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Slow cortical potentials and “inner time consciousness” — A neuro-phenomenal hypothesis about the “width of present”

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ABSTRACT

William James postulated a “stream of consciousness” that presupposes temporal continuity. The neuronal mechanisms underlying the construction of such temporal continuity remain unclear, however, in my contribution, I propose a neuro-phenomenal hypothesis that is based on slow cortical potentials and their extension of the present moment as described in the phenomenal term of “width of present”. More specifically, I focus on the way the brain's neural activity needs to be encoded in order to make possible the “stream of consciousness.” This leads us again to the low-frequency fluctuations of the brain's neural activity and more specifically to slow cortical potentials (SCPs). Due to their long phase duration as low-frequency fluctuations, SCPs can integrate different stimuli and their associated neural activity from different regions in one converging region. Such integration may be central for consciousness to occur, as it was recently postulated by He and Raichle. They leave open, however, the question of the exact neuronal mechanisms, like the encoding strategy, that make possible the association of the otherwise purely neuronal SCP with consciousness and its phenomenal features. I hypothesize that SCPs allow for linking and connecting different discrete points in physical time by encoding their statistically based temporal differences rather than the single discrete time points by themselves. This presupposes difference-based coding rather than stimulus-based coding. The encoding of such statistically based temporal differences makes it possible to “go beyond” the merely physical features of the stimuli; that is, their single discrete time points and their conduction delays (as related to their neural processing in the brain). This, in turn, makes possible the constitution of “local temporal continuity” of neural activity in one particular region. The concept of “local temporal continuity” signifies the linkage and integration of different discrete time points into one neural activity in a particular region. How does such local temporal continuity predispose the experience of time in consciousness? For that, I turn to phenomenological philosopher Edmund Husserl and his description of what he calls “inner time consciousness” (Husserl and Brough, 1990). One hallmark of humans’ “inner time consciousness” is that we experience events and objects in succession and duration in our consciousness; according to Husserl, this amounts to what he calls the “width of [the] present.” The concept of the width of present describes the extension of the present beyond the single discrete time point, such as, for instance, when we perceive different tones as a melody. I now hypothesize the degree of the width of present to be directly dependent upon and thus predisposed by the degree of the temporal differences between two (or more) discrete time points as they are encoded into neural activity. I therefore conclude that the SCPs and their encoding of neural activity in terms of temporal differences must be regarded a neural predisposition of consciousness (NPC) as distinguished from a neural correlate of consciousness (NCC).

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1. Introduction

What is consciousness? This is a question that is currently debated hotly by both philosophy and neuroscience in recent years (see Northoff, 2014a, b for an overview). Most generally put, consciousness describes the ability to subjectively experience. One central

component to such subjective experience is the continuity of time which William James presupposed in his concept of “stream of consciousness”. Central to the constitution of the “stream of consciousness” is the linkage and integration between different discrete points in physical time in the resulting neural activity that, as I suggested, results in temporal continuity.

How, though, is such an integration between different discrete points in physical time possible in neural activity? This is the question for the neural mechanisms underlying the construction of such temporal continuity. While there have been much recent investigations about the neural correlates of the perception and cognition of time in

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both neuroscience and philosophy (see for instance Wittmann, 2013; Wittmann et al., 2011; Wassermann et al., 2011; Craig, 2009, 2010a,b, c, 2011; Dainton, 2010; James, 1890; Lloyd, 2012; Seth et al., 2011; van Wassenhove et al., 2011; Wittmann, 2009; Wittmann et al., 2010), the neural mechanisms underlying the construction of such temporal continuity remain unclear.

The focus in the present paper is to develop a neuro-phenomenal hypothesis about the construction of temporal continuity and its phenomenal manifestation in consciousness. Since it combines direct linkage between both neuronal mechanisms and phenomenal features, I speak of neuro-phenomenal hypothesis that as such must be distinguished from neuro-cognitive, neuro-perceptual/sensory, neuro-affective, and neuro-informational hypotheses of consciousness in general (see Northoff, 2014a).

More specifically, I here hypothesize that low-frequency fluctuations, and more specifically the long phase duration and their large number of different discrete time points, may be central here. This explains the inclusion of different discrete time points, but it leaves open the question of how the different discrete time points within one phase duration are linked and integrated into each other. There must be a special neuronal mechanism and, more specifically, a particular coding strategy at work in how the brain encodes its neural activity during the long phase durations of the low-frequency fluctuations. This is the focus in the present paper. I will postulate that the temporal integration between different discrete points in physical time, such as within one phase duration, is made possible only by encoding temporal differences into neural activity thus presupposing what can be described as difference-based coding (as distinguished from stimulus-based coding) (see Northoff, 2014b). Most importantly, I will suggest that such difference-based coding predisposes not only the temporal continuity of neural activity, but also temporal integration on the phenomenal level of consciousness. In order to illustrate this in neuroscientific (and later in neurophenomenal) detail, I now turn to neuroscientist B. J. He and her paper with ME. Raichle from 2009 (He and Raichle, 2009).

2. Neuronal findings: intrinsic activity and slow cortical potentials

He et al. (He et al., 2008) investigated neurosurgical patients electrophysiologically with electroencephalography (EEG) in three different states of consciousness sequentially: wakefulness, slow wave sleep (SWS), and rapid eye movement sleep (REM). The data were low-pass filtered at <0.5 Hz to yield low-frequency fluctuations and, more specifically, spontaneous slow cortical potentials (SCPs). The correlation of SCPs across all electrodes was calculated by computing Pearson correlation coefficients between the SCPs in a seed electrode and all other electrodes.

What are SCPs? They are specific electrophysiological potentials in the low-frequency range (<0.5 Hz) and can thus be regarded as a form of low-frequency fluctuation (see Van Someren et al., 2011; Riedner et al., 2011; Mascetti et al., 2011 for excellent overviews). By correlating the SCP across different electrodes, she obtained correlation maps of SCP, signifying the occurrence of the SCP in the whole brain.

In addition, the patients also underwent resting-state functional magnetic resonance imaging (fMRI) to measure spontaneous resting-state activity and its low-frequency fluctuations. All voxels observed in fMRI that centered on a specific electrode (as the seed electrodes) were then correlated with those associated with the respective other electrodes. This yielded relationships between the SCPs' correlation maps as generated in EEG and the spontaneous BOLD correlation maps from the fMRI.

How were now the fMRI-BOLD signals related to the SCPs during the three different states of consciousness? SCP–fMRI correlation was observed in all three states: wakefulness, SWS, and REM. This distinguished the SCPs from higher frequency oscillations as the gamma oscillations (20–40 Hz). Unlike the SCP, the gamma oscillations only correlated with the BOLD signal in the awake state and

during REM sleep, but not during SWS, that is, NREM sleep, where consciousness is lost.

This let the author propose that the SCPs may be a very fundamental feature of neural activity. The SCPs as low-frequency fluctuations of neural activity may reflect the intrinsic organization of the brain's neural activity independently of its kind of neural activity, that is, resting-state or stimulus-induced activity (see also He et al., 2010; Van Someren et al., 2011; Riedner et al., 2011; Mascetti et al., 2011).

