs consisting of different network configurations during different phases of the peak amplitude of GS. Most interestingly, the specific network configurations remained the same during both rest and different task states, whereas the frequency in the occurrence of the different CAPs changed: the frequency of the CAP with a strong somatomotor focus that, during rest, was closely associated with the breathing frequency decreased in its frequency during the transition from rest to task states (see Fig. 3C).

Albeit tentatively, these data suggest that the ongoing whole brain fluctuations of GS (i.e., peaks and troughs) may structure their own topographical distribution during both rest and task states in a dynamic way. The basic topography of the CAPs seems to be carried over from rest to task states. At the same time, the frequency of their occurrence changes (i.e., increases or decreases) during the different task states, which suggests close but yet to be identified relationship with stimulus presentation. The overall suggestion seems to be that the resting state topography of the CAP serves as neuronal baseline for the task states as the former is carried over to the latter. Moreover, given that the frequency of the CAP changes during task states relative to their resting state supports the view that global brain activity with its topography (i.e., CAP) serves as a neuronal baseline for both rest and task states as well as for DMN and non-DMN.

Global Brain Activity and Its Topography II—Mediating Both Internally and Externally Oriented Cognition

Are the global signal and its topography relevant for both internally and externally oriented cognition? There is currently no direct evidence linking GS and its topography to different forms of internally and externally oriented cognition. However, indirect evidence comes from abnormal GS in neurologic and psychiatric disorders.

Consciousness includes both contents of internally oriented cognition and the ones of externally oriented cognition: we are aware of both external contents from the environment and our own internal contents like our memories (Northoff and Lamme 2020). If the ongoing activity's global signal and its topography do indeed serve as neuronal baseline, one would expect that its changes during the loss of consciousness, as in neurologic disorders,

should lead to the loss of both internally and externally oriented cognition.

That is indeed supported by two recent fMRI resting state studies (Huang and others 2016; Tanabe and others 2020), which, using fMRI, investigated GS and its topography during different degrees of loss of consciousness: sedation and anesthesia (sevoflurane, propofol), sleep with its different stages including REM, and minimally conscious states (MCS) and unresponsive wakefulness state (URWS). They measured a major general decrease in global brain activity during complete loss of consciousness in all three states: sleep N3, surgical anesthesia, and URWS (Huang and others 2016; Tanabe and others 2020). This suggests a role of global brain activity, that is, GS in consciousness and subsequently in both internally and externally oriented cognition (as both are broken down completely during the loss of consciousness) (Northoff and Lamme 2020).

Moreover, they observed that in intermediate states (like N1 and N2 sleep and sedation and MCS), subjects showed higher GS level and, interestingly, differences in their topography among each other and relative to their awake states (Tanabe and others 2020). Albeit tentatively, the authors associate such differences in GS topography to different configurations in their phenomenological and cognitive states, including distinct balances of internally and externally oriented cognition. Accordingly, these results support, although indirectly through consciousness and its loss, the involvement of GS and its topography in both internally and externally oriented cognition.

Global Brain Activity and Its Topography III—Connecting Internally and Externally Oriented Cognition through Their Balance

Yet additional evidence for the involvement of GS and its topography comes from psychiatric disorders. Psychiatric disorders like schizophrenia, bipolar disorder (BD), and major depressive disorder (MDD) can be characterized by abnormal shifts in the balance of internally and externally oriented cognition. For instance, internally oriented cognition dominates in schizophrenia delusion and hallucination, where it is confused with externally oriented cognition (Northoff and Gomez-Pilar 2021). Investigation of GS demonstrated abnormal decreases in GS topography in specifically sensory and motor cortex in schizophrenia while it was abnormally increased in association cortex like prefrontal cortex (Yang and others 2017)—this may reflect the abnormal shift toward internally oriented cognition and its confusion with externally oriented cognition in these patients.

Yet another instance is BD, which can be characterized by manic and depressive episodes. In manic BD, externally oriented cognition predominates over internally

oriented cognition, which, in part, may be related to abnormally high GS representation in sensorimotor cortex (Zhang and others 2018). Conversely, acute depressed subjects suffering from BD or MDD show abnormally high local-regional GS representation in hippocampus (Zhang and others 2018) and other regions of the DMN (Scalabrini and others 2020), which, most likely, reflects their abnormal increase in internally oriented cognition (Hamilton and others 2015; Northoff and others 2011; Northoff 2016a, 2016b). Together, the findings, albeit preliminarily and indirectly, suggest that GS and its topography modulate both internally and externally oriented cognition including their balance—that supports their role in mediating the ongoing activity's neuronal baseline on a cognitive level (i.e., internally and externally oriented cognition).

In sum, global brain activity as measured by the global signal and its topography may be a strong candidate feature for a shared spatial neural code to mediate the ongoing activity's role as neuronal baseline. That is supported by the fact that the GS and its topography strongly shape both rest and task states, DMN and non-DMN networks in their topography, and cognitive function with the balance of internally and externally oriented cognition. In short, GS topography is key in transition from rest to task, in consciousness, and in psychopathology. These findings point out the potential relevance of a global topographic organization in the brain's ongoing activity extending beyond specific networks like DMN and non-DMN. This global topographic organization of the brain seems to be a key feature in anticipating or predisposing the external environmental demands placed on the brain, thus acting as “spatiotemporal prior” (Pezzulo and others 2021).

Part III: Temporal Dynamics of Ongoing Activity—Intrinsic Neural Timescales

Intrinsic Neural Timescales I—Topography across DMN and Non-DMN

We so far focused on the ongoing activity's spatial neural code—how about its temporal neural code? The brain is characterized by a complex temporal organization that includes a wide range of regular faster frequencies (1–260 Hz) and more irregular slower frequencies (0.001–1 Hz) (Buzsáki 2006, 2019; Engel and others 2013; He and others 2010; Kiebel and others 2008; Palva and others 2018). The temporal organization can be measured either in the time domain by the autocorrelation window (ACW) (Chaudhuri and others 2014, 2015; Demirtaş and others 2019; Golesorkhi and others 2021a, 201b; Kiebel and others 2008; Murray and others 2014; Raut and others 2020; Zilio and others 2021) or in the frequency domain through scale-free activity with the power law exponent

(He 2011; He and others 2010; Huang and others 2016; Zhang and others 2018) (or the detrended fluctuation analysis [DFA]; Linkenkaer-Hansen and others 2001).

