It's Not Just About the Contents: Searching for a Neural Correlate of a State of Consciousness

A Commentary on Wolf Singer

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Global gamma band synchronisation is perhaps the most extensively studied candidate for a Neural Correlate of Consciousness (NCC). Yet despite numerous studies confirming its association with consciousness, it seems to be neither sufficient nor necessary for the presence of all subjective experiences. Analysis of gamma synchronisation studies suggests that it is a correlate of the initial binding of expected, attended, task-dependent contents of consciousness, whereas task-irrelevant contents do not seem to require gamma synchronisation. While discovery of such a content-related NCC is a remarkable achievement for the neurophysiological research of consciousness, it does not fully explain some of the fundamental structural properties of consciousness, namely the temporal and spatial integration of all available experiences into a coherent stream of consciousness. As an alternative, instead of focusing solely on the selected contents of consciousness, the neural mechanisms of the fundamental properties of consciousness could be studied by contrasting states of (un)consciousness. Recent research into the states of consciousness suggests that, for instance, informational complexity is a highly sensitive predictor of the presence of consciousness, possibly reflecting background structural properties of the unity of subjective experiences. As a limiting factor, though, such a state-related NCC does not seem to reflect the phenomenal diversity of the contents of consciousness. Arguably, these limitations could be overcome by devising experimental setups that would simultaneously probe the neural correlates of the contents and the state of consciousness.

Keywords
Contents of consciousness | Gamma band synchronisation | Neural correlate of consciousness (NCC) | Neural correlates of consciousness | Nonconscious states | Spatial binding | State of consciousness | Stream of consciousness | Temporal binding | Unconscious states

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1 Introduction

Even though the search for the neural correlates of consciousness is still an unresolved challenge of astonishing complexity (Crick 1994), the continuous efforts to crack the mystery are not expended in vain. Each year brings an increasing number of cognitive neuroscientific studies that reveal yet another piece of the puzzle of the neural basis of subjective experience. However, it often seems that individual findings are too diverse and sparse to form a coherent picture. In addition to the fundamental problem of the binding of conscious experiences (Singer 2001), we increasingly face the problem of how to bind the findings of consciousness-related studies. The present target paper by Prof. Wolf Singer serves such a discovery-binding function, bring-

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ing very diverse findings into a unified picture of how the neural correlates with the subjective.

In an impressively erudite manner, Singer (this collection) integrates a very broad range of anatomical and functional findings of the organisational principles of the brain, concluding that the high-level cognitive functions are supported by densely coupled, recurrent neural networks, interacting under the principles of non-linear dynamics. In the proposed framework, perception is treated as an active process, whose self-organisation is initially determined by genes, and later modified by post-natal development, learning, social interactions, and cultural influences. At the neuronal networks level, high-level integration and communication are achieved through synchronisation of oscillations in different electroencephalography (EEG) frequency bands, the most notable of which is gamma band (>30Hz) synchronisation (Engel et al. 1999). Given that an association between the widespread gamma-band synchronisation and conscious awareness is found in rather different experimental paradigms, such as visual masking (Melloni et al. 2007), binocular rivalry (Doesburg et al. 2009), and attentional blink (Gross et al. 2004), gamma synchronisation is often regarded as the main NCC (Singer this collection).

Yet the candidature of gamma synchronisation as the correlate of consciousness is challenged by some findings from research into the behavioural states of the brain. If gamma-range activity correlates with consciousness, it should diminish when consciousness ceases. Contrary to this, gamma band activity seems to increase rather than decrease in response to certain general anaesthetics, such as ketamine (Steriade et al. 1996). Furthermore, gamma synchronisation seems to be absent in some conscious brain states. For instance, it has been reported that large-scale neocortical gamma-band coherence is virtually absent during rapid eye movement (REM) sleep in cats (Castro et al. 2013), a state typically marked by the most intense dreaming in humans (Hobson et al. 2000) as well as in felids (Jouvet 1979).