2.1. Neuronal findings: slow cortical potentials and information integration

How can we determine the SCPs in further physiological detail? Negative shifts in the SCPs are supposed to index increases in cortical excitability. Such changes in cortical excitability have been shown to originate predominantly from synaptic activities at apical dendrites in superficial layers of the cortex where they reflect long-lasting excitatory postsynaptic potentials (EPSPs). In short, SCPs are closely related to the EPSPs in the superficial layers (layers 1 and 2) in the cortex.

Where do the superficial layers and thus the EPSPs get their input from? They get a major input from the lower layers of the cortex, layers 4, 5, and 6, that receive plenty of inputs from the thalamus (and other subcortical regions) leading subsequently to the excitation of the pyramidal cells, especially in layer 4. In addition to the lower layers' input, the superficial layers 1 and 2 also receive strong inputs from other cortical regions whose afferences terminate directly in layers 1 and 2. These cortico-cortical afferences and their respective neural excitation are then integrated and processed further in the superficial layers' abundant GABAergic inhibitory interneurons.

Let us sketch the pathway of neuronal processing by taking the example of thalamic input. The input from thalamic regions is first processed in deeper layers, layers 4 and 5 and 6, which leads subsequently to the excitation of the here located pyramidal cells. While also producing EPSPs, these deeper cortical signals have less impact on the activity changes in the superficial layers as measured in the SCPs. Besides the pyramidal cells, there are also many interneurons, GABAergic and inhibitory neurons in especially the superficial cortical layers. Due to their rather low amplitude of membrane flow changes, these interneurons do seem to have a minor impact, if at all, on the SCPs in particular and the local field potentials in general.

Taken together, this lets one propose that the SCPs as low-frequency fluctuations are related predominantly to long-lasting depolarization of apical dendrites in superficial cortical layers. Besides the thalamic input, which enters via deeper layers like layers 4 and 5, other long-range intracortical and cortico-cortical connections preferentially terminate in these superficial layers, layers 1 and 2. This means that the SCPs cannot be associated with the information from a single stimulus. Instead, they reflect rather the summation of many stimuli as conveyed by the different connections, intracortically and cortico-cortically, all terminating in the superficial layers.

Based on the connectivity pattern of the superficial layers and the long-lasting depolarization, the EPSPs, the resulting SCPs must reflect the integration of information from different stimuli processed in different cortical regions. This is quite compatible with the earlier reported correlation between the cortico-cortical (e.g., electrode–electrode) correlation maps of both SCP and fMRI signals. The aforementioned results are possible only if signals from different regions as measured in fMRI are integrated into the locally measured SCPs. The BOLD signals of the fMRI result from the integration of neural activity of different regions so that the correlating SCPs, as locally measured, must be related to integration of neural activities from different regions.

2.2. Neuronal findings: slow cortical potentials and consciousness

What do the SCPs as low-frequency fluctuations in the brain's resting state entail for the phenomenal features of consciousness? He and Raichle (He and Raichle, 2009) hypothesize that the SCPs are the neural correlate

of consciousness and are therefore a minimally sufficient neural condition of the contents in consciousness (see the second Introduction for the exact definition of the term “correlate”). More specifically, SCPs carry information from different cortical regions. The slow time scale, the slow frequency character (<0.5 Hz), and the integration of long-range intra- and cortico-cortical connections may allow the SCPs to temporally integrate and synchronize stimuli and thus information processed in different regions (despite the respective conduction delays) and sources.

Following He and Raichle, such integration may well account for the experience of a “unitary and undivided whole” in consciousness. This is supported, according to them, by recent findings from perception, attention, volition, and unconscious states (anesthesia, vegetative state) that all go along with changes in the SCPs and the level of consciousness (see He and Raichle, 2009; see also Riedner et al., 2011; Meissner and Wittmann, 2011 for further empirical support). This may be different, though, in patients with vegetative states where the opposite pattern can be observed with preserved low and infraslow frequencies and reduced high frequencies (see (Fingelkurt and Fingelkurts, 2014) for a recent review of their own and others results). That may suggest that it is the degree of cross-frequency coupling rather than the power of the single frequency band that may be central for making possible a certain level of consciousness.

Let us return to the SCP as slow frequency oscillation. The exact neuronal mechanisms underlying such integration and synchronization of information in SCPs remain unclear. More specifically, He and Raichle leave open the question of the way that the neural activity related to the SCP must be encoded and thus generated in order to allow for the alleged integration and synchronization of the stimuli and their different discrete points in physical time. This will be the focus of my first neuronal hypothesis.

2.2.1. Neuronal hypothesis: slow cortical potentials mediate “double temporal integration”

How does such local integration of transregional activity come about? He and Raichle claim that, due to their broad time window, the SCPs as low-frequency fluctuations are ideal candidates to integrate information from different regions. But how such purely neuronal integration leads to consciousness and its phenomenal features remains unclear. For that, as I claim, we need to go into further detail about the exact neuronal mechanisms of such temporal integration and, more specifically, the way neural activity during the SCP is encoded and thus generated.

What do I mean by “temporal integration”? I will distinguish between two different kinds of temporal information that need to be integrated—the temporal information related to the stimuli themselves, and the temporal information related to the brain's neural processing of the stimuli. This shall be explicated in the following discussion.

First, the temporal information related to stimuli and their different temporal properties must be integrated within the SCPs. More specifically, the stimuli and their respective information conveyed in the cortico-cortical connections are scaled on different discrete points in physical time. For instance, stimulus *a* may occur at time point *x* while stimulus *b* may occur at time point *y*. There are thus different discrete points in physical time associated with the occurrence of the different stimuli that need to be integrated in the superficial layers of the cortex where the SCPs are generated.

Second, different stimuli may be processed in varying degrees in different regions; this may occur closer or further away from the region where they are temporally integrated into an SCP. The differences in distance and regions may imply different biophysical–computational conduction delays between the region processing the stimulus and the one where it is temporally integrated with other stimuli.

For instance, stimulus *a* may be first processed in region *m*, which is closer to the integrating region *i* than the region *n* where stimulus *b* is processed. This means that the different biophysical–computational conduction delays associated with different stimuli and their respective regions

must also be integrated in the superficial layers where the SCPs are generated. There is consequently a need for what I describe in the following discussion as “double temporal integration”: the different discrete points of the different stimuli's occurrence in physical time need to be integrated in the same way the biophysical–computational conduction delays related to the stimuli's neural processing in the brain require integration.

Accordingly, the different discrete points in physical time related to both stimuli and the brain's conduction delays need to be integrated in neural activity. One may consecutively want to speak of “double temporal integration”: the concept of “double temporal integration” describes the need to integrate both the stimuli's different discrete points in their occurrence in physical time and the biophysical–computational conduction delays during their neural processing in the brain.

2.2.2. Neuronal hypothesis: difference-based coding mediates “double temporal integration”

How is such “double temporal integration” possible? I propose that the encoding of neural activity in terms of temporal differences between different discrete points in physical time as related to both the stimuli and the biophysical–computational conduction delays may be central here. In short, I suggest difference-based coding to be a necessary condition and thus a neural predisposition of “double temporal integration” in the brain's neural activity. If, in contrast, there were stimulus- rather than difference-based coding, such “double temporal integration” in neural activity would remain impossible.