Remarkably, the brain's temporal organization follows a certain spatial pattern as lower-order unimodal sensory regions display shorter timescales while higher-order transmodal regions as of the default-mode network and other higher-order networks (like central executive network) exhibit longer timescales (Chaudhuri and others 2015; Demirtaş and others 2019; Golesorkhi and others 2021a, 2021b; Honey and others 2012; Ito and others 2020; Kiebel and others 2008; Raut and others 2020; Runyan and others 2017; Stephens and others 2013; Watanabe and others 2019). Moreover, even subcortical regions like caudate, thalamus, cerebellum, and hippocampus display a certain hierarchical order of shorter and longer timescales in their resting state (Raut and others 2020).

These findings led to the assumption that the spontaneous activity in different regions and networks exhibits specific timescales as reflected in the concept of “intrinsic neural timescales” (Chaudhuri and others 2015; Deco and others 2019; Farzan and others 2017; Gollo and others 2015, 2017; Liégeois and others 2019; Murray and others 2014; Wasmuht and others 2018).

Interestingly, strong similarities in the unimodal and transmodal cortical distribution of intrinsic neural timescales have been observed on cellular levels in monkeys (Cirillo and others 2018; Chaudhuri and others 2015; Murray and others 2014) and mice (Fulcher and others 2019) and regional-network levels in human EEG/MEG and fMRI (Demirtaş and others 2019; Golesorkhi and others 2021a, 2021b; Ito and others 2020; Raut and others 2020; see below for details). Therefore, the concept of intrinsic neural timescales may offer a unifying principle for linking cellular (Murray and others 2014), population (Runyan and others 2017), and regional/network (Golesorkhi and others 2021a, 2021b; Ito and others 2020; Raut and others 2020) levels of activity (see Marom 2010).

There is strong evidence on both cellular and regional-network levels that the brain's ongoing activity exhibits different intrinsic neural timescales along a certain topography, that is, a unimodal to transmodal gradient spanning from sensory regions to DMN. The DMN seems to stand at one end of the temporal hierarchical gradient (i.e., showing long timescales), while the sensory and motor regions can be located at the other extreme as they display short timescales (see also Golesorkhi and others 2021a, 2021b; Huntenberg and others 2018; Ito and others 2020; Margulies and others 2016; Raut and others 2020). Importantly, as Golesorkhi and others (2021b) demonstrate, such gradient is a temporal continuum where different networks' temporal features are “located” right between the extremes of DMN and sensorimotor cortex (see Fig. 4A).

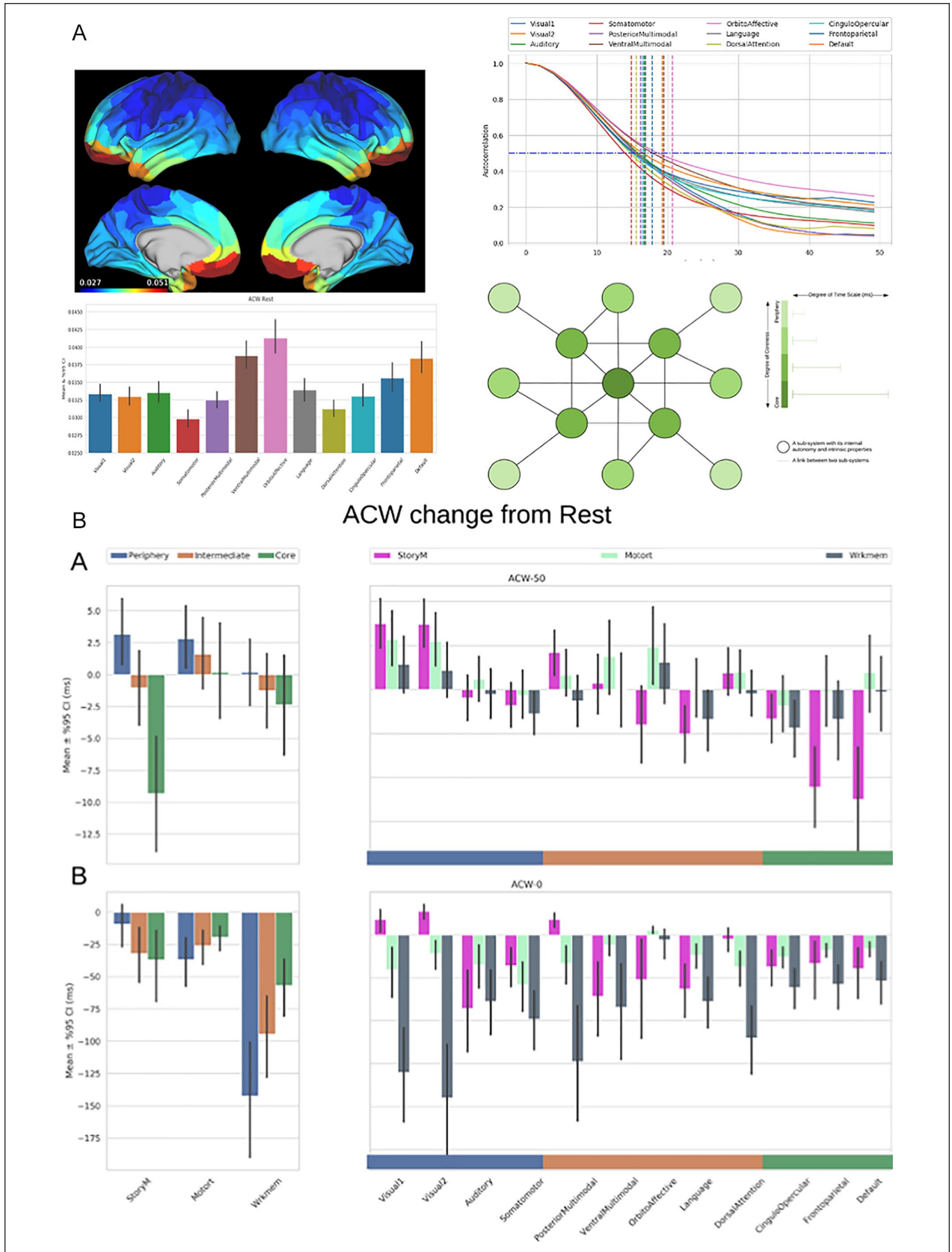


Figure 4. (continued)

