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How Does the Brain's Spontaneous Activity Generate Our Thoughts?: The Spatiotemporal Theory of Task-Unrelated Thought (STTT)

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The Oxford Handbook of Spontaneous Thought: Mind-Wandering, Creativity, and Dreaming

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Print Publication Date: May 2018 Subject: Psychology, Cognitive Neuroscience

Online Publication Date: Apr 2018 DOI: 10.1093/oxfordhob/9780190464745.013.9

Abstract and Keywords

Recent investigations have demonstrated the psychological features (e.g. cognitive, affective, and social) of task-unrelated thoughts, as well as their underlying neural correlates in spontaneous activity, which cover various networks and regions, including the default-mode and central executive networks. Despite impressive progress in recent research, the mechanisms by means of which the brain's spontaneous activity generates and constitutes thoughts remain unclear. This chapter suggests that the spatiotemporal structure of the brain's spontaneous activity can integrate both content- and process-based approaches to task-unrelated or spontaneous thought—this amounts to what is described as the “spatiotemporal theory of task-unrelated thought” (STTT). Based on various lines of empirical evidence, the STTT postulates two main spatiotemporal mechanisms, spatiotemporal integration and extension. The STTT provides a novel brain-based spatiotemporal theory of task-unrelated thought that focuses on the brain's spontaneous activity, including its spatiotemporal structure, which allows integrating content- and process-based approaches.

Keywords: task, thought, spatiotemporal theory of task-unrelated thought, brain, spatiotemporal, cognition

Introduction

Content Versus Process Models of Task-Unrelated Thought

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Our daily mental life is characterized by strong thoughts that are unrelated to various external tasks and distractions in 25%–50% of our waking hours (Christoff et al., 2016; Smallwood & Schooler, 2015). These thoughts have been described by various terms, including *spontaneous thoughts* (see Andrews-Hanna, Irving, Fox, Spreng, & Christoff, Chapter 13 in this volume), *mind-wandering* (Mason et al., 2007), *task-unrelated thoughts* (Doucet et al., 2012), *random thoughts* (Andreasen et al., 1995), *self-generated thoughts* (Smallwood & Schooler, 2015), or *stimulus-independent thoughts* (Christoff et al., 2016; Dixon, Fox, & Christoff, 2014; Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015). Regardless of how we name them, these thoughts imply that we no longer focus on some externally given task or stimuli and their respective external mental contents, but are instead drifting away to some internal mental contents that remain more or less unrelated to specific stimuli or tasks. These internal mental contents shall here be described as task-unrelated thoughts that, at the same time, are also stimulus-independent (Fox et al., 2015; Smallwood & Schooler, 2015). These task-unrelated thoughts (as implying stimulus independence) are the focus in the present chapter.

(p. 56)

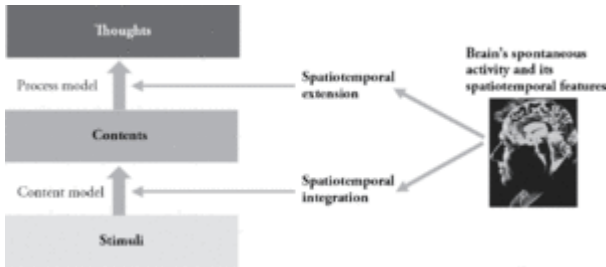
Different kinds of task-unrelated thoughts have been suggested. Smallwood and Schooler (2015), for instance, distinguish between self-generated and perceptually guided thoughts, with the former being generated internally by the self, while the latter originate rather externally in perceptions. Importantly, both forms of thought can occur either in the absence or presence of a task (i.e., task-related or -unrelated). The distinction between self-generated and perceptually guided thoughts seems to be more or less analogous to the one between internally and externally directed thoughts (Dixon et al., 2014). Both forms of thought may then be either spontaneous without any goal or with a goal, and thus unintentional or goal-directed (Dixon et al., 2014).

The various distinctions (i.e., self- vs. perceptually generated thoughts, as well as internally vs. externally directed thoughts) are mainly based on contents that either are self-related and thus internally or perceptually based, or are not related to self and thus externally based. Such content-based approaches have recently been complemented by focusing on induction mode and dynamic or process-related features (Andrews-Hanna et al., Chapter 13 in this volume; Christoff et al., 2016). The induction mode, for instance, is considered when distinguishing spontaneous versus deliberate thoughts, as well as unintentional versus intentional task-unrelated thoughts (Andrews-Hanna et al., Chapter 13 in this volume; Christoff et al., 2016)—these distinctions reflect different degrees of voluntary control when inducing task-unrelated thought, while the dynamic or process-related features pertain to, for instance, the duration and flow (“stream of consciousness” as based on W. James) of task-unrelated thoughts.

The different forms of task-unrelated thoughts suggest a basic distinction between content models and process models of task-unrelated thoughts (Andrews-Hanna et al., Chapter 13 in this volume; Christoff et al., 2016; Ellamil et al., 2016). The long dominating content models focus on different contents and our cognition, which supposedly determine task-unrelated thoughts—content models can therefore be considered

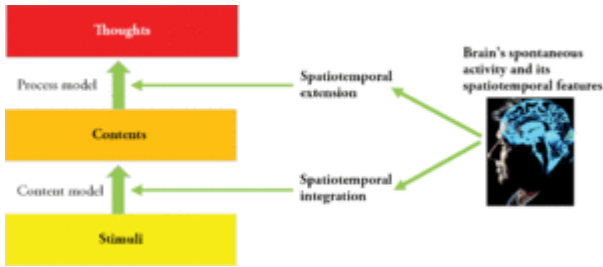
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cognitive models. Process models, on the other hand, emphasize the dynamic and process-based nature of task-unrelated thoughts (Andrews-Hanna et al., Chapter 13 in this volume; Christoff et al., 2016). How are both content and process models related to each other? I hypothesize that both contents and dynamic or process-based features of task-unrelated thoughts can be integrated and linked by spatiotemporal features. For that reason, I here suggest what I describe as the *spatiotemporal theory of task-unrelated thought* (STTT) (see Figure 6.1).



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Figure 6.1. Spatiotemporal theory of task-unrelated thought (STTT). (See Color Insert)



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Figure 6.1. Spatiotemporal theory of task-unrelated thought (STTT).

From the Brain's Spontaneous Activity to Task-Unrelated Thoughts

Psychologically, these different forms of task-unrelated thoughts have been associated with cognitive, affective, and social functions. For instance, self-generated thoughts have been associated with affective functions like anxiety and depression while, at the same time, being decoupled from perception (Andrews-Hanna et al., 2013; Baird, Smallwood, Lutz, & Schooler, 2014; Ruby, Smallwood, Engen, & Singer, 2013; Ruby, Smallwood, Sackur, & Singer, 2013; Smallwood & Schooler, 2015). In contrast, perceptually derived thoughts are closely linked to the perception of external events or objects in the environment (Smallwood & Schooler, 2015).