How can we describe difference-based coding in the here presupposed temporal context in more detail? I hypothesize that difference-based coding (as distinguished from stimulus-based coding) allows for encoding the temporal differences between different stimuli's occurrence at different discrete time points (as it is symbolically rather than mathematically expressed by letters and numbers in the following).

Let us start with the encoding of the temporal information related to the stimulus itself. What is encoded into neural activity is not the time point *x* of the stimulus *a* and the time point (*x* + 1) of the stimulus *b* but rather the temporal difference between the time points *x* and (*x* + 1). Hence, the subsequently resulting neural activity neither reflects the time point *x* nor (*x* + 1) but rather their temporal difference or integral, for example, $x - (x + 1)$.

This means that the neural activity does not correspond to (nor represent, as the philosophers may want to say) the discrete time point of the single stimulus by itself in an isolated and independent way. Instead, the neural activity may rather mirror the temporal difference between two (or more) discrete time points associated with different (or the same) stimuli across different discrete points in physical time. The single stimulus is thus no longer encoded into neural activity as isolated and independent from other stimuli as in stimulus-based coding. Instead, it is encoded into neural activity in relative temporal difference to other stimuli and thus in a relational and interdependent way.

How about the temporal information from the brain's biophysical–computational conduction delays? The same is supposed to apply for the temporal differences resulting from the brain's transregional processing, that is, the conduction delays, during the neural processing of stimuli *a* and *b* in regions *m* and *n* to region *i*: what is encoded and integrated in the region yielding the SCPs may be not so much the conduction delay from region *m* to region *i* and the one from region *n* to region *i* (as one would suggest in the case of stimulus-based coding).

Instead, what is encoded into the neural activity of region *i*, the one that yields the SCPs, may be the difference in conduction delays (that is, $[(m - i) - (n - i)]$), rather than the conduction delays themselves (that is, from *m* to *i* and from *n* to *i*). Accordingly, I propose difference-based coding to apply also to the neural processing of the biophysical–computational conduction delays related to the brain's neural processing of stimuli.

Taken together, both the different stimuli's different discrete points in physical time and their different biophysical–computational conduction delays in their associated neural processing are proposed to be encoded into neural activity in terms of temporal differences. Such

encoding in terms of temporal differences makes it possible to integrate the different discrete points in time related to both the different stimuli and the different conduction delays. I thus hypothesize difference-based coding rather than stimulus-based coding to predispose or make possible the temporal integration of both the different stimuli's time points and the different conduction delays in the brain's neural activity.

2.2.3. Neuronal hypothesis: "double temporal integration" and difference-based coding as intrinsic features of the Brain's neural activity

We have focused so far on the temporal integration of the different discrete time points related to both stimuli and conduction delays. This, though, has left open the question of how stimuli and conduction delays as different kinds of information with different origins can be temporally linked and integrated with each other.

How are stimuli and conduction delays temporally integrated in the neural activity of region i ? The encoding of both stimuli and conduction delays in terms of temporal differences into neural activity provides a common format for both, a temporal difference. This allows them to be integrated despite their occurrence at different discrete points in physical time.

The neural activity of region i , the integrating region that yields the SCPs, may consecutively be characterized by "double temporal integration" as signified by $([x - (x + 1)] - [(m - i) - (n - i)])$. Accordingly, the encoding of neural activity in terms of temporal differences allows the brain's neural activity to integrate the different kinds of information related to stimuli and conduction delays into one common format, temporal differences; this in turn makes possible their integration into one neural activity, the neural activity of the region that yields the SCP.

One may now be inclined to object that this may well hold for stimulus-induced activity as, for instance, the contingent negative variation (CNV) that can be characterized as stimulus-related SCPs while it may not apply to spontaneous SCPs generated intrinsically in the resting state itself. Why? Because the resting state cannot be simply characterized by stimuli but rather the absence of stimuli. One would thus wonder why there are SCPs at all in the resting state characterizing the brain's intrinsic activity.

This however, does not hold. Even the resting state itself receives plenty of input from stimuli generated intrinsically in the brain itself, the neuronal stimuli as I described them. In addition, the resting state receives continuous interoceptive stimuli from the body and the unspecific exteroceptive sensory stimuli from the environment. And very much like specific exteroceptive stimuli in the case of the CNV, these different stimuli—that is, their distinct time points and processing times—need to undergo "double temporal integration."

I consequently hypothesize that the spontaneous SCPs, as, for instance, observed by He et al. (He et al., 2008) (and others like (Van Someren et al., 2011; Riedner et al., 2011; Mascetti et al., 2011)), can be traced back to the "double temporal integration" during the encoding of the various stimuli in terms of temporal differences into neural activity during the resting state. This means that difference-based coding and "double temporal integration" operate continuously during both resting-state and stimulus-induced activity.

Both resting state and stimulus-induced activity must therefore be regarded as intrinsic features of the brain's operation, meaning that the brain cannot avoid encoding any kind of its neural activity in terms of difference-based coding and subsequent "double temporal integration." Accordingly, I postulate that difference-based coding and "double temporal integration" are necessary and therefore unavoidable features of the brain's neural activity in general including both resting state and stimulus-induced activity.

2.2.4. Neuronal hypothesis: encoding of the Stimuli's natural statistics predisposes neural activity to "going beyond" the single stimulus

How is the alleged encoding of temporal differences into the brain's neural activity, that is, difference-based coding, manifest in the phenomenal features of consciousness? Let us consider what

happens in difference-based coding. By encoding differences between different discrete points in physical time (and conduction delays) rather than the actual discrete time points themselves, the purely physical characterization of the single stimuli, for example, their discrete points in physical time and their respective conduction delays, is resolved into a difference, that is, a temporal difference. Hence, the encoding of the stimuli (and conduction delays) in terms of temporal differences allows for "going beyond" the single stimuli's physical features, that is, their different discrete points in physical time and their conduction delay.

What exactly do I mean by "going beyond"? By encoding the single stimuli's discrete points in physical time in relation to those of other stimuli, the resulting neural activity no longer reflects (*represents* as the philosophers may want to say) exclusively the single stimulus itself. Instead, the resulting neural activity contains some information about the same stimulus at other discrete points in physical time and/or other stimuli and their specific time points. The resulting neural activity thus "goes beyond" the single stimulus itself and its particular discrete point in time.

This means that the stimuli's distribution across the different discrete points in physical time and thus their "temporal statistics" is encoded into the brain's neural activity. Rather than reflecting the single stimulus itself, neural activity encodes the stimuli "statistical frequency distribution that is the stimuli's natural statistics" or more specifically their "temporal statistics" (see Northoff, 2013b for details). Accordingly, due to its encoding of the stimuli's "natural statistics," the neural activity "goes beyond" the single stimulus itself (see later for more details on the "going beyond").