Figure 4. (continued)

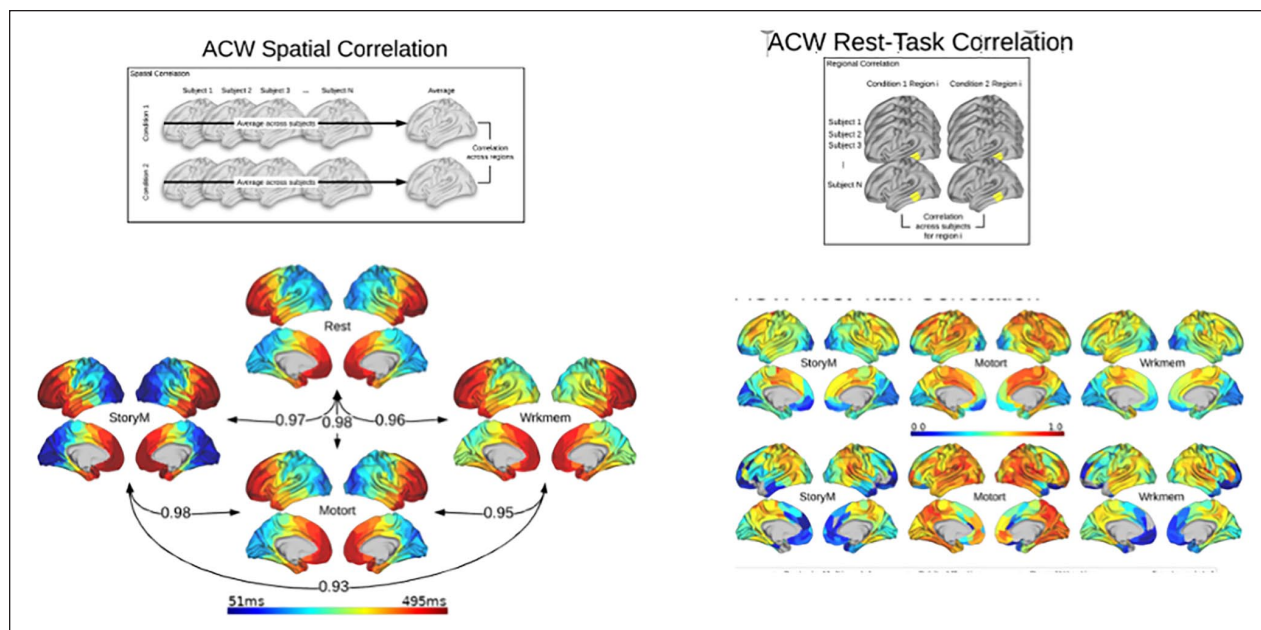


Figure 4. (A) Topography of intrinsic neuronal timescales in different networks (left) and core-periphery organization (right) (see also Golesorkhi and others 2021b). (B) Intrinsic neuronal timescales during task relate to rest (as measured by autocorrelation window [ACW] in two versions, ACW50 and ACW0) (see also Golesorkhi and others 2021b). (C) Correlation of intrinsic neuronal timescales between rest and task (ACW) in a spatial-topographic (left) and region based (right) (see also Golesorkhi and others 2021b).

Intrinsic Neural Timescales II—Serving as Neuronal Baseline for Both Rest and Task States

Establishing a temporal continuum with a hierarchical gradient, intrinsic neuronal timescales operate on a global or whole-brain level cutting across the distinction of DMN and non-DMN. Does this predispose the intrinsic neural timescales to serve as baseline (i.e., reference or standard for rest and task states as well as for internally and externally oriented cognition)?

One key question is whether the resting state’s intrinsic neural timescales modulate task states and their associated information processing. The relevance of intrinsic neural timescales for information processing is strongly suggested by the studies of the group around Hasson (Chen and others 2015, 2017; Hasson and others 2015 for review; Nguyen and others 2019; Regev and others 2018; Stephens and others 2013; Yeshurun and others 2017). They demonstrated that shorter temporal segments of external stimuli (like single words of stories or short episodes in movies) are processed preferentially in lower-order unimodal sensory regions while the longer intervals (like whole paragraphs in stories or longer episodes in movies) are related to activity changes in higher-order transmodal regions—they therefore speak of “temporal receptive windows” (Chen and others 2015, 2017; Hasson and others 2015; Stephens and others 2013) (that more or

less correspond to “temporal receptive fields” on the cellular level; Cavanagh and others 2016). This is compatible with the assumption of the topographical organization of the intrinsic neural timescales in the resting state as described above.

Are the task-related temporal receptive windows shaped by the topographical organization of the intrinsic neural timescales in the resting state? Conducting a modeling study with a synchronization (Kuramoto) model and simulation of transcranial magnetic stimulation (TMS), Gollo and others (2017) demonstrate that regions with longer ACW, as located in DMN and central executive network, show lower and more sluggish activity changes in response to external stimuli than sensory regions with their shorter ACW that exhibit higher amplitude and faster response to external stimuli (see also Cocchi and others 2016; Kiebel and others 2008). Analogous results were observed in the modeling study by Chaudhuri and others (2015), who applied electrical stimulation to V1 in visual cortex (see also Demirtaş and others 2019).

Does the same hold also in human data? This was confirmed in a recent human fMRI study by Ito and others (2020) who used the Human Connectome Project (HCP) data set to investigate both ACW in resting state and amplitude during different task states. They demonstrated negative correlation between ACW duration and the

magnitude of task-related activity (i.e., amplitude across the different regions): the longer the region's resting state ACW (i.e., transmodal regions), the lower its task-related amplitude while regions with shorter ACW (i.e., unimodal regions) exhibit higher amplitude during different tasks. These results support the assumption that the resting state's intrinsic neural timescales strongly shape brain dynamics and its information processing during task states (Gollo 2019; Gollo and others 2017).

