

3

Neuronal Oscillations, Coherence, and Consciousness

Andreas K. Engel¹ and Pascal Fries^{2,3}

¹Department of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, Hamburg, Germany ²Ernst Strüngmann Institute for Neuroscience in Cooperation with Max-Planck-Society, Frankfurt, Germany ³Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands

O U T L I N E

Relevance of Oscillatory Signals	49	Relation of Oscillations and Coherence to Contents of Consciousness	53
Dynamic Coupling by Neural Coherence	51	Conclusions: Coherence and Consciousness	57
Relation of Oscillations and Coherence to Levels of Consciousness	52	References	58

A large body of neuropsychological and physiological evidence suggests that consciousness has to be understood as a function of numerous interacting systems, such as sensory areas, memory structures, centers for executive control as well as circuits mediating emotion and motivation (Crick and Koch, 1990; Newman and Baars, 1993; Tononi and Edelman, 1998; Engel et al., 1999; Engel and Singer, 2001; Lamme, 2006; Dehaene et al., 2006; Tononi and Koch, 2008; Dehaene and Changeux, 2011). Thus, any theory about the neural mechanisms of consciousness must explain how multiple component processes can be integrated and how large-scale interactions can emerge within and across distributed neural systems. Furthermore, such a theory must specify mechanisms for the dynamic selection of subsets of neuronal responses, because only a fraction of all available information gains access to consciousness. In this chapter, we consider the potential relevance of oscillatory neural signals for the emergence of consciousness. We will suggest that changes in the strength or the coupling of oscillatory signals may relate to the

selection of signals for access to consciousness, to structuring of conscious contents, to large-scale integration across different brain regions, and to buildup of a “global workspace.” In recent years, empirical evidence is emerging which indeed suggests that coherent oscillatory activity may relate to these different prerequisites and, thus, may be critical to understanding the neural basis of consciousness.

RELEVANCE OF OSCILLATORY SIGNALS

Oscillatory brain signals are usually categorized into five frequency bands: delta (0.5–3.5 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (>30 Hz). A large body of evidence suggests that oscillatory activity in these frequency bands is linked to a broad variety of perceptual, sensorimotor, and cognitive operations (Singer and Gray, 1995; Engel et al., 2001; Palva and Palva, 2007; Fries, 2009; Engel and Fries, 2010; Siegel et al., 2012; Lisman and Jensen,

2013). Oscillatory activity in the delta-band has been related to motivational processes, the brain reward system, and is the predominant frequency during deep sleep phases (Başar et al., 2000; Knyazev, 2007). Activity in the theta-band has been linked to working memory functions, emotional arousal, fear learning, and attentional sampling (Knyazev, 2007; Jensen and Lisman, 2005; Fries, 2009; Landau and Fries, 2012; Lisman and Jensen, 2013). The prominent alpha-band rhythm, which has been discovered in the human electroencephalogram (EEG) by Hans Berger in the late 1920s, has been suggested to reflect cortical operations during the awake resting-state in the absence of sensory inputs. It has been proposed that alpha-band oscillations may relate to disengagement of task-irrelevant brain areas (Klimesch et al., 2006; Jensen and Mazaheri, 2010), as well as working memory function and short-term-memory retention (Palva and Palva, 2007). Neuronal responses in the beta-band have been frequently linked to sensorimotor processing (Roelfsema et al., 1997; Brovelli et al., 2004) as well as many other functions including, for instance, working memory and top-down processing (Engel and Fries, 2010; Bastos et al., 2015a,b).

Neural signals in the gamma-frequency range have received considerable attention in the past two decades. Although the phenomenon of fast neuronal oscillations had already been described 50 years earlier, it started to attract major interest only in the late 1980s, when it was shown to correlate with perceptual binding (Gray et al., 1989). Fast oscillations in the gamma-frequency range have been found in a large number of different neural systems and across a wide range of species (for review, see Singer and Gray, 1995; Engel et al., 2001; Fries, 2009; Siegel et al., 2012). In animal studies, early observations on gamma oscillations were made in the visual and olfactory systems (Fröhlich, 1913; Adrian, 1950; Freeman, 1968). In humans, gamma-band activity was demonstrated first in the auditory cortex (Galambos et al., 1981). In the past three decades, studies in animals and humans have reported gamma-frequency oscillations in all sensory systems, in memory systems, motor system, as well as in association regions (for review, see Singer and Gray, 1995; Engel et al., 2001; Fries, 2009; Siegel et al., 2012). The putative functions of synchronization in the gamma-band seem to be particularly diverse, ranging from perceptual integration, stimulus selection, sensorimotor integration, movement preparation to memory formation, attention, and consciousness (Singer and Gray, 1995; Engel et al., 2001; Engel and Singer, 2001; Fries, 2005, 2009; Engel and Fries, 2010; Siegel et al., 2012). Typically, the observed amount of gamma is positively correlated with increased processing load and, thus, with the level of attention, as well as with the difficulty or integrative nature of the processing (Fries, 2009).