2.2.5. Neuronal hypothesis: different degrees of difference-based coding during the encoding of neural activity

How can we further specify the encoding of the stimuli's "natural statistics" with regard to the here-discussed "double temporal integration"? Since it concerns the encoding of the stimuli's and their respective conduction delays' different discrete points in physical time, one may want to speak of "temporal statistics." The concept of temporal statistics describes the distribution and thus the frequency of different discrete points of time across physical time and their subsequent encoding into the brain's neural activity.

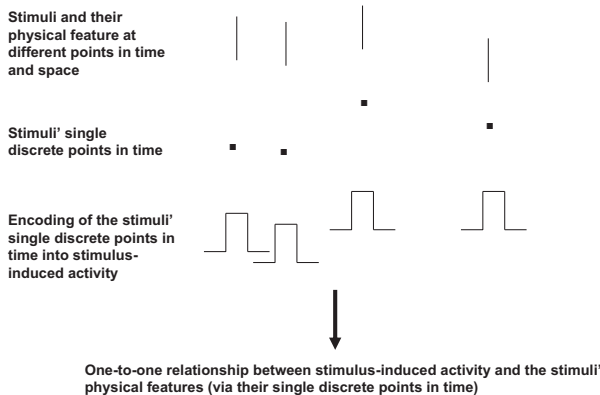
By encoding the stimuli's and their conduction delays' temporal statistics, the single stimulus and its respective conduction delays are encoded relative to the occurrence of itself and other stimuli at the same or different discrete points in physical time. This means that the single stimulus's physical features are no longer encoded as such, that is in an isolated and independent way: the single stimulus's physical features concern its specific discrete point in time and its specific conduction delay.

If these physical features are now no longer encoded in an isolated and independent way, the resulting neural activity cannot be based exclusively on the stimulus's physical features themselves. Instead of the stimuli's physical features themselves, their temporal relations, that is, temporal differences, and thus their temporal statistics are encoded into neural activity. What is encoded into neural activity is thus no longer stimulus and physically based but rather difference and statistically based (see Fig. A.1 and A.2).

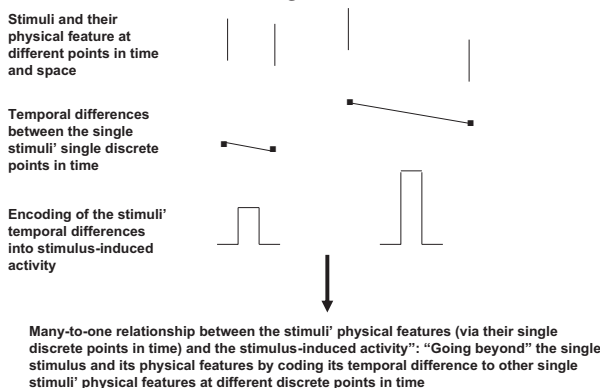
One should notice, however, that the distinction between physically and statistically based encoding strategies does not obey the law of all or nothing: either physically based encoding to 100% or statistically based encoding to 100%. Instead, there is rather a more-or-less distinction with a reciprocal balance between the possible degrees of physically and statistically based encoding and thus between stimulus- and difference-based coding: the more the stimuli's different discrete points in physical time are encoded in terms of temporal differences, the more this balance will be shifted toward the statistically based pole; that is, difference-based coding.

How will the balance be shifted in the converse case of increased encoding of the stimuli's discrete points in physical time? Most likely, the balance will be tilted toward the physically based pole; that is, stimulus-based coding. One may consequently propose a continuum of different possible degrees of statistically based encoding, or difference-based coding, that may be reciprocally related to the possible degrees of physically based encoding and thus stimulus-based coding (see Fig. A.3).

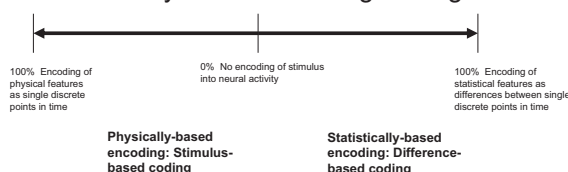
A.1 Physically-based coding strategy: Stimulus-based coding



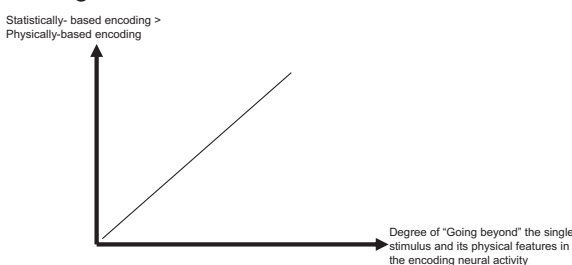
A.2 Statistically-based coding strategy: Difference-based coding



A.3 Reciprocal balance between physically- and statistically-based encoding strategies



A.4 Encoding strategies and the "Going beyond" the single stimulus



2.2.6. Neuronal hypothesis: difference-based coding predisposes neural activity to "going beyond" the single stimulus

Such statistically based encoding of the stimulus in relation to itself and others across different discrete points in physical time implies that the resulting neural activity "goes beyond" the single stimulus's physical features. The physical features of the single stimulus are somehow preserved in the encoded neural activity, not as isolated and independent features but rather as relative to the ones of the same or other stimuli across different discrete points in physical time.

To put the same idea in a different way: The single stimulus's physical features are not lost in the encoded neural activity but rather put in the wider context of the same and other stimuli's physical features occurring at the same and other discrete points in time. Accordingly, the encoded neural activity can be characterized by what I call "going beyond" in the following.

What does "going beyond" mean? Going beyond means that the encoded neural activity includes the physical features of the stimuli themselves, though in a wider way in relative difference from other stimuli by applying a statistically based rather than physically based encoding strategy. The neural activity induced by a single stimulus thus contains more information than the one related to that particular stimulus itself; the encoded neural activity thus "goes beyond" the single stimulus and its temporal (and spatial) information.

Such going beyond the encoded neural activity is well reflected in the following quote by Buzsaki (Buzsaki, 2006, 275): "Because of the additive contribution of the brain, the behavior of a neuron or local network does not faithfully reflect the physical features of the input." What Buzsaki describes as the "additive contribution of the brain" may be closely related to the brain's application of a particular encoding strategy—difference-based and statistically based encoding, as distinguished from stimulus-based and physically based encoding.

How does such an encoding strategy lead to what Buzsaki describes as "additive contribution of the brain"? Rather than encoding the stimuli's discrete points in time, the brain prefers to encode their temporal differences across different discrete points in physical time into its neural activity. This adds something to the single stimulus itself; namely, that the resulting neural activity "goes beyond" the single stimulus itself by encoding the single stimulus's temporal relation to itself and others across time.