These data support the assumption that resting state ACW shapes response to task states (i.e., their amplitude). However, they leave open whether the resting state ACW itself shapes its own changes during the transition from rest to task. This is addressed by Stephens and others (2013) and, in full detail, by Golesorkhi and others (2021b). Golesorkhi and others (2021b) investigated the ACW not only during MEG rest but also during three different task states (motor, story-math, working memory) (HCP MEG). Both DMN and sensory regions exhibited changes in their ACW during task states, with sometimes lengthening and sometimes shortening, which also depended upon the task (i.e., working memory, motor, and story-math) (see Fig. 4B).

In addition, Golesorkhi and others (2021b) also investigated the correlation of ACW rest with the ACW during task in both a spatial topographic way and within each region itself. This yielded extremely high correlation values in especially the spatial-topographic correlation of rest and task ACW. That suggests a strong shaping of task-related ACW by the resting state ACW with the latter serving as neuronal baseline for the former (see Fig. 4C).

Together, these findings suggest that the resting state's intrinsic neural timescales strongly shape task states. Moreover, the differential changes during the three different tasks underline the dynamic-adaptive nature of the intrinsic neural timescales to different task contexts. Since, at the same time, there was high correlation of rest and task ACW, these findings make it rather likely that the intrinsic neural timescales do indeed take on the role as neuronal baseline—they may provide a temporal neural code as internal reference or standard for both rest and task states, including rest-task transition.

Intrinsic Neural Timescales and Cognition— Serving as Neuronal Baseline for Internally and Externally Oriented Cognition

Do the intrinsic neural timescales serve as a temporal neural code that mediates cognition? There is increasing evidence that the resting state's intrinsic neural timescales mediate concurrent cognitive processing. Studies in monkeys demonstrated that longer duration of the resting state's intrinsic neural timescales (as obtained during baseline intervals sandwiched between task) was associated

with better behavioral performance in reward (i.e., longer duration of delay in delay discounting task) (Murray and others 2014), stronger spatial response coding in the delay period during a nonmatch-to-goal task (Cirillo and others 2018), and increased working memory performance during later periods (i.e., delay) (Wasmuht and others 2018).

How about humans? Human EEG studies show that subjects' degree of self-consciousness and their integration of temporal delays are positively related to the length of their resting state's ACW (Kolvoort and others 2020; Wolff and others 2019a, 2019b): the longer the ACW, the higher the degree of self-consciousness and the more self-specificity is preserved over longer the temporal delays. Moreover, other evidence for the role of intrinsic neural timescales in mediating mental features comes from consciousness research: intrinsic neural timescales as measured by PLE or ACW have been found to be altered during the loss of consciousness as in anesthesia, UWRS/MCS, and sleep (Huang and others 2018b; Tagliazucchi and others 2013, 2016; Zhang and others 2018; Zilio and others 2021).

Finally, indirect evidence for the involvement of intrinsic neural timescales in internally oriented cognition is emerging from psychiatric disorders. Autism exhibits changes in its intrinsic neural timescales during resting state in caudate and primary sensory regions (ACW in fMRI) (Watanabe and others 2019) as well as in resting thalamus, insula, and anterior cingulate (PLE in fMRI) (Damiani and others 2019). A recent EEG study observed abnormally long intrinsic neural timescales during specifically self-related tasks (and diminished rest-task difference) in schizophrenia (Northoff and others 2021; see also Wengler and others 2020). Since both autism and schizophrenia are characterized by abnormal balances of internally and externally oriented cognition (Northoff and Gomez-Pilar 2021), they, albeit indirectly, support the assumption that the ongoing activity's intrinsic neural timescales serve as neuronal baseline for both forms of cognition. Together with the more direct evidence from healthy subjects, we assume that the intrinsic neural timescales provide a temporal code that makes it possible for the ongoing activity to serve as neuronal baseline for both internally and externally oriented cognition.

Part IV: Baseline Model—Ongoing Activity Serves as Neuronal Baseline for Rest and Task, DMN and Non- DMN, and Internally and Externally Oriented Cognition

Going beyond the Dual Model

We will next formulate an alternative model of the role of the brain's ongoing activity. The inconsistencies of the

dual model suggest that the role and function of the ongoing activity extends beyond its role in resting state, DMN, and internally oriented cognition. There are no dual neural codes, one coding for internally and one for externally oriented cognition. Going beyond the dual model means to provide a broader and more comprehensive framework with a shared global neural code that allows integrating and connecting rest and task states, DMN and non-DMN, and internally and externally oriented cognition. Rather than representing dualities or dichotomies, they may be specific aspects or specifications of a yet not defined more fundamental or basic function of the brain. We attribute such more basic or fundamental function of the brain to its ongoing activity; the latter's spatiotemporal dynamics provide a global temporal and spatial code for both the brain's rest and task as well as for its internally and externally oriented cognition.

What is the ongoing activity's more basic or fundamental function? We propose that the ongoing activity serves as neuronal baseline, that is, as internal reference or standard on the neuronal level (i.e., rest and task states), network level (i.e., DMN and non-DMN), and cognitive level (i.e., internally and externally oriented cognition). We therefore speak of a "baseline model" (see Box 1 for a historical review). The concept of internal reference or standard is a key feature of the baseline model, which marks its main difference from the dual model.

What do we mean by internal or standard (i.e., baseline)? Let us first draw the comparison with the biological clock. The biological clock serves as the internal reference or standard for the timing of the organism, including its temporal relation to the environment. Analogously, the brain's ongoing activity serves as an internal spatial and temporal reference or standard for the brain's processing, including its cognition—the ongoing activity takes on the role of neuronal baseline as featured by its spatiotemporal dynamics.

Ongoing Activity Serves as Neuronal Baseline

The baseline model postulates that the ongoing brain activity serves as neuronal baseline and thereby as an internal reference or standard for the brain's processing during rest and task states, all networks including DMN and non-DMN, and both internally and externally oriented cognition. The role or function of the brain's ongoing activity thus extends beyond rest, DMN, and internally oriented cognition, as assumed in the dual model—the baseline model provides a more basic and fundamental view of the role of the brain's ongoing activity.