The target paper briefly mentions neural mechanisms supporting overall brain states, but dismisses them as modulatory systems that are too general to be considered the NCC (Singer this collection). In the following, I will argue that the relation between the neural mechanisms of the contents and states of consciousness is not straightforward, and that the puzzle of the neural mechanisms of consciousness cannot be completed without studying the neural mechanisms of conscious states.

2 Contents vs. states of consciousness

An important distinction in consciousness research is that between the contents and a state of consciousness (Chalmers 2000). The concept of the contents of consciousness refers to individual subjective experiences that occur in phenomenal consciousness, such as reading a word or hearing birdsong, and as such they are sometimes referred to as the phenomenal contents of consciousness (Revonsuo 2006). Most neural experiments on consciousness, especially in the dominant field of visual awareness studies, are concerned with the neural basis of such specific contents of consciousness, i.e., they select one or two subjective experiences within an overall stream of consciousness. In this type of experiment, participants may be presented with stimuli close to their perceptual threshold (Del Cul et al. 2009) or they may be instructed to observe ambiguous stimuli that may lead to perception of several alternating contents of consciousness (Kornmeier & Bach 2012). The brain responses are then contrasted between trials that differ in awareness of these stimuli. Notably, while participants in such experiments report being unaware of some contents of consciousness, they still maintain awareness of other experiences: such as seeing the edges of a computer screen, hearing the background noise of the Magnetic Resonance Imaging (MRI) scanner, or letting their thoughts wander away from the experimental task. Typically, such experiences are ignored as task-irrelevant, and consequently the so-called “unaware” or “unconscious” trials still bear very rich phenomenology.

Contrary to the selective contents of consciousness, the concept of the state of consciousness refers to an overall pattern of subjective psychological functioning that includes the totality of phenomenal contents of consciousness (Rosenthal 1986; Tart 1972). In addition to the relaxed waking state of consciousness in a healthy volunteer, which could be also regarded as a *baseline state*, altered, unconscious, and non-conscious states can be distinguished. In *altered states of consciousness*, such as dreaming or Lysergic Acid Diethylamide (LSD) psychomodulation, subjective experiences may undergo various perceptual and cognitive alterations, the neural basis of which can be studied by contrasting them with a baseline state of consciousness, e.g., by comparing brain activity before and after hallucinogen intake (Carhart-Harris et al. 2012). Given that there is no widely accepted definition and criterion for an altered state of consciousness (Móró 2010; Revonsuo et al. 2009), a rather common approach is to describe, classify, and study states that are traditionally called *altered*, avoiding a single definition that would grasp the core of all altered states of consciousness (Vaitl et al. 2005).

Contrary to the baseline and altered states of consciousness, unconscious states are deprived of subjective experiences, but they may still maintain the potential to become conscious. For instance, an unconscious state of dreamless sleep may turn into a conscious sleep once a sleeping participant begins to dream (for an alternative interpretation of dreamless seep, see Thompson this collection). Finally, nonconscious states are those completely deprived of a capacity to support phenomenal consciousness, such as an irreversible coma. In clinical neuroscience, the most extensively studied contrast between a pathological altered state of consciousness and an unconscious or non-conscious state is a comparison between minimally conscious and vegetative state patients (Sitt et al. 2014). When states of (un)consciousness are contrasted, neural representations of specific experiences are typically ignored, making it difficult or even impossible to assess the phenomenal specificity of findings, e.g., if participants were aware of particular external stimuli or what internally generated experiences they had. Nevertheless, research into these states may reveal neural patterns that are common to all subjective experiences without individuating them.