Taken all together, this leads me to suggest the following hypothesis. I propose the degree of the going beyond to be directly dependent upon the balance between statistically and physically based encoding strategies: the more the balance tilts toward statistically based

Fig. A. Different encoding strategies. (1) Physically-based coding strategy: stimulus-based coding. This figure shows the strategy of physically-based encoding. Here the stimuli including their physical features are encoded into neural activity in orientation on their different single discrete points in time (and space). There is thus one-to-one correspondence between the stimuli' discrete points in time and the number of stimulus-induced activities. The stimulus-induced activity thus corresponds in a one-to-one way to the stimulus, its physical features and its single discrete point in time. Therefore, the physically-based encoding strategy can be described as stimulus-based coding. (2) Statistically-based coding strategy: difference-based coding. This is different in statistically-based encoding. Here, the temporal differences between the stimuli's different discrete points in time are encoded into neural activity. Depending on the degree of temporal difference, the resulting stimulus-induced activity will vary in its degree. The encoding of neural activity depends here no longer on the single stimulus itself and its discrete point in time but rather on the occurrence of stimuli across time and thus their statistical frequency distribution. Hence the name statistically-based. Since that is possible only on the basis of encoding temporal difference, one can speak of difference-based coding. (3) Reciprocal balance between physically- and statistically-based encoding strategies. The figure depicts the relationship between physically-based and statistically-based encoding strategies. There is a balance between both with increases in the degree of the one going along with decreases in the respective other. (4) Encoding strategies and the 'going beyond' the single stimulus. The figure shows the relationship between the different encoding strategies and the degree of, 'going beyond' the single stimulus. The higher the degree of statistically-based encoding when compared to physically-based encoding (y-axis), the higher the degree to which the resulting stimulus-induced activity, 'goes beyond' the single stimulus and its physical features (x-axis). Hence, I assume that what metaphorically is described by, 'going beyond' has its origin in the balance between physically- and statistically-based coding strategies.

encoding, the more likely the resulting neural activity will go beyond the single stimulus. But the converse case of the balance shifting toward physically based encoding will go along with a reduced degree of going beyond the single stimulus in the resulting neural activity (see Fig. A.4).

We should be careful, however. Buszaki seems to use the concept of “going beyond” in a more theoretical sense as description and interpretation of data rather than providing direct empirical support in correspondingly designed experiments. This is what I will claim in the following.

2.2.7. Neuronal hypothesis: low-frequency fluctuations encode temporal differences

One may now want to object that some stimuli may temporally be so different, due to both different occurrence in time and different conduction delays, that their encoding into neural activity in terms of a temporal difference and thus their temporal integration remains impossible. This may be so because the time span that needs to be integrated may exceed the degree of temporal differences that can possibly be linked and integrated.

This means that the degree of temporal differences that are to be integrated may exceed the length of the phase (or cycle) durations of even the low-frequency fluctuations like the SCP. The temporal difference between the to-be-integrated different discrete points in physical time may simply exceed the one that is available within one phase duration of the SCP. Integration of the different discrete time points and thus the encoding of the stimuli's temporal statistics remain impossible in this case.

What is the ultimate limit, the time window, beyond which different discrete points in time can no longer be encoded in terms of their temporal differences via difference-based coding? I propose that the frequency range of the SCP sets biophysical–computational limits to the degree of temporal differences that can possibly be linked, integrated, and encoded into neural activity. The lower the frequency range of the SCPs, the more temporally extended are their time windows, and the longer are their phase durations.

And the longer the phase durations, the larger the temporal differences between different discrete points in time that can still be encoded in terms of temporal differences into the same neural activity change. Accordingly, longer phase duration predisposes the brain's neural activity to integrate temporally more distant stimuli under the umbrella of the same neural activity change.

Conversely, higher frequency ranges above the SCPs go along with shorter phase durations (for example, time windows) and can therefore encode only smaller temporal differences (see Fig. B.1). This means that temporally more distant stimuli can no longer be linked and integrated into the same neural activity and do instead induce rather two (or more) different neural activity changes.

I propose the following hypothesis: the lower the frequency range in the fluctuations of the neural activity, the larger the temporal differences that can possibly be encoded into neural activity. And the larger temporal differences can be encoded into neural activity, the higher the possible degrees of statistically based encoding (while at the same time decreasing the possible degrees of physically based encoding).

2.2.8. Neuronal hypothesis: from the encoding of temporal differences to local and global temporal continuity of neural activity

Based on these considerations, I propose stronger (and lower) low-frequency fluctuations to go along with higher possible degrees of going beyond, while the possible degree of going beyond may decrease when the higher frequency fluctuations are stronger (see Fig. B.2).

By allowing for the encoding of larger temporal differences in the low-frequency fluctuations' longer phase durations, the different discrete points in physical time become linked and connected to each other and thus integrated. The physically based temporal discontinuity of the stimuli themselves becomes consequently superseded by their

processing in terms of the statistically based temporal continuity in the brain's neural activity.

Stronger degrees, that is, power and range, of low-frequency fluctuations should then go along with higher degrees of statistically based encoding and going beyond, which ultimately leads to higher degrees of temporal continuity. Accordingly, I propose the possible degree of temporal continuity of neural activity to be directly dependent upon the range and power of low-frequency fluctuations and the degree of difference-based and statistically based encoding (see Fig. B.3 and 4).

In sum, I propose that “temporal continuity of neural activity” refers to the difference-based and statistically based temporal integration between the different stimuli's different discrete points in physical time during their encoding into the brain's neural activity. Hence, I regard the concept of temporal continuity to be a purely neuronal concept. As such, it is based on the specific encoding strategy the brain applies to encode and generate its own neural activity during both resting state and stimulus-induced activity when processing the different stimuli (or its own intrinsic activity changes) and their different discrete points in physical time.

Finally, one may also need to further distinguish between “local” and “global” temporal continuity of neural activity. “Local” temporal continuity concerns the statistically based integration between different particular stimuli in a specific region; that is, like the region *i*, and its superficial layers with the consecutive generation of a regionally specific SCP. “Global” temporal continuity, in contrast, refers to the integration of all stimuli the brain encounters across time and its different regions' neural activities as, for instance, manifest in its low-frequency fluctuations. I focused so far only on the neuronal mechanisms of local temporal continuity, which in the further course of this paper shall be complemented in phenomenal regard.

3. Phenomenological excursion: “width of present”

How is the local temporal continuity, as a purely neuronal feature of the brain's intrinsic activity, manifest in experience and thus consciousness? This is the question for the phenomenal manifestation of the neuronal mechanisms underlying the constitution of local temporal continuity. For that, I turn to phenomenological philosophy, which provides excellent descriptions of the experience of time in consciousness.

The chief founder of phenomenological philosophy was E. Husserl, who found successors, among others, in M. Merleau-Ponty, Jean-Paul Sartre, and Martin Heidegger as well as more current ones like Dan Zahavi, Alva Noe, and Evan Thompson (and see also Dainton, 2008). Among other phenomenal features of consciousness like intentionality, they aim to reveal the specific structure of time in experience and thus in consciousness, that is, phenomenal time, as what Husserl (Husserl and Brough, 1990) described as “inner time consciousness.”