The baseline model is based on the following empirical data: nonadditive rather than additive interaction of rest and task states, suggesting that rest serves as internal

reference for external task states (He 2013; Huang and others 2017; Wainio-Theberge and others 2020); occurrence of activation in DMN and deactivation in non-DMN regions, which is dependent upon the general task-context (Chen and others 2015, 2017; Simony and others 2016; Vatansever and others 2015, 2017); recent findings on the brain's global activity showing how, during the rest-to-task transition, it modulates the frequency of the regional/network pattern as measured by dynamic CAP of DMN and non-DMN networks (Liu and others 2018; Zhang and others 2020); association of internally oriented cognition like self and mind wandering with activation in non-DMN (i.e., seemingly task-positive networks like salience and control-executive networks) (Christoff and others 2009b; Christoff and others 2016; Qin and others 2020; Scalabrini and others 2017, 2019; Smallwood and Schooler 2015; Vatansever and others 2020); and, at the same time, externally oriented cognition that also induces activation in DMN as a seemingly task-negative network (Chen and others 2015, 2017; Simony and others 2016; Vatansever and others 2015, 2017; Zhang and others 2020).

Following these and other data, the baseline model proposes that the ongoing activity serves as an internal reference or standard for the brain's processing during rest and task states. The baseline model postulates that both rest and task states are based on the ongoing activity as it is manifested in both (see above). This suggests that the ongoing activity, through its spatiotemporal dynamics, provides a global shared spatial and temporal neural code that is more basic and fundamental than the binary neuronal differentiation of rest and task states.

The same holds analogously for DMN versus non-DMN whose differentiation, as the baseline model postulates, can be traced to the brain's overall or global activity and its dynamics with a specific topographical pattern and dynamic CAP of networks (Liu and others 2018; Zhang and others 2020) (see above for details). Finally, both internally and externally oriented cognition may be based on the brain's ongoing activity and its global neural code (i.e., its spatiotemporal dynamics): the latter serves as internal reference or standard for both while, at the same time, allowing for their differentiation into two distinct forms of cognition (Northoff and Gomez-Pilar 2021).

Taken together, the baseline model overcomes the dichotomies on neuronal (i.e., rest versus task), network (i.e., DMN versus non-DMN), and cognitive levels (i.e., internally and externally oriented cognition). This is achieved by integrating these dualities through their commonly shared reference to the ongoing activity; through its spatiotemporal dynamics, the ongoing activity provides a global shared neural code that allows it to operate as neuronal baseline for both brain and cognition (see Fig. 5).

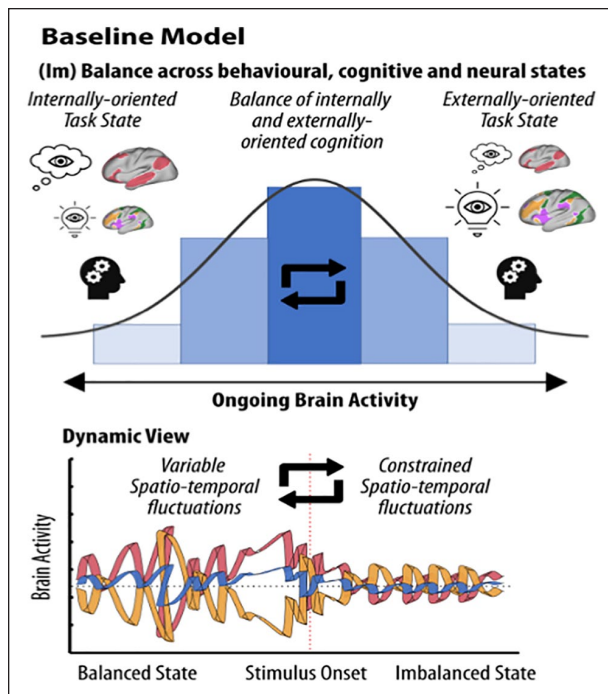


Figure 5. The baseline model of brain and cognition. In contrast to the dual model, we propose that the ongoing brain activity acts as a neuronal baseline that provides a precursor for the emergence of distinct spatiotemporal patterns that are in service of variable cognitive processes. Rather than a dichotomy, this model suggests that the differential brain activity patterns observed between behavioral and cognitive states may originate from a context-dependent relative imbalance in the spatiotemporal dynamics of the brain. This dynamic view proposes that both internal and external task states may constrain the ongoing brain activity in a manner that surpasses the arbitrary dichotomies introduced by psychological ontologies (i.e., internally and externally oriented cognition) as well as neurobehavioral duality of rest and task states (see Fig. 6).

Probability Space Serves as Internal Reference or Standard—Neural Predisposition Rather Than Neural Correlate

What exactly do we mean by internal reference or standard? Let us illustrate that by the example of the interaction of rest and task (Northoff and others 2010a, 2010b). Traditionally, task-related activity is supposed to be added onto the level of the ongoing activity—this amounts to additive rest-stimulus interaction (Fox and others 2006; He 2013; Huang and others 2017). Additive rest-stimulus interaction means that the activity related to stimulus or task is simply added onto the activity level of the ongoing activity like its prestimulus activity. Importantly, the degree to which the stimulus or task elicit activity is supposed to remain independent of the prestimulus activity