(p. 57) Neuronally, spontaneous or resting state activity (see later discussion for details) in the default-mode network (DMN; Raichle, 2015a, 2015b) and especially the cortical midline structures (Northoff & Bermpohl, 2004) has been highlighted in thoughts or mind-wandering (Andrews-Hanna, Smallwood, & Spreng, 2014; Doucet et al., 2012; Mason et al., 2007). However, other regions and networks like temporal cortical regions and the central executive network (CEN) have also been shown to be recruited during spontaneous or task-unrelated thought (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Fox et al., 2015). These data suggest widespread recruitment of regions and networks across the entire brain in the resting state during task-unrelated and stimulus-independent thought.

Spontaneous thoughts are clearly related to and based on the brain's resting state or spontaneous activity (see later discussion for conceptual differentiation). The brain's resting state can be characterized spatially by different neural networks (including DMN and CEN) and temporally by different frequency fluctuations in the range between 0.001 and 200 Hz (Cabral, Kringelbach, & Deco, 2013; Northoff, 2014a for details). This suggests that the brain's spontaneous activity shows an elaborate spatiotemporal structure, whose details will be discussed later.

How does the brain's spontaneous activity constitute or generate our thoughts? Or in other words, how does something neuronal like the brain's spontaneous activity generate or constitute something that is psychological (i.e., thoughts)? The question for transforming neuronal activity into something psychological (i.e., thoughts) must be distinguished from the question of how those same thoughts and their contents stand in relation to sensorimotor, cognitive, affective, or social functions.

My focus here is on the first question, the one for transformation, which encounters a serious problem. When measuring the brain's spontaneous activity, we do not detect any thoughts at all; all we see are firing rates of neurons, different networks, and different frequency fluctuations. Beyond that, we will not detect anything else in the brain's spontaneous activity. How is it possible for the brain's spontaneous activity and its

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neuronal features to generate or constitute task-unrelated thoughts? This is the central question guiding the present chapter.

To address this question, one may want to suppose a common denominator that makes it possible to transform the brain's spontaneous activity into task-unrelated thought. I here suggest spatiotemporal features to be one such common denominator underlying both neuronal and psychological activity. This leads me to suggest the spatiotemporal theory of task-unrelated thought (STTT), which postulates two spatiotemporal mechanisms. First, the STTT supposes that the brain's spontaneous activity integrates (and thereby transforms) different stimuli into content—this amounts to “spatiotemporal integration” and the contents of task-unrelated thoughts. Second, the STTT postulates that the brain's spontaneous activity and its spatial and temporal features allow the extension of the contents beyond their original points in time and space—this amounts to “spatiotemporal extension,” by means of which contents are transformed into thoughts. Taken together, as in its name, the STTT can be conceived a spatiotemporal (rather than cognitive) theory that links content and process models, as well as neuronal and psychological levels of task-unrelated thoughts.

“Spatiotemporal Integration”: Transformation of Stimuli into the Contents of Thoughts

The Brain's Spontaneous Activity: Different Stimuli and Their Baselines

How can we better describe the brain's spontaneous activity? I here understand the concept of the brain's spontaneous activity in a purely neuronal sense, as distinguished from a cognitive sense (as is often presupposed in the context of task-unrelated thought). Often the brain's spontaneous activity is considered to be devoid of the processing of specific stimuli or tasks, for instance the absence of a particular visual picture during task-evoked activity. In that case, the concept of spontaneous activity is more or less equated with the “resting state” that is defined by the absence of specific external stimuli (Logothetis et al., 2009; Northoff, 2014a). However, it is important to note that the absence of specific stimuli or tasks does not imply the complete or total absence of any kind of stimuli (or tasks). Even in the resting state, there are still plenty of stimuli that are processed.

When closing the eyes, as during the resting state, there is the continuous interoceptive input or stimuli from the body that need to be processed. There is, for instance, continuous input from the heart (heartbeat) and lungs (respiration). One would therefore expect that neural activity in the resting state is related to the interoceptive activity in the body. This possibility is supported by a study that demonstrated that resting state

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functional (p. 58) connectivity in the resting state is directly related to (i.e., correlates with) heart variability (Chang et al., 2013), and by a recent meta-analysis of functional neuroimaging studies of spontaneous thought showing that the insula—the key interoceptive cortex—is consistently recruited (Fox et al., 2015). The close link between interoceptive stimuli from the body and the brain's spontaneous activity is further supported by recent studies from the group around Tallon-Baudry that show how the heartbeat and the gastral dynamics (as related to slower frequencies) are directly related and coupled to neural activity in the brain's spontaneous activity (Babo-Rebelo et al., 2016; Park and Tallon-Baudry, 2014; Richter et al., 2016).

Due to the strong input of the body's interoceptive stimuli, Marx and colleagues (2004) therefore characterize the resting state as obtained during eyes closed as an "interoceptive state" where neural activity is strongly determined by and reflects the predominant processing of interoceptive stimuli from the body by the brain. Correspondingly, Barry, Clarke, Johnstone, Magee, and Rushby (2007) speak of an "arousal baseline," referring to an unspecific level or state of arousal as triggered mainly by the body's interoceptive input.

What happens if subjects open their eyes? In that case, additional exteroceptive input (e.g., visual input) is added to the ongoing exteroceptive input stemming from gustatory, olfactory, auditory, and tactile input (that is already ongoing in the interoceptive state). The balance between the continuous interoceptive and exteroceptive input may thus shift toward the latter when opening the eyes. The primarily interoceptive state and its "arousal baseline" is then transformed into a primarily "exteroceptive state" and a corresponding "activation baseline" (Barry et al., 2007).

In addition to the continuous interoceptive and exteroceptive input from body and environment, there is also input from the brain itself and its intrinsic activity. The thalamus, for instance, generates its own activity pattern with oscillations that may be imputed into other regions. Analogously to interoceptive and exteroceptive input, one may want to speak here of "neural input" with a "neural state" and a corresponding "neural baseline" (Northoff, 2014a). These different baselines (i.e., activation, arousal, and neural baseline) may be prevalent throughout the whole brain and thus in all regions and networks.

Different brain regions and networks may show different balances between the three different states, though. For instance, subcortical regions in the brain stem receive strong interoceptive inputs from the body such that the interoceptive state and its arousal baseline may predominate here in the resting state. On the other hand, sensory regions and their respective sensory networks receive rather strong exteroceptive input so that the exteroceptive state and the activation baseline may predominate here. Finally, the "neural state" and its neural baseline may predominate in regions like the cortical midline structures that neither receive direct stimulus input (either interoceptive or

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exteroceptive) nor send out stimulus output (like the motor cortex and the executive control network) (Northoff, 2014a).