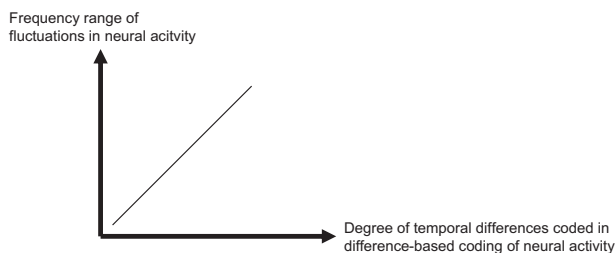
How does Husserl describe “inner time consciousness”? We perceive and experience objects in the world in succession; that is, we perceive a flow of changing objects independent of whether they are stable or changing—there is continuous temporal flux entailing change and thus succession. On the other hand, we perceive and experience fixed and stable objects, objects persisting over time, implying temporal extension and duration. Succession and duration can be considered crucial features of our subjective experience of objects in time and thus of our inner time consciousness. This is captured by William James and his description of a “stream of consciousness” (as well as by Henri Bergson who uses the same term, ‘duration’ to describe the temporal dimension of our subjective experience, i.e., consciousness, as distinguished from the merely physical time; to elaborate this would dent strongly into more philosophical issues, however, which are beyond the scope of this book; see (Northoff, 2014c).

Consider Husserl's (Husserl and Brough, 1990) example of a melody. We experience tones in continuous succession and change with one tone leading to the next tone. At the time, however, we retain the melody with the tones becoming temporally extended, overlapping and

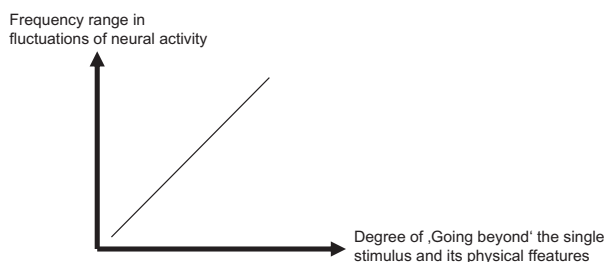
superseding each other. This first and foremost makes possible the experience of a melody while hearing the tones. Succession and duration of the melody imply that our consciousness must encompass more than that which is given right now. This means that the present moment cannot be considered an isolated and punctual moment detached from both the previous and the next moment.

Instead of being isolated and punctual, the present moment may be characterized by what Husserl called the “width of present.” The concept of the width of present describes our ability to experience objects and events in our consciousness for a certain duration while succeeding the previous ones. “Succession” and “duration” do consecutively characterize the width of present in our experience of objects and events in consciousness.

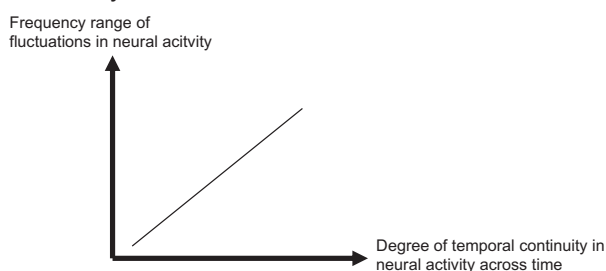
B.1 Difference-based coding and frequency fluctuations of neural activity



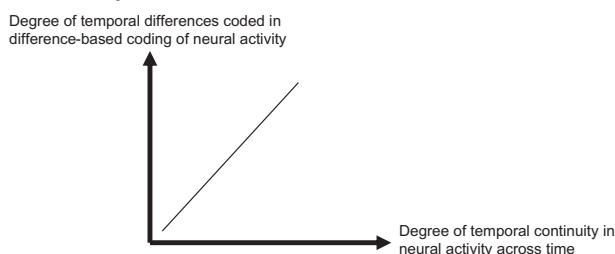
B.2 Frequency fluctuations and local temporal continuity



B.3 Frequency fluctuations and local temporal continuity



B.4 Frequency fluctuations and local temporal continuity



3.1. Phenomenological excursion: “width of present” versus “knife-edge present”

Both succession and duration would remain impossible if the present lacked any “width of present”; the present of objects and events in consciousness would then be characterized as “knife-edge present,” which includes only one single discrete point in time, rather than as the “width of present” and its inclusion of several integrated single discrete points in time.

Let us detail this aspect further. Both succession and duration would be impossible if consciousness provided us only with access to the pure now-points of the objects. The same would hold if our experience were a mere series of unconnected now-points of experiences. This would resemble the loss of pearls when the chain is taken away. In this case we would be confronted with a series of isolated, punctual states without any interconnections. This would make both change, for example, succession, and duration and thus width impossible. Experience and thus consciousness would altogether be impossible in this case.

Let us apply this to our example of the melody. If our consciousness provided us with merely isolated and punctual states, that is, single discrete points in time, experience of a melody would become impossible. The experience of change and succession, which are essential to reveal a melody across the series of different tones, would no longer be given. The experience of a melody would then be replaced by hearing merely isolated and unconnected tones. There would no longer be any succession. In short: no succession, no melody.

At the same time, no tone would be temporally extended anymore in our experience. That would make any overlap and superseding of the tone right now with previous and next tones impossible. Hence, there would be no duration either. Due to the absence of both duration and succession, there would only be a series of right-now tones, which we would no longer be able to link and connect to a melody. In short, we would hear only tones but no melody. There would be no longer any width of present but only knife-edge present.

4. Neurophenomenal hypothesis: encoding of temporal differences into neural activity predisposes “succession” in consciousness

How now does the phenomenal concept of the “width of present” stand in relation to the neuronal concept of local temporal continuity? Let us recall: local temporal continuity described the integration

Fig. B. Difference-based coding and local temporal continuity. (1) Difference-based coding and frequency fluctuations of neural activity. The figure shows the relationship between the frequency range of fluctuations in the neural activity (i.e., the differences in the time span of the phase durations between the highest and the lowest frequency fluctuation) and the degree of temporal differences that can be encoded into neural activity: The larger the degree of frequency ranges in the fluctuations of the neural activity, the larger the degree of temporal differences across the different discrete points in time that can be encoded into neural activity. (2) Frequency fluctuations and local temporal continuity. The figure shows the relationship between the frequency range of fluctuations in the neural activity (i.e., the differences in the time span of the phase durations between the highest and the lowest frequency fluctuation) and the degree to which the resulting stimulus-induced activity can “go beyond” the single stimulus and its physical features: the larger the degree of frequency ranges in the fluctuations of the neural activity, the larger the degree of “going beyond” the single stimulus and its physical features. (3) Frequency fluctuations and local temporal continuity. The figure shows the relationship between the frequency range of fluctuations in the neural activity (i.e., the differences in the time span of the phase durations between the highest and the lowest frequency fluctuation) and the degree of temporal continuity of neural activity: the larger the degree, i.e., power and range, of frequency ranges in the fluctuations of the neural activity, the larger the degree of temporal continuity of neural activity across different discrete points in time. (4) Frequency fluctuations and local temporal continuity. The figure shows the relationship between the degree of difference-based coding and the degree of temporal continuity of neural activity: the larger the degree of difference-based coding (when compared to stimulus-based coding), the larger the degree of temporal continuity of neural activity across different discrete points in time.

(linkage and connection) of different discrete points in physical time into statistically based temporal differences. The phenomenal concept of the width of present in contrast can be characterized by two phenomenal features, succession and duration.