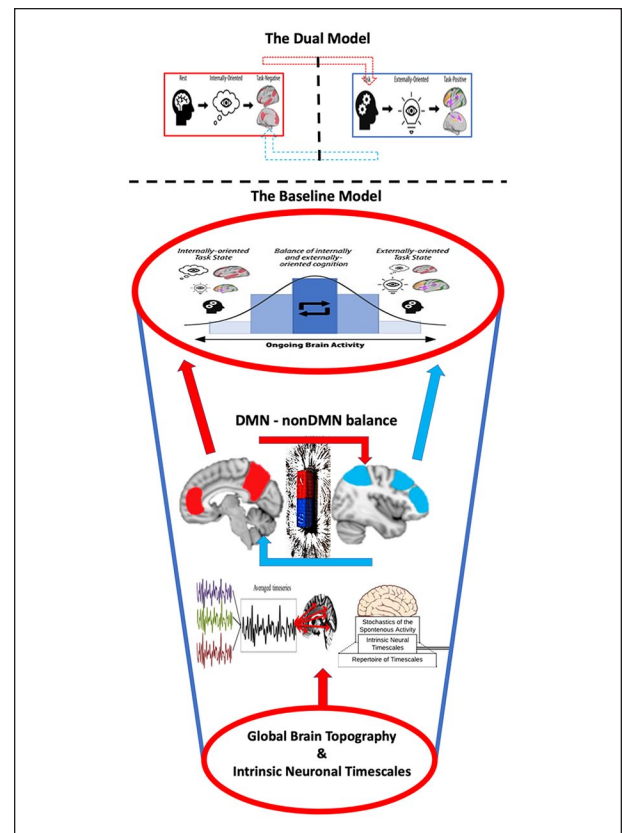


Figure 6. Summary of the transition from the dual model (on the top) to the baseline model (on the bottom).

level—the stimulus itself—is conceived as sufficient for the level of stimulus-induced activity (He 2013). However, different lines of evidence shed doubt on such purely additive rest-stimulus interaction. Various studies in both fMRI and EEG/MEG demonstrate that prestimulus activity levels strongly affect both stimulus-induced activity and associated externally oriented cognition (i.e., perception) (He 2013; Hesselmann and others 2008; Huang and others 2017; Sadaghiani and others 2009, 2010, 2015; Keitel and others 2017; Wainio-Theberge and others 2020; Wolff and others 2019a, 2019b). Even more interesting, prestimulus activity levels also affect internally oriented cognition like self-referential processing (Bai and others 2015; Mayer and Lieberman 2018; Qin and others 2016) and internally oriented decision making (Nakao and others 2019; Wolff and others 2019a, 2019b). These data strongly suggest the nonadditive interaction of rest/prestimulus and stimulus-induced activity (He 2013; Huang and others 2017; Wainio-Theberge and others 2021; Wolff and others 2019a, 2019b).

Even more important, these data demonstrate that the brain's ongoing activity, through nonadditive rest-stimulus interaction, shapes both internally and externally

oriented cognition. This means that the ongoing activity serves as internal reference or standard relative to which it can change its own spatial and temporal coordinates: the level of the ongoing activity sets a probability space (see also Cocchi and others 2017) for the possible (and impossible) degrees of its own spatial and temporal changes during task states and cognition.

Together with the findings described above, we suppose that such probability space is constituted by the ongoing activity's spatiotemporal dynamics serving as internal reference or standard. Such dynamic probability space indexes the ongoing activity's capacity or neural predisposition (rather than as neural correlate) for change and ultimately for cognition. This is paradigmatically exemplified in the concept of neural predispositions of consciousness (NPCs) as distinguished from the neural correlates of consciousness (NCCs) (Northoff 2013; Northoff and Heiss 2015; Northoff and Lamme 2020).

Part V: Related Models—Metabolic-Energetic, Inside-Out, and Predictive Models

Metabolic-Energetic Model (Raichle) I—Metabolic-Energetic Baseline as Precursor of the Baseline Model

Taking an energetic-metabolic view, Raichle and others argue for a “metabolic-energetic baseline” (Gusnard and Raichle 2001; Hyder and Rothman 2010; Hyder and others 2011; Shine and Breakspear 2018; Shulman and others 2010; van Eijsden and others 2009) or “physiological baseline” (Gusnard and Raichle 2001; Raichle 2015a, 2015b). The assumption of such metabolic-energetic baseline is strongly supported by observations of high metabolic-energetic consumption in the resting state with only maximal 5% incremental increase during task states (Aiello and others 2015; Bodart and others 2017; Gusnard and Raichle 2001; Hyder and others 2011; McAvoy and others 2019; Nugent and others 2015; Raichle and others 2001; Raichle and Mintun 2006; Raichle 2015a, 2015b; Soddu and others 2015; van Eijsden and others 2009). Therefore, Raichle and others (2001) suggest that the high resting state metabolism in DMN regions serves as the “default mode of brain function,” as explicitly stated in the title of his 2001 article (Raichle and others 2001). Such default mode or baseline is supposed to provide a metabolic-energetic reference or standard for its own activity changes (Andrews-Hanna 2012; Raichle and others 2001; Raichle and Gusnard 2001; Raichle 2015a, 2015b).

Is the metabolic-energetic baseline identical with internally oriented cognition? Raichle himself, in his earlier work, associates the high resting state metabolism in the task-negative regions not only with internally oriented

cognition but also with externally oriented cognition (i.e., attention to the external environment) (Gusnard and Raichle 2001; Raichle and others 2001; Simpson and others 2001). This becomes even more explicit in a recent review article (Raichle 2015a, 2015b), where he contests the identification of metabolic-energetic and cognitive baselines with respect to the DMN: “However, several factors lead this author to believe that focusing solely on spontaneous cognition ignores the possibility of a much more fundamental role for the default-mode network in brain function” (Raichle 2015a).

Metabolic-Energetic Model (Raichle) II—Empirical Evidence

Supported by additional recent evidence, as cited, these factors include occurrence of the DMN in nonhuman species like nonhuman primates (Vincent and others 2007), mice, and rats (Raichle 2015a, 2015b) that exhibit a different cognitive profile than humans; persistence of the DMN with somewhat modified functional connectivity in anesthetic states (Fransson 2006; Huang and others 2014, 2016; Huang and others 2018b) where consciousness, including internally oriented cognition, is lost; and task-related activity, with task requiring externally or internally oriented cognition, only requires maximal 5% incremental increase of the brain's overall metabolic energy.