Taken together, these short deliberations show that the brain's spontaneous activity is far from a true "resting" state in the literal sense of the term. There are many different stimuli being processed, interoceptive and exteroceptive and neural, which leads to different balances between interoceptive and exteroceptive and neural states (and their respective baselines) across different regions and networks in the brain. This raises the question of how the integration of these different stimuli ultimately results in the brain's spontaneous activity (or resting state, if taken in an operational way). How are the different continuous inputs, interoceptive and exteroceptive and neural, linked or bound together such that they constitute what we observe as spontaneous (or resting state) activity? I suggest in the following section that "spatiotemporal integration" and, more specifically, "spatiotemporal binding" may be central for that.

"Spatiotemporal Binding": Transforming Stimuli into Contents

What is spatiotemporal binding? The concept of binding has been used often in the context of consciousness, where it describes the linkage (e.g., binding) between different stimuli into one content by means of which the latter is supposed to become conscious (Crick & Koch, 2003). This has been called the "binding hypothesis" of consciousness (Crick & Koch, 2003; Rhodes, 2006). For instance, stimuli are supposed to be bound together by 40 Hz (i.e., gamma band) oscillations in the visual cortex that allow the stimuli to be synchronized, amounting to "binding by synchronization" (Mudrik et al., 2014). However, the association of such binding of different stimuli into contents with conscious awareness has been contested. Studies have demonstrated that the linkage or binding between different stimuli, for instance during (p. 59) multisensory integration, can occur in the absence of consciousness (Mudrik et al., 2014; Revonsuo, 2006; Zmigrod & Hommel, 2011).

Independent of the association with consciousness, one can conceive binding nevertheless as a central mechanism to link different stimuli. I suggest that such binding occurs in the brain's spontaneous activity: the different continuous interoceptive and exteroceptive and neural inputs are temporally and spatially linked and thus bound together in that they result in contents that later resurface as the contents of thought. Such binding between the different contents occurs, I propose, on the grounds of the spatiotemporal features of the brain. Let us detail the mechanisms of such "spatiotemporal binding," as I call it (I will distinguish it from other forms of binding in the next section).

Each region in the brain shows specific spatial and temporal features in its spontaneous activity. Spatially, brain regions may show a certain functional connectivity pattern with other regions. For instance, cortical midline structures, the core part of the DMN, have shown a rather high (if not the highest) degree of functional connectivity within the

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brain's spontaneous activity (when compared to other regions and networks) (de Pasquale et al., 2012; Hagmann et al., 2008; Honey et al., 2009). In contrast, sensory regions show a much lower degree of functional connectivity. Temporally, each region (and network) seems to have its own range of time windows within which it can bind or integrate different stimuli into one pattern of neural activity. These intrinsic time windows may surface in what has been described as "temporal receptive windows" (Hasson, Chen, & Honey, 2015; Honey et al., 2009; Murray et al., 2014) that have been shown to be rather short in sensory cortex (60–80 ms), whereas they seem to be rather long in other areas, especially the cortical midline structures (up to 250–300 ms).

What do these spatial and temporal features imply for the binding of interoceptive and exteroceptive and neural inputs in the brain's spontaneous activity? They suggest that different regions may bind different inputs in different ways, depending on their respective spatial and temporal profile. For instance, the sensory cortices, with their low degrees of functional connectivity and short intrinsic time windows, may not be able to bind as many and or as wide a range of stimuli, including their different points in time and space, together as the cortical midline structures, with their high degree of functional connectivity and long intrinsic time windows. There consequently may be different spatiotemporally based "neural binding patterns" for integrating different stimuli across the brain's different regions and networks.

How are these different neural binding patterns related to thoughts and their contents? I propose that the contents of thought result from and are constituted or generated on the basis of the binding between different stimuli, including their different points in time and space. By binding different stimuli and their different points in time and space together, a certain unity (an "objectual unity," as philosophers would call it; cf. Bayne & Chalmers, 2003) is constituted, which may correspond to what we describe as the content (or object) of thought.

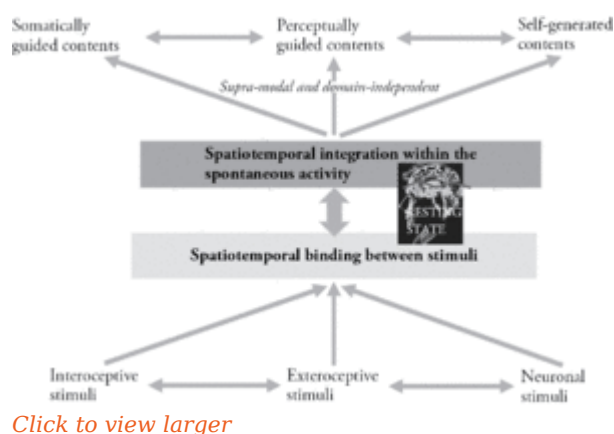
Contents may then be distinguished on the basis of their neural binding pattern and its spatiotemporal features. Different contents (or objects) of thought may consequently be assumed to correspond to different neural binding patterns and different spatiotemporal features. Depending on the predominant content, one may want to distinguish between somatically guided, perceptually guided, and self-generated thoughts.

If, for instance, interoceptive input prevails over exteroceptive input in the brain's spontaneous activity, the contents of our spontaneous thought may more likely concern one's body rather than referring to the environment. Such somatically guided thoughts may, for instance, predominate in psychiatric patients with anxiety, panic, or depression, who can be abnormally preoccupied with their body (or parts of it, such as the heart), resulting in various somatic symptoms. In that case, one would expect that the balance of spontaneous activity shifts toward the subcortical or interoceptively involved regions like

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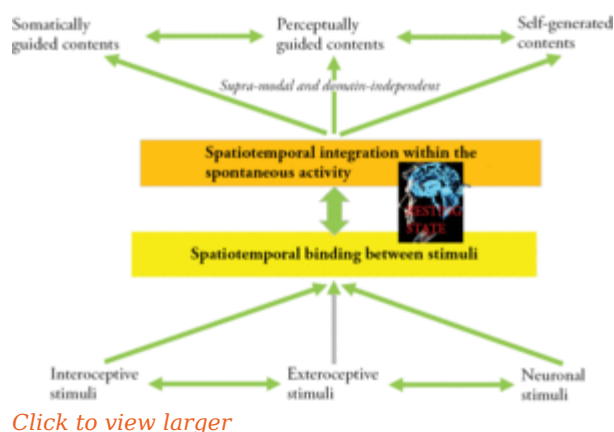
the insula and the somatosensory cortex, which is indeed the case (Andrew-Hanna et al., 2016; de Greck et al., 2012).