Crick and Koch (1990) were the first to suggest a relation between the occurrence of synchronized oscillations and consciousness. Inspired by the finding that visual stimuli can elicit synchronized oscillatory activity in the visual cortex (Gray et al., 1989), they proposed that an attentional mechanism induces synchronous oscillations in selected neuronal populations, and that this temporal structure would facilitate transfer of the encoded information to working memory. According to their view, only appropriately bound, or integrated, neuronal activity could enter short-term memory and, hence, become available for access to awareness, that is, the conscious experience of sensory signals.

In the past two decades, numerous authors have advocated a relationship between consciousness and integration of signals across neural populations. Damasio (1990) suggested that conscious recall of sensory contents requires the binding of distributed information stored in spatially separate cortical areas. Llinas and Ribary (1994) have argued that arousal (i.e., an increased level of consciousness) and awareness result from the activation of nonspecific thalamocortical circuits which serve to bind sensory contents encoded by specific thalamocortical loops. Newman and Baars (1993) have suggested that unspecific and specific thalamocortical systems interact to form a global workspace, where bound contents become globally available and, hence, lead to the emergence of conscious states. A related view has been expressed by von der Malsburg (1997) who postulated that the degree of consciousness attributable to a whole cognitive system may covary with the degree of coherence, or functional coupling, between different neural subsystems. Tononi and Edelman (1998) have suggested that consciousness requires binding or, in their terms, re-entrant interactions between systems performing perceptual categorization and brain structures related to working memory and action planning. Early on, we have suggested that coupled neuronal oscillations may underlie the large-scale interactions supporting consciousness (Engel et al., 1999; Engel and Singer, 2001), a notion that will be further elaborated in the remainder of this chapter.

Several authors have emphasized that interaction of bottom-up and top-down processing may be a prerequisite for the emergence of conscious states. Grossberg (1999) has proposed that conscious states result from a resonance, or match, between top-down priming and bottom-up processing of incoming information, which allows learning and binding of information into coherent internal representations. Similarly, on the basis of the global workspace hypothesis, Dehaene et al. (2006) have argued that consciousness requires large-scale reverberating interactions involving frontoparietal networks that implement top-down processing. Lamme (2003, 2006) has also emphasized the large-scale nature

of neural processing required for consciousness and has proposed that recurrent processing between high- and low-level areas has to occur. This notion is also a key ingredient of the integrated information theory of consciousness (Tononi and Koch, 2008).

Taken together, all these authors seem to imply (i) that consciousness results from a cooperative process in a highly distributed network, and is not attributable to a single brain structure or process; and (ii) that only coherent activity, resulting from the operation of integrative mechanisms, could become functionally salient, causally efficacious and globally available, and, thus could lead to the emergence of conscious mental states and their respective behavioral manifestations. The critical point is that dynamic integration may not only help to achieve the “unity” of consciousness but may also gate the access to awareness and, hence, turn subconscious information into conscious mental contents. In what follows, we will discuss evidence that demonstrates the relevance of dynamic coupling by coherent neuronal oscillations to key processes that seem to be required for the emergence of conscious mental states.

DYNAMIC COUPLING BY NEURAL COHERENCE

Originally, the notion that temporal correlations might be important for dynamic integration of neural signals was proposed in the context of perceptual processing and integration of object features (von der Malsburg, 1994; Singer and Gray, 1995). This hypothesis has been strongly motivated by the insight that perception, like most other cognitive functions, is based on highly parallel information processing involving large neural assemblies spread across numerous brain areas. According to this hypothesis, synchronization of spatially separate neurons is a key principle of brain function since it allows the formation of functionally coherent activity patterns supporting particular cognitive functions.

A critical assumption in this framework is that synchrony in a distributed network of neurons is subject to both bottom-up and top-down influences (Engel et al., 2001; Engel and Fries, 2010). Thus, temporal correlations might subservise a dual function in such networks. On the one hand, synchrony could permit the rapid and reliable selection of perceptually or behaviorally relevant information. Because precisely synchronized discharges have a high impact on the respective postsynaptic cells, the information tagged by such a temporal label could be rapidly and preferentially relayed to other processing centers (Fries, 2005, 2009). On the other hand, formation of assemblies is not only constrained by stimulus-related information, but much more strongly by the intrinsic dynamics of the system (Engel et al., 2001, 2013). Factors

like attention, predictions, or previous knowledge are often crucial for the processing and integration of sensory information. Therefore, we assume that temporally coordinated signals from other regions of the network can have a strong impact on sensory regions by modulating the local neural dynamics in a top-down manner (Engel et al., 2001; Bastos et al., 2015a,b). Such modulatory top-down signals implementing dynamic contextual predictions could arise, for instance, from regions involved in memory and action planning. Thus, both bottom-up routing of signals and top-down modulation of processing call for highly selective neuronal communication that is thought to be mediated by correlated oscillatory fluctuation of the activity of the cell populations involved (Engel et al., 2001; Fries, 2005, 2009; Bastos et al., 2015a,b).