How are neuronal and phenomenal descriptions related to each other? I hypothesize that the encoding of statistically based temporal differences in neural activity predisposes and thus makes possible not only the constitution of temporal continuity of neural activity, but also of both succession and duration, and thus ultimately of the width of present on the phenomenal level of consciousness.

Let me be more specific. By linking and connecting two different discrete points in physical time and their respectively associated tones, the two tones can no longer be segregated from each other in the resulting neural activity. This is so because the tones are encoded into neural activity in terms of their temporal difference from each other that is past and future, tones, so that the neural activity “goes beyond” the single tone itself.

This implies that the tone occurring at a later discrete point in physical time is no longer arbitrarily and purely contingently tied to the previous tone and its particular discrete point in physical time. Instead, the later discrete point in time seems to be specifically tied to the preceding one, as defined by their specific temporal difference as distinguished from others. How is such non-arbitrary and non-contingent linkage between the two different tones possible? By encoding their specific temporal difference, the later tone is put into a relationship to its preceding tone. Most important, this relationship and thus their temporal difference are specific for the relationship between these two tones and may not hold for the same tone's relationship to another tone. This decreases the degree of contingency, or arbitrariness, in their relationship. Therefore, the later tone and its particular discrete point in time cannot avoid anymore standing in a relationship of succession to the previous tone and its particular discrete point in physical time.

Accordingly, by encoding the different tones in terms of their temporal differences, the resulting neural activity “glues” (links and integrates) different tones together and generates a neural relationship between them that supersedes their physical features. Such a neural relationship in turn predisposes and thus makes possible a non-arbitrary and non-contingent relationship between the different tones in our experience; that is, in our consciousness.

How is that related to the degree of the encoding of statistically based temporal differences into neural activity? I propose the following: the more distinct and specific the degree of the encoded temporal difference between earlier and later tones is when compared to other temporal differences (between the same and other tones), the lower the degree of contingency and the higher the degree of succession that can possibly be associated with that particular tone sequence. How is that manifested in phenomenal consciousness? Very simple: we will hear the tones as connected and thus as a melody.

If, conversely, many other tone sequences also encode the same temporal difference into neural activity, their degree of succession will be rather low, while their degree of contingency will be high. In that case, the tones may not be connected to a melody in our consciousness any more. I propose the degree of succession to be directly dependent on the degree of specificity of the temporal difference encoded between two (and more) different discrete time points and their associated stimuli.

For instance, hearing the same or closely related constellation of tones over and over again will become boring so that one no longer hears any melody anymore. This is obviously different if the same constellation or sequence of tones is played only once and preceded and followed by different, more or less unrelated, tones and sequences. In that case, the particular sequence of tones stands out and may therefore be more probably experienced as melody.

4.1. Neurophenomenal hypothesis: encoding of temporal differences into neural activity predisposes “duration” in consciousness

How about the second phenomenal feature of the “width of present,” duration? For that, we now take the perspective of the preceding tone and its particular discrete point in physical time. By being linked to the discrete point in time of the later tone, the single discrete point in physical time associated with the previous tone becomes extended and “stretched” toward the single discrete time point of the later tone.

Thereby, the degree of extension or stretching of the earlier discrete time point may depend on the degree of temporal difference between the two discrete time points: the larger their temporal difference that is encoded into neural activity, the more the previous tone can be extended in its associated neural activity, and the longer its subsequent duration in experience. If, in contrast, the temporal difference from the next tone's discrete time point is rather small, the degree of temporal extension of the preceding tone and its duration will decrease. I thus propose the degree of duration to be directly dependent on the degrees of temporal differences encoded between two (or more) different discrete time points and their associated stimuli.

Taking all this into consideration, I postulate that the width of present is directly related to the possible degree of local temporal continuity of neural activity and, more specifically, to the degree of statistically based temporal differences during the encoding of neural activity. The encoding of larger and more specific statistically based encoded temporal differences into neural activity is supposed to predispose higher degrees of “duration” on a phenomenal level and consequently a more extended width of present in consciousness (see Fig. C.1).

Conversely, the encoding of smaller and less specific statistically based temporal differences into neural activity leads to lower degrees of succession and duration on the phenomenal level of consciousness. This implies a lower degree of the width of present with reduced temporal extension and thus a higher degree of knife-edge present. The less the encoded neural activity “goes beyond” the stimulus's single discrete point in physical time, the more likely the present moment will shrink to a knife-edge present in consciousness (see Fig. C.2–4).

4.2. Neurophenomenal hypothesis: encoding of temporal differences into neural activity determines the level or state of consciousness

I have so far focused only on the temporal characterization of the contents in consciousness, while I neglected its second dimension—the level or state of consciousness (see Introduction, this volume). The “level or state” means the degree of consciousness by itself and thus in terms of what psychologically is described as “arousal” independent of any contents (see Introduction, and Northoff, 2013a, 2013b).

How is my neurophenomenal hypothesis related to the level or state of consciousness? Following the phenomenological philosophers, higher degrees of the width of present should go along with higher degrees of (possible) consciousness. Conversely, this means that lower degrees of the width of present and consecutively higher degrees of the knife-edge present should lead to a decrease in, and ultimately loss of, consciousness.

I consequently claim that disorders of consciousness like the vegetative state and being under anesthesia should show lower degrees of succession and duration with subsequently low degrees of width of present and high degrees of knife-edge present. If so, they should show low degrees of difference-based and statistically based encoding of stimuli, while at the same time exhibiting a high degree of stimulus-based and physically based encoding of the stimuli's single discrete points in time. They should consequently show low degrees of temporal continuity in their neural activity.

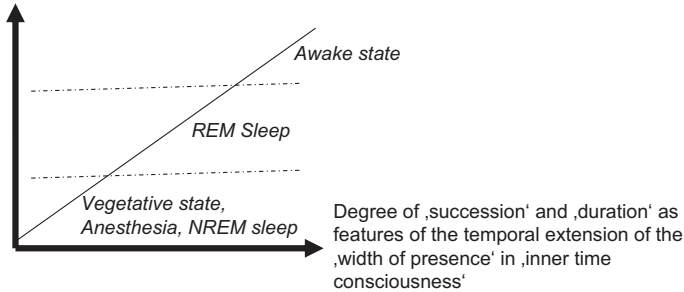
This is exactly what can indeed be observed neuronally in these patients. And that, by definition, goes along with extreme reduction in the level or state of consciousness. Accordingly, the example of disorders of consciousness provides empirical support (albeit indirectly) to my neurophenomenal hypothesis of the relationship between difference-based coding, temporal continuity, and state/level of consciousness.