Further lines of evidence include the rest of the brain's “dark energy” (80%–90%) may, by itself, not necessarily or always be accompanied by specific cognitive functions, including internally oriented cognition (Raichle and others 2001; Raichle and Menon 2006; Raichle 2015a, 2015b); involvement of the DMN in externally oriented cognition like attention to external stimuli (Andrews-Hanna 2012; Raichle and others 2001) and complex external naturalistic stimuli (Chen and others 2015, 2017; Simony and others 2016); and changes in DMN and both internally and externally oriented cognition in various psychiatric disorders (Anticevic and others 2012; Northoff and Gomez-Pilar 2021; Scalabrini and others 2020).

Together, these observations speak against the identification of the ongoing activity's role as baseline with cognition—the ongoing activity provides a metabolic-energetic baseline that transforms into neuronal activity (i.e., neuronal baseline) but is not identical with cognitive activity (i.e., cognitive baseline). Raichle's concept of metabolic-energetic baseline operating as default is consequently compatible with the here postulated baseline model: the latter extends the former's primarily metabolic-energetic stance by showing that the ongoing activity's spatiotemporal dynamics may be key in serving as neuronal baseline (i.e., internal reference or standard).

Future studies may thus want to investigate both metabolic-energetic features and spatiotemporal dynamics of the ongoing activity during rest and task states (see He 2011 for a first step).

Inside-Out Model (Buzsáki)—Brain-Based Approach and Spatiotemporal Neuroscience

The dual model's starting point is the distinction between internally and externally oriented cognition. It then proceeds from that cognitive distinction to its underlying neural correlates on both neuronal (i.e., rest versus task) and network (i.e., DMN versus non-DMN) levels. Hence, following Buzsáki (2019), the dual modal proceeds from the outside of the brain (i.e., its cognition) to its inside (i.e., its neuronal and network activity). He characterizes such approach as “outside-in,” which is the standard approach in cognitive neuroscience as paradigmatically reflected in the dual model of the brain's ongoing activity.

However, Buzsáki conceives such outside-in approach as deeply flawed as it reverses the relationship of brain and cognition in the “wrong direction.” Rather than inferring cognition at the outside from the brain's inside, it bases the latter upon the former—hence its name outside-in approach. That neglects the brain's inside itself, though, which may be key in mediating its outside, namely, cognition. He therefore contrasts the currently dominating outside-in approach with what he describes as an “inside-in” approach that, methodologically, is primarily based on the brain (i.e., brain based) rather than on cognition or the mind (i.e., cognition—or mind based) (Northoff 2014a; Northoff and others 2010a).

Which features of the brain's inside play a key role in mediating cognition at its outside? The answer of the baseline model is clear: it is the ongoing activity that, operating as neuronal baseline through its spatiotemporal dynamics, shapes our cognition. The key feature of the brain's inside are, according to our view, the spatiotemporal dynamics of the brain's ongoing activity that, serving as global shared spatial and temporal neural code, provide the neuronal baseline for the outside, that is, behavior and cognition. This requires one to complement the baseline model by what we recently described as “spatiotemporal neuroscience” (Northoff and others 2020, 2021). In a nutshell, spatiotemporal neuroscience investigates how the ongoing activity's spatiotemporal dynamics structures cognition in a spatiotemporal way like in a scale-free way as manifest in both brain and behavior (Kolvoort and others 2020; Palva and others 2013; Smith and others 2013). Put into Buzsáki's terms, spatiotemporal neuroscience serves as bridge, “glue,” or “common currency” of inside and outside (i.e., brain and cognition).

Predictive Coding (Friston) I—Converging with Spatiotemporal Dynamics

How does our baseline model of brain featured by STD stand in relation to one of the major theories of brain function, namely, predictive coding as complemented by the free energy principle (FEP) (Friston 2010; Hohwy 2013)? Following Bayesian statistics, predictive coding, in a nutshell, postulates that task-related activity is based on the comparison of the predicted input and the actual input with their difference yielding the prediction error. Predictive coding is compatible with the spatiotemporal approach focusing on STD: what is dynamically described as prestimulus activity featured by STD may well yield the predicted input (i.e., the empirical prior), as referred to in predictive coding.

One would, for instance, expect that the spatiotemporal dynamics (as measured by GS, global signal correlation [GSCORR], ACW, and/or PLE) of the resting state or the prestimulus interval may encode predictions (i.e., predicted inputs or empirical priors). The degree of relative change (i.e., mostly reduction) of GS and PLE (and other dynamics measures; see above) during the transition from rest/prestimulus to task may indicate the degree of the prediction error: large rest/prestimulus task changes in GS and ACW/PLE may signal high prediction error, whereas low degrees of rest/prestimulus task change in the same measures may indicate low prediction error. However, the relationship of GS and ACW/PLE and, more generally, of spatiotemporal dynamics and predictive coding remains to be investigated. Predictive coding may thus be complemented by a primarily spatial and temporal neural code of the ongoing activity's spatiotemporal dynamics.

How does predictive coding stand in relation to the ongoing activity's potential role as neuronal baseline? For that, we need to consider what Friston (2010) describes as FEP. Technically, the free energy principle casts neuronal dynamics as a gradient flow on a quantity known as *variational free energy* in Bayesian statistics. FEP crucially focuses on variational free energy of the coupling of the dynamics in both brain and environment: the brain minimizes variational free energy by aligning to its respective environmental context through, for instance, synchronization or entrainment (Lakatos and others 2019). We will now see that FEP unravels another potential role of the brain's ongoing activity beyond its role as neuronal baseline.

The free energy principle is used as a powerful formalism for modeling and understanding diverse forms of internally and externally oriented cognition, including consciousness (Hohwy 2013; Seth 2015), affect/emotion (Clark and others 2018; Gu and others 2013; Seth and

Friston 2016; Smith and others 2019), and self (Gallagher 2020; Seth and Tsakiris 2018). Importantly, the link of free energy to mental features like self can be predicated on temporospatial dynamics, as, for instance, by relying on “deep temporal models” (Friston and others 2017; Kiebel and others 2008) featured by what is described as *temporal thickness* or depth, which is the capacity to make inferences about present, past, and future (Seth 2015). Future studies are warranted that connect FEP and STD with the ongoing activity’s function as neuronal baseline, including its modulation of internally and externally oriented cognition (Northoff and others 2020).