If, in contrast, exteroceptive input predominates, the spontaneous activity balance may shift more toward the sensory cortices, resulting in the predominance of external thoughts contents, for example “externally guided cognition” (Dixon et al., 2014) or alternatively, “perceptually guided thought” (Smallwood & Schooler, 2015). Finally, the neural input from the brain's spontaneous activity itself and especially that from the cortical midline structures may predominate in the brain's spontaneous activity. In that case, one would expect internally guided cognition (Dixon et al., 2014), with thought contents strongly related to the self, (p. 60) amounting more or less to self-generated thoughts (Smallwood & Schooler, 2015) (see Figure 6.2).



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Figure 6.2. Spatiotemporal integration and binding. (See Color Insert)



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Figure 6.2. Spatiotemporal integration and binding.

How are the three different kinds of content related to each other? Since interoceptive, exteroceptive, and neural stimuli are all integrated and bound together within the brain's spontaneous activity, there are no exclusively somatically or perceptually guided thoughts, nor solely self-generated thoughts. Instead, the contents of our thoughts are supra-modal and domain-independent and can therefore be traced to the balance between interoceptive, exteroceptive, and neural stimuli. Rather than considering each type of stimulus independent of the others, it is rather a

matter of their balance and the degree to which one predominates over the others. The hypothesis of such a balance is consistent with recent findings of decoupling from sensory processing, including sensory cortex, during self-generated thought (Andrews-Hanna et al., 2014; Baird et al., 2014; Gorgolewski et al., 2014).

“Spatiotemporal Integration”: Basic and Fundamental Form of Integration

I have suggested that “spatiotemporal integration” and, more specifically, “spatiotemporal binding” are central in constituting the contents of our thoughts. What exactly do I mean by integration? One can describe different forms of integration, such as multisensory integration, perceptual integration, semantic integration, cognitive integration, and formal mathematical integration (see Mudrik, Faivre, & Koch, 2014, for an excellent overview). These forms of integration implicate sensory and perceptual functions like multisensory integration and perceptual integration, as well as cognitive functions such as semantic and cognitive integration, or even higher-order cognitive functions as required in mathematical integration.

Those more complex forms of integration must be distinguished from the kind of integration proposed here. The integration between different stimuli in spontaneous brain activity does not yet implicate any specific active recruitment of sensorimotor, perceptual, cognitive, or higher-order cognitive functions. Instead, the integration by the spontaneous activity occurs in an automatic way, by default, due to the nature of the spontaneous activity's spatiotemporal structure. The interoceptive and exteroceptive and neural stimuli constituting the different baselines are by default (i.e., automatically) integrated within the brain's spontaneous activity. No recruitment of sensory, perceptual, motor, cognitive, or higher-order cognitive functions is required.

Instead, the different stimuli and their spatial and temporal features are integrated by and within the spatiotemporal features of the brain's spontaneous activity so that one may want to speak of “spatiotemporal integration.” Such spatiotemporal integration features a most basic and fundamental level of integration that is inherent in the spontaneous activity and its spatiotemporal structure prior to and independent of any subsequent sensorimotor, affective, cognitive, and social function, including their respective forms of integration (i.e., multisensory, cognitive, etc.). Accordingly, taken together, spatiotemporal integration can be characterized by (1) its automatic nature occurring by default (p. 61) because of the spontaneous activity's spatiotemporal structure; and (2) prior to and independent of the recruitment of specific sensorimotor, affective, cognitive, and social function.

One may want to argue that such spatiotemporal integration is trivially true. Any integration between different stimuli occurs at one particular or discrete point in time and space within the brain, for instance at a particular region or cell population, as well as in a specific frequency range. This is not contested here. Taken in this sense, the characterization of integration as spatiotemporal is indeed trivially true. However, that is not the sense that I mean by the concepts of space and time as the core of spatiotemporal integration. Rather than referring to discrete points, here the concepts of space and time

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refer to a distribution of different points across space and time entailing a stochastic or statistically based and ultimately neural, rather than mental, meaning of time and space.

Let us illustrate such stochastic meaning of space and time by the example of multisensory integration (Ferri et al., 2015; Stein et al., 2009). Multisensory integration is assumed to rely on different principles, including spatial and temporal coincidence between the cross-modal stimuli: if the two cross-modal stimuli coincide at the same point in space, as for instance in a particular cell population or region, their likelihood of being integrated is much higher than when they do not spatially coincide (see Stein et al., 2009, as well as Chapter 10 in Northoff, 2014a, for details). The same holds analogously for temporal coincidence: if the two stimuli temporally coincide and do thus occur stochastically at the same point in time, they can be much better integrated with each other than when occurring at different points in time. This makes it clear that multisensory stimuli are integrated with each other on stochastically based spatial and temporal grounds.

I now assume the same in an analogous way to hold for the integration of the ongoing interoceptive and exteroceptive and neural stimuli with each other into the brain's spontaneous activity. The more the temporal and spatial features of interoceptive stimuli coincide with the spatial and temporal features of the brain's spontaneous activity, the better the former will be integrated within the latter. The same holds, obviously, for the integration of exteroceptive and neural stimuli into the spontaneous activity, which also occurs on purely spatial and temporal grounds.

Instead of the single stimulus itself and its specific points in time and space, the spontaneous activity encodes the relation (e.g., difference) of the former's points in time and space to its own points in time and space (i.e., its own spatial and temporal features). The resulting neural activity is thus based on the stochastically based spatiotemporal difference between stimulus and spontaneous activity—this presupposes difference-based coding (as distinguished from stimulus-based coding) (Northoff, 2014a). I now postulate that such stochastically based spatiotemporal encoding strategy (i.e., difference-based coding) allows for the kind of spatiotemporal integration and binding that transforms simple stimuli into contents.

Such encoding strategy (i.e., difference-based coding) is based on the spatiotemporal features of stimuli; this distinguishes it from other strategies that are rather based on the nature of the stimuli themselves, like their origin, as in body, environment, or brain, or, alternatively, on associated sensorimotor, cognitive, affective, or social function, as in more complex forms of integration (see earlier discussion). Therefore, the concept of "spatiotemporal" as presupposed in spatiotemporal integration cannot be considered trivially true but rather substantial in that it describes a most basic and fundamental form of integration. I postulate that spatiotemporal integration in this most basic and fundamental sense (i.e., prior to and independent of other more complex forms of

integration) is central for integrating and binding and thus transforming stimuli into contents as essential ingredients of task-unrelated thought.