It is possible that these two lines of research may eventually reveal rather different, if not independent, NCC systems: a neural correlate of the state of consciousness and a neural correlate of the contents of consciousness (Chalmers 2000). If these exist, any neuroscientific program of consciousness research would be incomplete without searching for a state NCC. Furthermore, even if a separate state NCC did not exist, there is currently no evidence for this, and thus NCC research is incomplete if it does not investigate this possibility. This view is often dismissed on the basis that some of the most plausible candidates for a state NCC, such as the brainstem reticular formation (Merker 2007; Parvizi & Damasio 2001), are rather low-level neural systems, whereas converging evidence shows that consciousness is a cortical process (Singer this collection). Furthermore, it could be argued that a conscious state may be nothing more than the sum of individual experiences, in which case revealing the NCC of specific contents would automatically explain the state NCC. Yet a brief analysis of the fundamental structural properties of consciousness—see the following section—shows that the necessary and sufficient NCC cannot be revealed by an exclusive focus on the contents of consciousness. Notably, the arguments presented in this commentary will be confined to the biological nature of human and animal consciousness, and as such they are not applicable to the problem of machine, extraterrestrial, or silicon-brain consciousness.

3 Unity as the fundamental property of the stream of consciousness

Given that subjective experiences can accompany almost any sensory, cognitive, emotional, and behavioural function of the brain, phenomenal consciousness turns out to be an extremely complex and multi-dimensional process. Nevertheless, introspection shows that despite its qualitative richness, phenomenal consciousness appears to us as a unified and coherent model of the external and internal environment (Bayne 2010; Revonsuo 2006). The continuity in the diversity of subjective experiences is famously referred to as the stream of consciousness (James 1890). This metaphor points to the unification of experiences occurring at different points in time and space, which is achieved through temporal and spatial binding.

At the cognitive level of description, temporal binding, i.e., integration of subjective experiences over time, is realised through the perception of simultaneity, duration, and successiveness (Kiverstein 2010; Pöppel 1997). Perception of simultaneity may integrate several experiences, e.g., seeing a cat and hearing a birdsong in the park, as occurring at the same time. Perception of duration of selected experiences may extend them in time, e.g., the birdsong might seem to last for a certain period of time. Finally, perception of successiveness may signal the end of one temporally-extended experience, and the beginning of another one, e.g., as the cat reaches the bush and the birdsong ceases, we may notice a cone under the bush. Notably, the change does not typically involve all experiences, and as we are aware of some changing contents, some other experiences continue to endure in time, e.g., we still see the same bush. In addition to the timing-specific functions, temporal binding seems to depend on the iconic memory that contains the just-experienced contents of consciousness, and on the anticipation of subsequent ones, forming the temporally-extended phenomenal experience of now, sometimes referred to as the *specious present* (Dainton 2006; Kelly 1882). Temporal extension of subjective experiences have a simple, yet very important and often overlooked implication for NCC research: if there is a single neural mechanism generating phenomenal consciousness, it should be present as long as we are conscious of at least one single content. Given that our experiences do not cease at a fixed rate, i.e., some are shorter and some longer, and that the change does not happen abruptly for all experiences at once, the NCC should persist for the duration of the stream of consciousness. Thus, a temporary-confined correlate of awareness, such as a negative Event Related Potential (ERP) waveform briefly peaking at about 200ms from the onset of visual stimuli (Railo et al. 2011), cannot be a sufficient correlate of consciousness, as awareness of visual contents lasts for a much longer period of time.

Spatial binding, i.e., integration of subjective experiences in space, is realised through several complimentary processes, through which each subjective experience occupies a specific location in relation to other experiences, which is sometimes referred to as *location binding* (Treisman 1996). In the baseline state of consciousness, one experience never occurs in isolation from other experiences; and when some experiences cease, we do not experience emptiness, because other experiences fill in their place. Furthermore, individual experiences are spatially integrated not only with respect to each other in phenomenally external space, but also with respect to the common egocentric reference point (Revonsuo 2006). The reference point is typically located in the phenomenal head or chest, and all other experiences are realised in the space as taking a certain distance and angle from this point. While typical phenomenological analysis of 3D space considers visual and auditory experiences, it has recently been shown that emotions and feelings are also experienced as taking certain location with respect to our body parts (Nummenmaa et al. 2014). For instance, anger is overrepresented in hands and arms when compared to sadness. Arguably, even thoughts, which are often regarded as non-spatial entities (Clarke 1995), are usually experienced as occurring within the head rather than somewhere else. Given that the whole phenomenal space is bound together, the NCC should also represent awareness of the whole space rather than, for instance, selected regions on the computer screen. That is, a promising candidate for an NCC should not cease when a specific experience vanishes as long as the spatial and temporal unity of the stream of consciousness is maintained.