5. Neuroconceptual remark: do slow cortical potentials process the contents of consciousness?

I started from the SCPs and He and Raichle's assumption of SCPs being central for consciousness. Thereby I shed a more detailed light on the kind of neuronal mechanisms that must occur to predispose

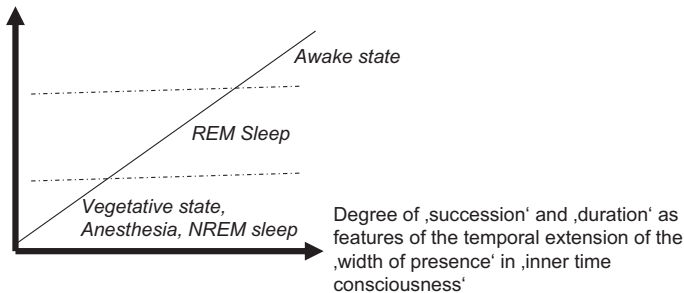
C.1 Difference-based coding and the “width of presence”

Degree of statistically-based temporal differences in difference-based coding of neural activity across different discrete points in time



C.2 Power of low frequency fluctuations and the “width of presence”

Degree of power of the low frequency ranges in the fluctuations of neural activity (like slow cortical potentials)



C.3 Local temporal continuity and the “width of presence”

Degree of local temporal continuities in neural activity across time

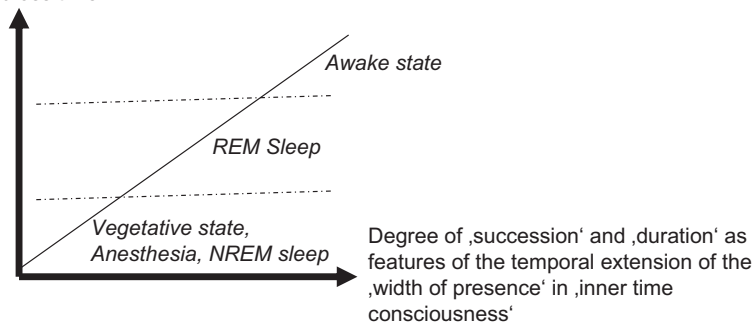


Fig. C. Neuronal mechanisms of the ‘width of presence’. (1) Difference-based coding and the ‘width of presence’. The figure shows the relationship between the degree of temporal differences coded in difference-based coding of neural activity across time and the degree of temporal extension (‘succession’ and ‘duration’) of the ‘width of presence’ in ‘inner time consciousness’, i.e., the latter’s extension beyond the single discrete time point in the present moment: the higher the degree of temporal differences, the more the single discrete time point can be extended beyond the present moment. I assume a low degree of temporal differences being coded in neural activity in vegetative state, anesthesia, and NREM-sleep which thus leads to a low degree of temporal extension in the ‘width of presence’ (and consecutively to reduced ‘inner time consciousness’). (2) Power of low frequency fluctuations and the ‘width of presence’. The figure shows the relationship between the power of low frequency fluctuations and the degree of temporal extension of the ‘width of presence’ in ‘inner time consciousness’, i.e., the latter’s extension beyond the single discrete time point in the present moment: the higher the power of low frequency fluctuations, the more the single discrete time point can be extended beyond the present moment. Presupposing, I assume a low degree of difference-based coding into low frequency power in neural activity in vegetative state, anesthesia, and NREM-sleep which thus leads to a low degree of temporal extension in the ‘width of presence’ (and consecutively reduced ‘inner time consciousness’). (3) Local temporal continuity and the ‘width of presence’. The figure shows the relationship between the degree of local temporal continuity and the degree of temporal extension of the ‘width of presence’ in ‘inner time consciousness’, i.e., the latter’s extension beyond the single discrete time point in the present moment: the higher the degree of local temporal continuity of regional neural activity across different discrete points in time, the more the single discrete time point can be extended beyond the present moment. I assume a low degree of local temporal continuity of regional neural activity in vegetative state, anesthesia, and NREM-sleep which thus leads to a low degree of temporal extension in the ‘width of presence’ (and consecutively to reduced ‘inner time consciousness’).

and thus make possible the SCP's role in consciousness. This let me propose that SCPs and low-frequency fluctuations may indeed have a central role in consciousness, more specifically in constituting the width of present as the phenomenal hallmark of inner time consciousness.

Christoph Koch (Koch, 2009) critically remarks that the hypothesis of SCP as the neural correlate of consciousness cannot account for the specificity of contents in consciousness. The contents surfacing in consciousness are highly specific, and (following his argument) this content specificity must be reflected in the underlying neuronal mechanisms. Each specific phenomenal content should correspond to a specific neuronal mechanism, as is presupposed in the hypothesis of the NCC. The NCC is thus a content-based hypothesis about the neuronal mechanisms of consciousness (see though, Haynes, 2009; de Graaf et al., 2012; Aru et al., 2012; Neisser, 2011a, 2011b; Northoff, 2013b, 2014a; Hohwy, 2012; for recent discussion about the concept of NCC with criticism resembling in part the one voiced here in the Introduction).

Koch argues that the hypothesis of the SCP violates the assumption of content specificity. The content specificity on the phenomenal level does not correspond to a neuronal specificity, since the SCPs are too unspecific. Why? The SCPs integrate information from various sources; therefore, they cannot mediate any specific content and consequently remain unable to account for content specificity on the phenomenal level. The hypothesis of the SCP thus implies a mismatch between specific contents on the phenomenal level and unspecific neuronal mechanisms in the gestalt of the SCP.

Koch's argument targets the SCP hypothesis with regard to the contents of consciousness that are supposed to correspond to certain neuronal states. The contents of consciousness, including their corresponding neuronal activities, are the result of a process that generates and yields them. This process may by itself be mediated by neuronal mechanisms that precede and must therefore be distinguished from those neuronal mechanisms that are directly related to the contents (of consciousness) themselves.

One may consequently need to distinguish between the encoding of neural activity as it is generated for the subsequent processing of any kind of content from the neuronal activities related to the actual processing of a specific content: I suppose the former, the encoding strategy during the generation of neural activity, to predispose consciousness itself independent of any particular contents. In contrast, the latter, the neuronal activities related to the actual processing of specific contents, are the neural correlates of the contents of consciousness rather than of consciousness itself. This shall be more explicated in further detail in the last section.

5.1. Neuroconceptual remark: slow cortical potentials are a neural predisposition of consciousness!

What does this imply for the hypothesis of the SCP as the neural correlate of consciousness? Koch's critic targets the assumption that the SCPs are the neuronal activities that correspond to specific contents in consciousness. However, his rejection of the SCP as the neural correlate of the contents of consciousness does not rule out that they have another yet-to-be-defined role in constituting consciousness itself independent of its contents.

Accordingly, Koch may be right in that the SCPs may not be involved in the neuronal activities underlying the contents of consciousness, while he may be wrong in that they have no role in consciousness at all. I hypothesize that the SCP may be a necessary neural condition that predisposes and makes possible the subsequent association of stimuli and their related contents with consciousness.

How can the SCP a necessary condition of the possible association of stimuli with consciousness? This is possible, as I propose, by the role of the SCP in constituting local temporal continuity as neural predisposition of the width of present on the phenomenal level of consciousness. In short, the SCP and their essential role in "double temporal integration" (see earlier) are a neural predisposition of consciousness.

Accordingly, instead of accounting for the contents themselves, SCPs seem to provide the very formal temporal structure and organization within which the contents (associated with the stimuli and their different discrete time points) are integrated such that they can be associated with consciousness. This means that the SCPs and their "double temporal integration" are necessary in temporally structuring and organizing the brain's neural activity in such a way that the latter can predispose and thus make possible consciousness.

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