“Spatiotemporal Extension”: Transformation of Contents into Thoughts

The Brain's Spontaneous Activity: Spatial and Temporal Features

The brain's intrinsic activity (or spontaneous activity) can spatially be characterized by various neural networks that consist of regions showing close functional connectivity with each other. There is, for instance, the DMN that includes mainly the cortical midline structures (Andrews-Hanna et al., Chapter 13 in this volume; Northoff et al., 2006), which show strong low-frequency fluctuations (Northoff, 2014a; Raichle, 2009; Raichle et al., 2001). Other neural networks include the sensorimotor network, the salience network, the ventral and dorsal attention network, the cingulum-operculum network, and the CEN (see Menon, 2011, for a review). These neural networks are related to each other in continuously dynamically changing constellations (de Pasquale et al., 2010, 2012), resulting (p. 62) in what may be described as a spatial structure that, through its functional nature, supercedes the anatomical structure.

In addition to such spatial structure on the functional level, the spontaneous activity can also be characterized by fluctuations in its neural activity in different frequency bands, ranging from infraslow (0.0001–0.1 Hz) through delta (1–4 Hz), theta (5–8 Hz), alpha (8–12 Hz), and beta (12–30 Hz) to gamma (30–180 Hz). Most important, these different frequency bands are coupled with each other, with for instance the phase of lower frequency bands being coupled to the phase or power of higher ones (Buzsaki, 2006; Buzsaki, Logothetis, & Singer, 2013; Northoff, 2014a). This amounts to a complex temporal structure in the brain's intrinsic activity that, as shown most recently, is related in some yet unclear ways to the spatial structure and its various neural networks (e.g., Ganzetti & Mantini, 2013; Northoff, 2014a).

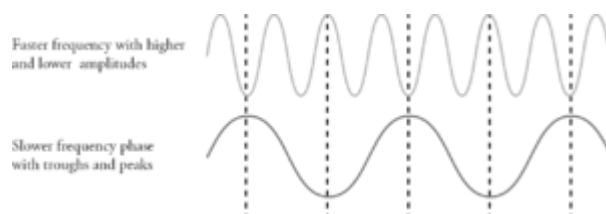
To be more specific, the spontaneous fluctuations as observed in the functional magnetic resonance imaging (fMRI) signal, i.e., BOLD, are found in lower frequency ranges, including the delta band (1–4 Hz), up- and down-states (0.8 Hz), and infraslow fluctuations (ISFs) (0.001–0.1 Hz) (Logothetis, 2008, Zhigalov et al., 2015). The slow-frequency fluctuations observed in fMRI have been assumed to correspond to what is measured as slow cortical potentials (SCPs) in electroencephalography (EEG) (He & Raichle, 2009; Khader, Schicke, Röder, & Rösler, 2008). These SCPs are not easy to obtain in EEG because they are subject to artifacts caused by sweating, movements, and electrode drift; their measurement therefore requires a more direct approach by so-called

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direct current (DC) recording. There is some evidence that what is measured as SCP in EEG corresponds, or is even identical, to the low-frequency fluctuations obtained in fMRI (He & Raichle, 2009; Khader et al., 2008).

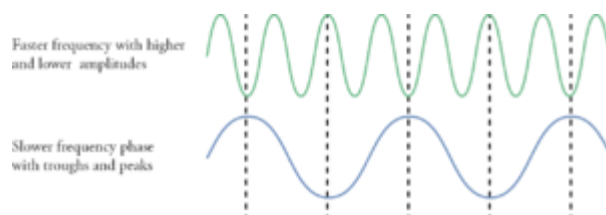
In addition to such low-frequency fluctuations, there are also higher frequency fluctuations in the brain's resting-state activity. These cover 1 Hz and higher frequency ranges, thus including delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (>30 Hz) (Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Sadaghiani, Hesselmann, Friston, & Kleinschmidt, 2010). This raises the question of how low and high frequencies are related to each other in the brain's resting state (Canolty & Knight, 2010; Fell & Axmacher, 2011; Fries, 2009; Sauseng & Klimesch, 2008). For instance, Vanhatalo et al. (2004) conducted an EEG study in healthy and epileptic subjects during sleep using DC-EEG to record low-frequency oscillations. All subjects showed infraslow oscillations (0.02–0.2 Hz) across all electrodes—and thus the whole brain—without any specific, visually obvious spatial distribution evident.

Most interestingly, Vanhatalo et al. (2004) observed phase-locking or phase-synchronization between the phase of slow (0.02–0.2 Hz) oscillations and the amplitudes of the faster (1–10 Hz) oscillations: the amplitudes of the higher frequency oscillations (1–10 Hz) were highest during the negative phases or deflection (e.g., during periods in the fluctuating cycle of the low-frequency oscillation that show higher degrees of excitability for subsequent stimuli when compared to positive periods in the cycle) of the slow oscillations (0.02–0.2 Hz) (see Figure 6.3).



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Figure 6.3. Schematic illustration of cross-frequency coupling. (See Color Insert)



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Figure 6.3. Schematic illustration of cross-frequency coupling.

Such phase-locking of high-frequency oscillations' power to the phases of lower ones is described as *phase-power coupling*, with phase-phase and power-power coupling also being possible (Canolty & Knight, 2010; Sauseng & Klimesch, 2008). Generally, the coupling seems to occur in the direction from low- to high-frequency fluctuations as well as from phase to amplitude/power (Buzsaki, 2006;

Buzsaki et al., 2013)—the phase of the lower (p. 63) frequency entrains the amplitude of the higher frequency. Such low-high frequency entrainment may be central in integrating

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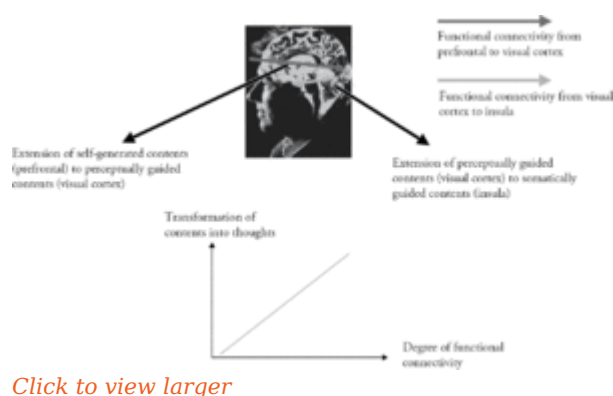
and embedding the stimuli (and their respective contents) into the ongoing temporal structure of the brain's intrinsic activity.

“Spatial Extension” of Contents: Functional Connectivity

What does the spontaneous neural activity's spatiotemporal structure imply for the constitution or generation of thoughts? Thoughts are based on contents. However, thoughts are more than contents, since we can have contents that do not transform into thoughts. Therefore, we need to consider additional mechanisms that transform contents into thoughts. For that, the STTT supposes yet another spatiotemporal mechanism, that is, *spatiotemporal expansion*.