So, what type of neural processes should we be looking for when searching for the NCC? If we take the unity of consciousness seriously, we should be looking for a neural process that steadily represents the whole phenomenal space, and sustains its activity over periods of time longer than the existence of a single experience. Arguably, the neural correlate of unified consciousness cannot be discovered by studying and contrasting only isolated contents of consciousness, as the unity of spatiotemporal interactions simply cannot be derived from solitary experiences. Thus, while continuing to search for the neural mechanisms of the contents of consciousness, the NCC program should be extended by carrying out systematic contrasts between unconscious, baseline, and/or altered states, which would consider the whole stream of consciousness. A possible objection to this proposal is that the unity of consciousness is not fundamental in the strong form of fundamentalism, i.e., some forms of consciousness may still exist despite the possible disintegration of its unity, which seems to happen in states like schizophrenia, sleep onset, or a minimally conscious state. For instance, the stream of consciousness may occasionally undergo a sudden, unpredictable alteration in terms of inner speech and imagery (Noreika et al. 2014). Nevertheless, if one aims to explain the neural mechanisms of normal waking consciousness, the unity thesis, with its NCC-related implications, cannot be ignored. With these considerations in mind, let us examine now the proposal of global gamma synchronisation as the NCC (Singer this collection).

4 Is gamma band synchrony sufficient and necessary for consciousness?

A sufficient and necessary NCC (or perhaps a set of NCCs) should be generic enough to cover all conscious contents and states, and should also be specific enough to cover only conscious contents and states. Notably, gamma synchronisation does not meet the second specificity requirement, as it can be associated with almost any perceptual and cognitive function that depends on the formation of temporary associations of distributed neuronal networks. Among numerous cases, increased gamma-band synchronisation is found to be associated with such tasks as perceptual learning (Gruber et al. 2002), self-paced movement (Pfurtscheller et al. 2003), mental rotation (Bhattacharya et al. 2001), viewing of unpleasant stimuli (Martini et al. 2012), deductive reasoning (Zhang et al. 2014), auditory attention control (Doesburg et al. 2012), face integration (Kottlow et al. 2012), and memory encoding and retrieval (Osipova et al. 2006). Gamma-band synchronisation thus seems be a generic process that contributes to complex cortical computations involved in most if not all of the higher cognitive functions (Fries 2009).

Singer (this collection) proposes that only global, widespread synchronisation of gamma oscillations is associated with consciousness, whereas local, spatially-restricted synchronisation is not necessary related to conscious awareness. This might refute studies reporting local synchrony; however, some of the above-mentioned studies found increased global gamma-synchrony when observing unpleasant stimuli (Martini et al. 2012) or carrying out a mental rotation task (Bhattacharya et al. 2001). It could be argued, though, that gamma synchronisation is present in these experiments as a correlate of task-related subjective experiences, such as awareness of memory retrieval. In fact, even though most of these studies did not even mention consciousness or awareness, their participants were not unconscious, and gamma synchronisation could have been associated with the task-dependent subjective experiences. Yet, this line of reasoning is challenged by the simple fact that participants remained conscious in all contrast conditions throughout the experiments. Why would consciousness-related gamma synchronisation increase in some, but not other conditions? This leads us to the question of what exactly gamma synchrony correlates with in studies that specifically manipulate awareness? Let us take a closer look at two key studies, also examined by Singer (this collection).