Predictive Coding (Friston) II—Free Energy and Environmental Stochastics

The FEP links the brain and, as in our case, the ongoing activity closely to its environmental context. As so well described in the concepts of FEP (Friston 2010) and entrainment (Lakatos and others 2019), the ongoing activity synchronizes with the stochastic structure of its respective environmental (and bodily) context (see also Northoff 2018a, 2018b). There is consequently no need any more for the living organism and its brain to represent a model of the environment in their head: “An agent does not *have* a model of its world—it *is* a model. In other words, the form, structure, and states of our embodied brains do not *contain* a model of the sensorium—they *are* that model” (Friston 2013, 213). Given such *self-similarity* between brain and environment, we may better focus on “what our head’s inside of” rather than searching for “what inside our heads” (Bruineberg and Rietveld 2019).

Self-similarity and free energy exchange of brain and environment imply that the structure and hierarchies of the latter must be somehow encoded in the STD of the former. Albeit tentatively, we propose that the brain’s ongoing activity and consequently the neuronal baseline may encode the spatiotemporal hierarchies of its environmental context (as understood in a broad sense)—this is supported by the observation that the intrinsic neural timescales are evolutionarily preserved across different species regardless of their brain weight (Buzsáki and others 2013). Taken in this way, the intrinsic neural timescales and subsequently the neuronal baseline itself are not purely neuronally shaped but strongly shaped by experiential exposure and learning, which renders them neuroecological (i.e., neuroecological baseline) (Northoff 2018a, 2018b, chapter 8). That is, for instance, supported by the relationship of the ongoing activity’s STD with early traumatic childhood events (Duncan and others 2015; Nakao and others 2013; Wang and others 2021).

Together, we propose that converging FEP and STD unravels a second role or function of the brain’s ongoing

activity. In addition to its role serving as neuronal baseline, as outlined in the baseline model, the ongoing activity may also encode stochastic models or presentations of the ongoing spatiotemporal dynamics of its respective environmental (and bodily) context—this reflects the free energy balance of brain and environment. Investigation of such second more neuroecological function of the brain’s ongoing activity and its relevance for the brain’s neuronal baseline, including its modulation of cognition and mental features, is warranted in the future. Future work is needed, though, to converge FEP with the ongoing activity’s spatiotemporal dynamics and its encoding of environmental stochastics.

It shall be noted that the epistemic level is akin to the radical embodiment (RE) as introduced by Barsalou (Barsalou 2008; Barsalou and others 2003), who considers how cognition can be described by, for instance, the dynamical system theory (e.g., Spivey and others 2008), then, only afterward, by representational explanations. Our approach moves one step further and considers how the brain is always placed in context and embedded in the relation with the world (see Northoff 2016a, 2016b, 2018a, 2018b; Scalabrini, Xu, and others 2021; Zilio 2020). We aim to search for the *common currency* between brain and psyche (Northoff and others 2020, 2021; Northoff and Scalabrini 2021) investigating how the spatiotemporal features of neuronal and psychological components can be considered the “baseline” for the subsequent development of mental features like thought modes and dynamics. Moreover, it has been recently shown how at the psychological level, also the self (Box 4), as compared to the role of default mode functionality, may be considered a psychological baseline shaping its inner thoughts and cognitions (Scalabrini and others 2022).

Conclusion

The brain’s ongoing activity is extensively investigated. Despite all progress, its exact function or role for both brain and cognition remains elusive. The currently predominant, most often tacit, background assumption is to characterize the ongoing activity by resting state, DMN, and internally oriented cognition. That triad is contrasted with a corresponding triad of task states, non-DMN, and externally oriented cognition. Together, these corresponding triads amount to a dichotomy of rest versus task, DMN versus non-DMN, and internally versus externally oriented cognition; for that reason, we speak of an existing dual model.

However, various lines of evidence shed doubt upon such dual coding of rest versus task, DMN versus non-DMN, and internally versus externally oriented cognition. We may therefore need to extend our model beyond these

dichotomies. The baseline model steps into this void. The terms *neuronal baseline* and *internal reference/standard* are key concepts here. A biological clock provides a temporal code that serves as internal baseline or reference for the timing of the rest of the organism, including its relation to the environment. Analogously, extending Raichle's original search for the default mode of brain function (Raichle and others 2001), the baseline model proposes that the brain's ongoing activity provides a global shared temporal and spatial code that allows it to serve as neuronal baseline and thus as internal reference or standard for the brain's processing and its cognition.

Specifically, the brain's ongoing activity provides a global shared spatial and temporal code that consists of a dynamic probability space as determined by its predisposition or propensity of neuronal change (i.e., balance of DMN and non-DMN) and, ultimately, cognition (i.e., balance of internally and externally oriented cognition). Exerting its role as neuronal baseline through a global shared spatial and temporal code pits the ongoing activity on a more basic and fundamental level out of which the triad of dualities on neuronal (i.e., rest and task), network (i.e., DMN and non-DMN), and cognitive (i.e., internally and externally oriented cognition) levels emerge.

Moreover, albeit tentatively, we assume that the ongoing activity's role or function as neuronal baseline is mediated by the brain's temporospatial topography and dynamics like global brain activity and intrinsic neural timescales—these provide a global shared spatial and temporal code. That is supported by recent observations that these spatiotemporal topographic and dynamic features operate in both rest and task, cut across DMN and non-DMN in their hierarchies, and modulate both internally and externally oriented cognition. The behavioral relevance of the ongoing activity's spatiotemporal dynamics is further supported by its direct involvement in mental features like self and consciousness as well as their alterations in neurologic and psychiatric disorders.

We conclude that recent empirical evidence favors the baseline model over the dual model. The role and function of the brain's ongoing activity extends beyond rest, DMN, and internally oriented cognition by providing the necessary framework for their integration with task, non-DMN, and externally oriented cognition. The brain's ongoing activity and its spatiotemporal topography and dynamics provide a yet not fully explored deeper and more basic and fundamental layer of the brain's neural activity and coding that may be key in understanding the brain and how it yields cognition and mental features. Taken in this sense, the baseline model provides a novel more comprehensive view on one of the most pressing scientific issues of our time, namely, the role or function of the ongoing activity for both brain and mind.

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