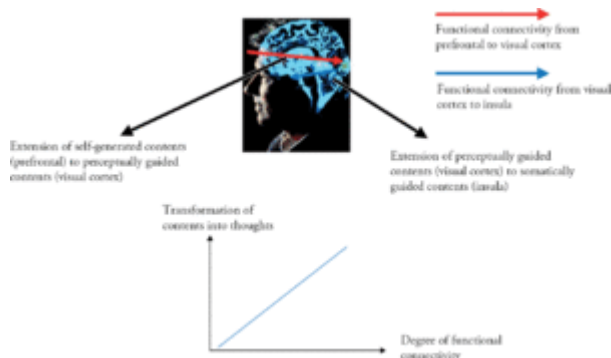
We discussed earlier the different inputs into the brain's spontaneous activity, including their binding into contents. Contents can consequently be determined as the linkage or binding of different stimuli into one unity, the unity of content (the “objectual” unity to which philosophers refer). This, however, leaves open the question of how contents can become thoughts. For that I assume that contents need to be *spatiotemporally extended*. This shall be explicated in the following. For that, we first need to consider the regions that have been shown to be recruited during task-unrelated thought. Most prominent among them are the cortical midline structures.

The cortical midline structures show the highest degree of functional connectivity within this region, as well as to all other regions in the brain (de Pasquale et al., 2012; Hagmann et al., 2008; Honey et al., 2009). This suggests that any content generated in, for instance, sensory regions gets somewhat linked and bound to midline regions. Conversely, it means that the contents generated in the midline impact contents elsewhere (see later in this chapter for details of what will be described as *self-expansion*). The original content is thus spatially extended beyond itself and its local origin at one particular point in space, entailing what I describe as spatial extension of content. The higher the degree of functional connectivity, the more the content can be spatially extended beyond its single discrete point in space, and the stronger the respective thought contents will be experienced or perceived as spatially extended across self, body, and environment. (See Figure 6.4).



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Figure 6.4. Spatial extension of contents into thoughts. (See Color Insert)



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Figure 6.4. Spatial extension of contents into thoughts.

The assumption of such spatial extension is in accordance with an early study by Mason and colleagues (Mason et al., 2007). They demonstrated a direct correlation between cortical midline neural activity in the DMN and the degree of mind-wandering: the stronger the midline activity in the DMN, the stronger the degree of mind-wandering (as sampled by a

questionnaire). Unfortunately, they (p. 64) did not include functional connectivity measures of the midline regions, which, as I suggest, may be directly proportional to the degree of recruitment of midline structures during task-unrelated thought.

We have to be careful, though. In addition to cortical midline structures, various other regions and networks have been implicated in task-unrelated thought. A subsequent study by Christoff and colleagues (Christoff et al., 2009) observed that other regions, for instance the lateral prefrontal cortex and the CEN, are also recruited during mind-wandering (see Fox et al., 2015, for a recent meta-analysis, as well as Dixon et al., 2014, for a discussion of competition vs. co-occurrence between internally and externally directed cognition). Relevant neuronal measures like inter- and intra-regional synchronization (as measured by functional connectivity and regional homogeneity), neuronal variability, and positive and negative BOLD responses, have been shown to be modulated by episodes of mind-wandering in both the DMN and CEN (and other networks like the dorsal attention network and the salience network) (Allen et al., 2013; Andrews-Hanna et al., 2014, Chapter 13 in this volume; Christoff et al., 2016; Doucet et al., 2012; Fazelpour & Thompson, 2015; Gorgolewski et al., 2014; Zabelina & Andrews-Hanna, 2016).

Additionally, other regions like the dorsomedial prefrontal regions, the insula, the dorsal anterior cingulate cortex (as part of the salience network), and the medial temporal regions/network (that includes the hippocampus and its central role in episodic memory retrieval) have also been shown to be activated during mind-wandering (see Andrews-Hanna et al., 2014, as well as Fox et al., 2015, for a recent meta-analysis). The involvement of non-DMN regions is further supported by a recent meta-analysis of neuroimaging studies on mind-wandering (Fox et al., 2015).

The authors reported involvement of typical DMN regions (like ventromedial prefrontal cortex, medial prefrontal cortex, precuneus/posterior cingulate cortex, bilateral inferior parietal lobule, and left medial temporal lobe/parahippocampal cortex). In addition, they

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observed many regions from the executive control network, including dorsal anterior cingulate cortex, right rostro- and left ventrolateral prefrontal cortex, right anterior inferior parietal lobule, and precuneus. Finally, regions outside both the DMN and CEN were also implicated, including right secondary somatosensory cortex, left mid-insula, and left lingual gyrus. This further suggests that mind-wandering is not limited to the DMN but involves brain regions and different networks and, ultimately, can involve more or less the entire brain, which may reflect the heterogeneity and complexity of task-unrelated thought (Fox et al., 2015).

Why is the involvement of different regions and networks relevant for task-related thought? The different regions and networks show different functional connectivity patterns. For instance, as pointed out, the cortical midline structures show the highest degree of functional connectivity when compared to other regions like sensory regions (see earlier discussion). I now postulate that each region will contribute to the spatial extension of contents into thoughts based on its respective functional connectivity pattern. By showing a high degree of functional connectivity to other and more distant regions, the point in space featuring the respective content can be extended further, that is, connected with others, and thereby put into a larger spatial context.

Based on their functional connectivity patterns, different regions like sensory and midline regions may contribute to the spatial extension of contents in different ways. The spatial point of a content originating strongly in sensory cortex (i.e., perceptually derived content) may not be as spatially extended as a content related to the self (i.e., self-guided content). The different regions' functional connectivity patterns, including their balance, may then strongly impact the degree to which a particular content and its particular point in space are extended to others and thus put in a larger spatial context. And, importantly, the larger the degree of spatial extension of the content, the more likely the content will be transformed into a thought. Accordingly, I hypothesize direct proportional relationship between the degree of functional connectivity (of particular regions or networks) and their recruitment during task-unrelated thought.