Melloni et al. (2007) presented pairs of words and asked participants to report on whether both words were the same. Visibility of the first word was manipulated by adjusting the luminance level of the forward and backward masks, which rendered the words visible only in some of the trials. Global gamma-phase synchronisation between the fronto-centro-parietal electrodes was observed within the 40–182ms time-window after the presentation of the first word only in visible trials, which coincides with the time when conscious perception of the words is expected to emerge. In the latter time-windows, visible words were marked by more localised gamma synchronisation, higher P300 amplitude, and higher amplitude of frontal theta oscillations than invisible words. These findings confirmed that gamma synchronisation is a correlate of visual-semantic awareness, and showed that other electrophysiological processes may also correlate with consciousness.

Doesburg et al. (2009) investigated the role of gamma-phase synchronisation in conscious awareness using a binocular rivalry paradigm, in which a different visual stimulus is presented to each eye. Instead of seeing both stimuli at the same time, people report perceiving only one of the stimuli that continues switching in time. An increase in the gamma-band synchronisation over the fronto-parietal regions was observed in the 600–540ms and 280–220ms time-windows before responses indicating a perceptual switch. Assuming that reaction time was about 250ms, the synchronisation increase coincided with a new percept reaching awareness. Interestingly, gamma synchronisation oscillated at the theta rhythm, suggesting a cross-frequency interaction.

In both of these experiments (Doesburg et al. 2009; Melloni et al. 2007), gamma synchrony peaked around the time when participants began experiencing a new content of consciousness, following which Singer (this collection) draws the well-justified conclusion that gamma synchronisation is associated with a transfer of the new contents into awareness. Given that increased synchronisation may reflect the neural and phenomenal binding required for the fundamental unity of consciousness to emerge, it seems to be an ideal candidate for the NCC. Yet the duration of increased synchronisation is relatively brief and seems to last a much shorter time than the awareness of stimuli. For instance, P300 distinguished visible and invisible words around 300ms post-stimulus, whereas gamma-band synchronisation became local during this time-window (Melloni et al. 2007). Such brevity of synchronisation suggests that it is involved only in the initial binding of the new contents of consciousness, while a further maintenance of these contents is supported by other neural mechanisms, in particular theta oscillations (Doesburg et al. 2009; Melloni et al. 2007; Singer this collection). Given that the global gamma synchronisation correlates with a spatially- and temporally-local change in the stream of consciousness, its association with an overall unity of consciousness is uncertain and, at least currently, it cannot be accounted as the only or even as the major NCC. If it were such, it would not cease as long as the participant were aware of a particular content of consciousness.

Furthermore, gamma synchrony does not seem to increase in response to each of the new contents of consciousness. In each trial, Melloni et al. (2007) presented a series of stimuli, including a fixation cross, a masking noise, a target word, and a blank screen. Each of these stimuli should have entered consciousness, and even when the target word was unreadable, participants should have perceived something, e.g., an unreadable word, incoherent letters, or a flashing mask. However, the global gamma synchronisation increased only in response to perceived visible words, suggesting that it is a correlate of the initial binding of a selected, expected, attended, coherent, task-relevant content of consciousness. As such, in addition to the lack of specificity, gamma synchrony does not seem to be generic enough to cover all the different contents of consciousness, even within the paradigmatic visual modality. Thus, it seems that the global gamma synchronisation is neither necessary not sufficient for consciousness to emerge, as subjective experiences may exist without gamma synchronisation, and even when synchronisation is involved in the generation of awareness, other neural processes are needed to maintain its presence.

As discussed in the previous section, the unity of consciousness emerges from the interaction of all experiences available at a time. Gamma synchronisation cannot account for the unity of a state of consciousness, simply because it is involved only in the generation of new task-dependent contents, and it does not seem to bind these contents within the broader stream of consciousness. Arguably, instead of focusing on selected stimuli, we may be able to detect the neural correlates of the unity of consciousness by contrasting states of consciousness with unconsciousness, since such a contrast would consider the whole stream of phenomenal contents, including their structural unity.