“Temporal Extension” of Content: Cross-Frequency Coupling

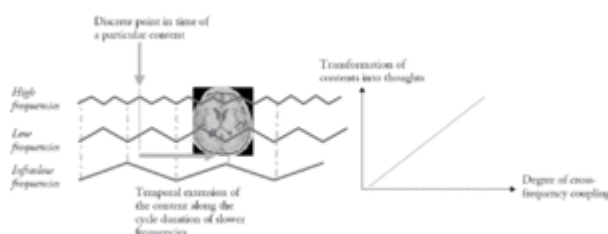
The same kind of extension of the contents of thought may analogously occur on the temporal side. The different frequencies are not isolated from each other, but can become coupled. Accordingly, the infraslow-frequency fluctuations with their long cycle durations may couple to the shorter, higher-frequency fluctuations entailing cross-frequency coupling (Huang et al., 2017; Zhiaglov et al., 2015). Especially the long cycle durations of the infraslow-frequency fluctuations may provide the perfect means to extend the single thought beyond (p. 65) its own temporal features at one particular point in time into a longer duration: the longer the cycle duration and hence the lower the frequency range, the more and thus longer the respective content can be temporally extended beyond its

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own original discrete point in time, and the more the thought will be perceived or experienced as temporally continuous.

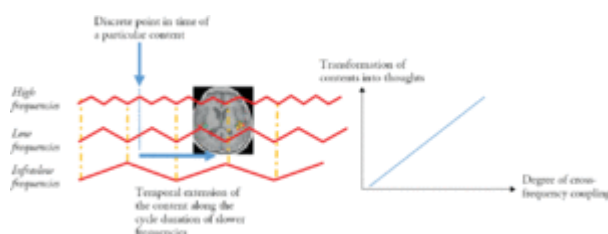
As discussed earlier, the long cycle durations of the infraslow-frequency fluctuations may be especially central here. If the timing of a content falls into the beginning of the phase of an infraslow-frequency fluctuation with a cycle duration of, for instance, 100 s (as in 0.01 Hz), the content's initial and discrete point in time (at 5 s into the onset of cycle duration) may be extended into the high excitability phase of the ongoing fluctuations (e.g., the trough, as distinguished from the peak). Since the trough covers half the cycle duration (e.g., 50 s of the 100 s total cycle duration), the content will be extended for an additional 45 s beyond its occurrence of 5 s into the cycle duration. In contrast, the shorter cycle durations of higher frequencies (like delta at 1 Hz) may not be able to temporally extend the thought to such a degree.

One could consequently hypothesize that regions and networks with a high degree of infraslow-frequency fluctuations may be able to temporally extend contents to a much higher degree than regions and networks with low degrees of the same frequency fluctuations. Investigations have indeed shown that the cortical midline structures that are part of the DMN show the highest and strongest degree of infraslow-frequency fluctuations, and sensory regions and networks exhibit a much lower degree of these frequency ranges while showing relatively stronger power in higher frequency ranges (Huang et al., 2016; Lee, Northoff, & Wu, 2014). One may now hypothesize that these temporal features may contribute to the often observed recruitment of cortical midlines structures in spontaneous thoughts and the overlap with the DM (Fox et al., 2015) (see Figure 6.5).



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Figure 6.5. (See Color Insert) Temporal extension of contents into thoughts.



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Figure 6.5. Temporal extension of contents into thoughts.

How can we link such temporal extension to thoughts? Future investigations may want to directly relate the infraslow-frequency fluctuations to the duration of spontaneous thought contents. One would expect that thought contents that last longer show stronger recruitment of infraslow-frequency fluctuations and cortical midlines regions than short-duration thought contents that may implicate higher

frequencies and eventually the sensory regions to a higher degree. Methodologically, one

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may want to ultimately establish spatial and temporal features of the thoughts themselves, including their contents, for instance on the basis of subjective reporting and timing. These spatial and temporal features of the thought contents can then be related to corresponding spatial and temporal features in the brain's spontaneous activity. For instance, self-guided thought, as mainly based on midline regions and their strong infraslow frequencies, may last longer when compared to perceptually derived thought as it involves mainly sensory cortex that shows less power in infraslow frequencies.

“Spatiotemporal Extension” and the “Virtual” Nature of Thoughts

Spatiotemporal extension allows for the content to be extended beyond the discrete point in time and space of its original generation. This constitutes *spatiotemporal continuity* of contents. As based on the preceding evidence, I assume that the degree of (p. 66) spatiotemporal extension and thus the spatiotemporal continuity of thought contents are directly proportional to the degree of functional connectivity and cross-frequency coupling in the brain's spontaneous activity: the higher the degrees of functional connectivity and cross-frequency coupling, the higher the degree to which contents and their single discrete points in time and space can be spatiotemporally extended and thus constituted in a spatiotemporally continuous way, and the more we will perceive the respective thought content to be spatially and temporally continuous (rather than discrete).

This description, however, applies merely to the extension of contents into space and time of the brain's spontaneous activity. How and why are these contents transformed into thoughts? By virtue of its spatial and temporal features, spontaneous activity may extend content beyond its single discrete point in time and space. That means that the single content becomes detached from its original origin, including its discrete point in time and space, at the same time that it becomes linked to other contents.

Conceived in spatiotemporal terms, this means that the contents become by default “virtual” within the spatiotemporal structure of the spontaneous activity. “Virtual” means that the content can no longer be located at one particular discrete point in time and space within the spontaneous activity. Instead, due to its spatiotemporal extension, the content occupies several discrete points in time and space, thus being stochastically distributed across different regions/networks and frequencies in the brain's spontaneous activity. In that sense, the concept of “virtual” can be more or less equated with being distributed: task-unrelated thoughts and their contents are spatiotemporal distributed.

However, there is more to task-unrelated thoughts. They constitute relations between different points in time and space (i.e., relational time and space) that as such can no longer be observed by us (in a direct way). Such a relational component allows the simulation of objects, events, or scenes (in a more or less realistic way); the constitution of such relational time and space (as distinguished from mere observational time and space) with subsequent simulation allows the transformation of mere content into task-

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unrelated thought. Based on its spatiotemporally relational and simulative nature, I describe task-unrelated thought as “virtual.” How can we explain the virtual nature of task-unrelated thought in more detail? The contents become stochastically and virtually extended in a three-dimensional way across different points in time and space within the spontaneous activity's spatiotemporal structure. Due to spatiotemporal extension into the three-dimensional space of the spatiotemporal structure, the original content becomes distributed and “virtualized.” That, I postulate, is the moment when the mere content transforms into a thought: the higher the content's degree of stochastic spatiotemporal extension within the three-dimensional spatiotemporal structure of the brain's spontaneous activity, the more virtual the content will become in spatial and temporal terms, and the more likely the content will be transformed into a thought.

Based on this assumption, one may want to suggest the following neuronal hypotheses. The stronger the degree of functional connectivity of regions such as cortical midline structures with the strongest infraslow-frequency fluctuations, the higher the degree to which contents are transformed into thoughts and the longer those thoughts should last. This is supported by an example from psychiatry where patients with depression show an abnormally high degree of functional connectivity of cortical midline structures, while they suffer from excessive thoughts with abnormally long duration—described as rumination (Berman et al., 2011; Kaiser et al., 2015; Northoff, 2015a, 2015b, 2015c, 2015d; Northoff & Sibille, 2014; see Hamilton et al., 2015, for an excellent overview).

Moreover, the degree to which contents are transformed into thoughts should also be related to the degree of cross-frequency coupling. The higher the degree of cross-frequency coupling, especially between infraslow and higher frequency fluctuations, the more likely it is that contents will be transformed into thoughts. One would consequently expect increased cross-frequency coupling in disorders like depression where patients suffer from increased amounts of thoughts, as in depressive rumination (Northoff, 2015a). In contrast, a decrease in cross-frequency coupling, observed for instance in schizophrenia, should then go along with a blockade of and decrease in thoughts, which are frequently observed in these patients (Northoff, 2015c, 2015d; Northoff & Duncan, 2016).

Spatiotemporal extension not only allows for extending particular contents in stochastic or virtual time and space, but also may link different contents. This should result in a continuous flow of thoughts, a “stream of thoughts” (as analogous to James's “stream of consciousness”) with both internally and externally directed contents (Smallwood & Schooler, 2015). One would assume that such (p. 67) a “stream of thoughts” recruits the entire spontaneous activity's spatiotemporal structure and its full extension. Again, especially the infraslow-frequency fluctuations with their long cycle durations may be central in linking different contents and consequently thoughts. By being linked to other contents, the single content becomes even more stochastically virtual and extended beyond itself, which makes its transformation into a thought even more likely. Ideally, one would then want to investigate the spatiotemporal dynamics of the spontaneous activity as whole (see Fox et al., 2015, for a discussion of this issue). In that case, one would want

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to apply, for instance, measures of global temporal structure like power law spectrum and exponent to characterize both the spontaneous activity's spatiotemporal structure (Huang et al., 2016) and the time series of the spontaneous thoughts. Higher degrees of temporal structure in the spontaneous activity should then lead to a higher probability of contents being transformed into thoughts.

Are the transformation of content into thought and the supposed involvement of the entire brain accompanied by consciousness? This is a separate question, which I leave open here. The Global Neuronal Workspace Theory (GNWT) by Dehaene (Dehaene & Changeux, 2011; Dehaene et al., 2014) postulates that the degree of neuronal globalization in spatial (i.e., prefrontal and parietal cortex) and temporal (i.e., late potentials like P300) terms is central for eliciting consciousness. How does such *neuronal globalization* compare to *spatiotemporal extension* as postulated here? The GNWT argues that neuronal globalization is necessary to recruit cognitive functions that, in turn, are necessary for consciousness. This is different in the case of spatiotemporal extension. Spatiotemporal extension does not refer to cognitive functions, as in neuronal globalization in the GNWT. Instead, it refers to the degree of spatial and temporal extension of a particular content and its point in time and space prior to and independent of recruiting cognitive functions. The concept of spatiotemporal extension must therefore be distinguished from neuronal globalization and, as one may want to say, *cognitive extension*. In a nutshell, neuronal globalization as in the GNWT is cognitive, while spatiotemporal extension as in the STTT is strictly spatiotemporal rather than cognitive. How much such spatiotemporal extension is related to consciousness remains then to be discussed on separate grounds (Northoff, 2014b).

Conclusion

I here introduced a novel theory of thought, the spatiotemporal theory of thought (STTT). The STTT is primarily a spatiotemporal rather than a cognitive, sensorimotor, or semantic theory of thought. The STTT shifts the focus from the cognitive features of task-unrelated thought to its spatiotemporal features. The spatiotemporal features of task-unrelated thought are supposed to provide a common denominator that underlies both content and process. Therefore, STTT may be ideally suited to link and integrate content models and process models of task-unrelated thought.

Moreover, the STTT is strongly based on the brain and the spatiotemporal structure of its spontaneous activity. Unlike in cognitive theories, the STTT focuses not so much on the contents of thought, but rather on the temporal and spatial features of those contents and how they are integrated into each other on the basis of their spatial and temporal features. I directly link the spatial and temporal features of task-unrelated thought to the spatiotemporal structure of the brain's spontaneous activity, including its concrete physiological mechanisms, such as functional connectivity and cross-frequency coupling.

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Future psychological investigation may want to characterize our thoughts not only in terms of their contents, but also with respect to their stochastically based spatial and temporal features, such as their spatial and temporal continuity (i.e., extension in our experience). Tackled in this way, thoughts and their contents are understood as stochastically based distributed and virtual three-dimensional spatiotemporal structures that are continuously sculpted and shaped by the spontaneous activity's spatiotemporal structure: the more the contents are spatiotemporally extended by the stochastically based spatial and temporal features of the spontaneous activity's spatiotemporal structure, the more distributed and virtual they become, and the more likely it is that they will be transformed into thoughts.

Such a spatiotemporal approach to thoughts can be tested experimentally on both neuronal and perceptual-experiential levels. Neuronally, one may want to focus not so much on the neuronal correlates of specific contents like sensorimotor, affective, and cognitive contents, but rather on those neuronal mechanisms related to the respectively underlying spatial and temporal features of thought contents. Correspondingly, one may also sample the spatial and temporal features underlying the contents, in addition to the contents themselves, (p. 68) on the perceptual-experiential level. This allows us to examine the relationship between the spatiotemporal features of the thoughts and their contents, on the one hand, to different aspects of the brain and its spontaneous activity, on the other hand. The STTT postulates spatiotemporal correspondence (and, even stronger, spatiotemporal isomorphism; Fell, 2004) of the spatial and temporal features at the neuronal level with those at the perceptual-experiential level of thoughts.

Finally, it should be mentioned that I have left out a number of dimensions of thought. For instance, our thoughts show a higher or lower degree of personal relevance or self-relatedness. Our thoughts are frequently highly personal and thus individual in nature. This raises the question of the relationship between thoughts and the self, with the latter expanding to the former. This expansion has been referred to as "self-expansion" (Sui & Humphreys, 2015), and has been shown to be closely linked to the cortical midline structures (Northoff, 2015, 2016, 2017; Northoff et al., 2006). Moreover, we can become consciously aware of our thoughts. This raises the question of the relationship between thoughts and consciousness. Both spatiotemporal integration and extension occur automatically and therefore remain unconscious. One would consequently need to search for an additional mechanism by means of which awareness or consciousness is assigned to the thoughts. These questions remain important subjects for future research (Northoff, 2014a, 2014b).

Acknowledgments

I thank Wendy Carter for sorting the references. Financial contributions to GN are acknowledged from the Canada Research Chair program (CRC), the Canadian Institute of

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Health Research (CIHR), the Michael Smith Foundation, and the National Science Foundation of China.

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