5 Studying the contents and states of consciousness: Let's probe them together!

Perhaps the most powerful contrast conditions for studying a neural correlate of a state of consciousness are comparisons between wakefulness and slow-wave sleep, as well as between wakefulness and general anaesthesia. A notable clinical contrast is a comparison between vegetative state and minimally conscious state patients. Furthermore, new paradigms are available for comparing consciousness with unconsciousness when an overall physiological state of the brain is controlled, such as dreamless vs. dreamful non-rapid eye movement sleep (NREM sleep; Noreika et al. 2009; Siclari et al. 2013) or dreamless vs. dreamful anaesthesia (Noreika et al. 2011). Let us examine several exemplary papers that compare an overall stream of consciousness with its absence.

Sitt et al. (2014) studied auditory-evoked potentials and endogenous fluctuations of EEG signal in 75 vegetative state and 68 minimally-conscious patients. None of the studied evoked potentials (P1, MMN, P3a, P3b, CNV) were able to discriminate patient groups, indicating that task-dependent brain activity does not necessarily distinguish between conscious and unconscious states. Contrary to this, analyses of spontaneous EEG activity showed that unconscious patients had higher power of delta and lower power of theta and alpha oscillations, especially over parietal regions. Furthermore, EEG complexity indices derived from the compressibility of a sequence of data points indicated increased signal complexity over the parietal region in the minimally conscious patients compared to the vegetative state patients. Finally, electrode connectivity measures derived from information theory showed that vegetative-state patients had lower-weighted symbolic mutual information exchange in the range of theta and alpha oscillations than minimally-conscious patients. Interestingly, none of the EEG connectivity measures in the gamma frequency range, including phase lag index and imaginary coherence, could discriminate patient groups, coinciding with other independent observations that gamma synchrony does not necessarily differentiate conscious and unconscious states of the brain (Castro et al. 2013; Steriade et al. 1996).

The finding that the presence of consciousness is associated with an overall complexity of EEG signal and the magnitude of inter-electrode information exchange (Sitt et al. 2014) seems to support the information integration theory of consciousness (Tononi 2012), which predicts that consciousness depends on information complexity and integration in the system. The information integration theory was recently tested by Casali et al. (2013), who investigated the consciousness-related electrodynamics of the distributed cortical networks in a wide range of states of (un)consciousness, including wakefulness (eyes open, eyes closed), sleep (NREM sleep, REM sleep), anaesthesia (midazolam, xenon, propofol), and consciousness disorders (locked-in syndrome, minimally conscious state, patients who have emerged from a minimally conscious state, vegetative state). In a series of experiments, transcranial magnetic stimulation (TMS) pulses were delivered to different cortical sites, which perturbed spontaneous EEG activity (Massimini et al. 2010). Complexity of such TMS-induced EEG perturbations was then calculated, and its index successfully differentiated the states of consciousness and unconsciousness, even at the individual participant's level (Casali et al. 2013). As predicted, the presence of consciousness was associated with a higher level of information complexity.

In these and similar experiments, the contents of consciousness were not systematically manipulated or controlled for, and conscious participants probably underwent very diverse experiences. Consequently, the reported EEG complexity as the NCC seems to be independent of particular phenomenal contents, and it may reflect some structural aspects of the whole stream of unified subjective experiences. It seems that phenomenal consciousness emerges in a state of the brain that is capable of generating the required level of information complexity and integration. As requested in the previous sections, such an NCC is stable in time and does not depend on an experience isolated from the rest of phenomenal space. Arguably, this type of study tackles the fundamental unity of consciousness much more directly than typical paradigms for studying the selected contents of consciousness. However, approaching one side of the bridge takes us further away from the other side, and the better characterization we have of the neural mechanisms of the state of consciousness, the less we can say about the neural mechanisms of particular contents of consciousness. For instance, the perturbational complexity index can differentiate conscious and unconscious states, but it is extremely insensitive when it comes to distinguishing between different contents of consciousness. For instance, the values of the complexity index did not systematically differ between the "eyes closed" and "eyes open" conditions in the standard waking state (Casali et al. 2013; Noreika 2014). Arguably, any NCC that cannot distinguish between experiences occurring in the "eyes closed" and "eyes open" conditions cannot be fully satisfactory, as the quality of subjective experiences is the core of the scientific problem of consciousness. Yet even though informational complexity does not reflect qualities of phenomenal contents, it is a promising candidate for an NCC of the background properties of consciousness that enable the emergence of subjective experiences and/or necessitate their structural unity.

We are thus left with studies of the contents NCC, such as focusing on the gamma synchrony, and studies of the state NCC, such as focusing on the information complexity. The first group of studies seems to explain the neural binding of concrete selected contents of consciousness, but it does not have a capacity to address the unity of consciousness. The second group seems to capture neural processes involved in the whole stream of consciousness, but it ignores differentiation or phenomenal diversity of consciousness. Ideally, research into the NCC would combine both of these complementary approaches. Unfortunately, a systematic combination of the contents- and states-focused paradigms is almost never tested in cognitive neuroscientific studies of consciousness.

The combined *contents-states paradigm* would contrast baseline and altered states, or consciousness and unconsciousness, or the transition between the two, while participants carry out experiments that tackle the neural mechanisms of the contents of consciousness. For instance, one could study binocular rivalry while participants lose consciousness in response to an anaesthetic agent. This could, for instance, provide data to investigate how global gamma synchrony as a correlate of the binding and transfer of new contents to awareness depends on or interacts with a changing level of neuronal information complexity. Another promising avenue is research into awareness-related performance in the transition from wakefulness to sleep (Goupil & Bekinschtein 2011). In a recent attempt, Bareham et al. (2014) demonstrated that healthy individuals show neglect-like loss of awareness of the right side of their space in a drowsy state of consciousness. Thus, spatial awareness and unity seem to depend on the state of alertness, as defined by the relative amplitude of theta and alpha oscillations, which confirms that the contents are not wholly independent of the state. That is, despite the external physical stimuli and environment remaining stable, phenomenal contents may appear, disappear, or reorganise depending on the overall state of consciousness. More such studies are expected to be carried out in future, aiming to integrate the content NCC, the state NCC, and altered states of consciousness research programs under one unified framework of the content-state NCC research.

6 Conclusion

Global gamma-band synchronisation, research into which was largely triggered and continues to be advanced by Prof. Wolf Singer, is one of the most promising NCCs. Synchronisation seems to increase in most cases when a new, task-dependent content of consciousness is formed. Yet a larger number of complications prevents its acceptance as the main NCC, namely: gamma synchronisation does not persist for as long as the contents of consciousness, some of the contents of consciousness emerge without gamma synchronisation being modulated, and, finally, gamma synchronisation may increase in unconscious or unresponsive states of mind. These complications show that gamma-band synchronisation cannot fully account for the existence of a unified stream of consciousness. Given that consciousness is integrated over cognitive time and space, a sufficient and necessary NCC should persist even when some but not all of the experiences cease to exist in time, or change their location. Nevertheless, even though gamma-band synchronisation seems to be neither necessary nor sufficient for all contents of consciousness to arise, it should be regarded as one of the NCCs specifically involved in the binding of new attended experiences. Future research may also develop more accurate characterization of gamma synchronisation, including its spatial scale, precision, and stability (Singer this collection), and certain forms of synchrony might be necessarily accompanied by consciousness; yet such evidence is not currently available.

Given that gamma synchronisation cannot be the only NCC, research efforts and resources should be distributed to search for the other NCCs, some of which might be responsible for the maintenance of already-bound single contents, and some of which might contribute to the unity of the whole stream of consciousness. Research paradigms should be developed that allow simultaneous manipulation and testing of both the contents and the states of (un)consciousness. Most likely, none of the discovered NCCs alone will be necessary and sufficient for all forms of subjective experiences to exist. How many of the neural correlates will be sufficient for the stream of consciousness to flow, and whether the sufficient ones will also be necessary, remains to be studied in future. For now, an exciting program of NCC research should continue searching for the new avenues. Among various proposals, such as a focus on how social interactions and culture modulate neural networks supporting phenomenal contents (Singer this collection), the present one claims that it's not just about the contents, and that a state of consciousness deserves a treatment of its own.

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