As mentioned already, the basic phenomenon of correlated oscillatory activity is well documented for a wide range of neural systems and species. Numerous studies have shown that neurons in both cortical and subcortical centers of the visual system typically respond with fast oscillatory activity that can be synchronized with precision in the millisecond range (for review, see Singer and Gray, 1995; Engel et al., 2001). Direct support for the relevance of oscillatory coupling for perceptual integration comes from studies showing that neuronal synchronization in the cortex depends on the stimulus configuration. In the visual systems of cats and monkeys, it could be demonstrated that spatially separate cells show strong synchronization only if they respond to the same visual object. However, if responding to two independent stimuli, the cells fire in a less correlated manner or even without any fixed temporal relationship (Gray et al., 1989; Kreiter and Singer, 1996; Castelo-Branco et al., 2000). The experiments demonstrate that Gestalt criteria such as continuity or coherent motion, which have psychophysically been shown to support perceptual grouping, are important for the establishment of synchrony among neurons in the visual cortex. In humans, coherent visual stimuli have been shown to lead to augmentation of gamma-band power, reflecting enhanced neural interactions in this frequency range (Siegel et al., 2007).

Beyond the visual modality, coherent oscillatory activity has also been observed in the auditory (Brosch et al., 2002; Debener et al., 2003), somatosensory (Bauer et al., 2006), and olfactory (Wehr and Laurent, 1996) systems. Moreover, synchrony has been implicated in processes such as attentional selection (Fries et al., 2001; Gross et al., 2004; Buschman and Miller, 2007; Gregoriou et al., 2009, 2012; Bosman et al., 2012; Grothe et al., 2012), sensorimotor integration (Roelfsema et al., 1997; Brovelli et al., 2004; Womelsdorf et al., 2006), decision making (Donner et al., 2009), movement preparation (Sanes and Donoghue, 1993; Baker et al., 1999; Jenkinson et al., 2012), and memory formation (Fell et al., 2001; Csicsvari

et al., 2003; Gruber and Müller, 2005; Herrmann et al., 2004; Jensen and Lisman, 2005). Collectively, these data provide strong support for the hypothesis that synchronization of neural signals is a key mechanism for integrating and selecting information in distributed networks (Singer and Gray, 1995; Engel et al., 2001). What they suggest is that coherence of neural signals allows to set up highly specific patterns of effective neuronal coupling, thus enabling the flexible and context-dependent binding, the selection of relevant information and the efficient routing of signals through processing pathways (Salinas and Sejnowski, 2001; Fries, 2005; Womelsdorf et al., 2007).

RELATION OF OSCILLATIONS AND COHERENCE TO LEVELS OF CONSCIOUSNESS

Evidence from both animal and human experiments suggests that neural synchrony may be of critical relevance for the emergence of consciousness in at least two respects. First, oscillations of different frequency ranges may relate to the buildup of conscious states and, thus, to changes in the *level* of consciousness; second, oscillations may facilitate the selection of sensory information for access to awareness and, thus, have an impact on the *contents* of consciousness. In this section, we discuss the relation between oscillatory activity in specific frequency ranges and the level of consciousness. Substantial evidence demonstrates that state changes leading to alterations in the level of consciousness are associated with variations in oscillatory signals and large-scale neural coherence. Well-studied examples include changes in arousal resulting from sleep-waking cycles and transitions between wakefulness and anesthesia.

It has long been known that the frequency ranges of cortical oscillatory activity are modulated with arousal (Moruzzi and Magoun, 1949). More recent studies have clearly established that high-frequency oscillations are particularly prominent during epochs of higher vigilance and that synchronization across neuronal populations increases during states characterized by arousal (for review, see Urbano et al., 2012). Thus, experiments in rats (Franken et al., 1994; Brankačk et al., 2012) and cats (Steriade et al., 1996; Steriade, 1997) have shown that gamma-band synchronization is enhanced during rapid-eye movement (REM) sleep and waking compared to deep sleep. In addition, REM sleep is associated with enhanced theta-gamma cross-frequency coupling (Brankačk et al., 2012). Moreover, electrical activation of the midbrain reticular formation (one of the structures responsible for change of vigilance states) has been shown to induce a shift from low to high oscillation frequencies and an increase of stimulus-induced

synchronization in the visual cortex (Munk et al., 1996). It seems likely that the increasing availability of faster coupling patterns reflects an enhanced readiness for specific neural communication in states of higher arousal.

As in other mammals, cortical activity in humans shows an enhancement of high-frequency EEG components during states of increased arousal, sleep-waking transitions and REM sleep. Several studies using EEG or magnetoencephalography (MEG) in healthy humans indicate that in the awake state and during REM sleep, gamma-band frequencies are present which are diminished during deep sleep (Llinás and Ribary, 1993, 1994; Uchida et al., 2001; Le Van Quyen et al., 2010). The similarity of high-frequency activity during REM phases and the awake state suggests that, in both cases, synchrony in this frequency band correlates with similar processes leading to consciousness, which are just differently modulated by external stimulation (Llinás and Ribary, 1994). Similar evidence for high-frequency cortical activity related to arousal is available from intraoperative human recordings (Moll et al., 2009). It should be noted, however, that bursts of gamma-band activity have also been observed to precede states of unconsciousness during epileptic seizures (Worrell et al., 2004). This suggests that high-frequency oscillations *per se* are not sufficient to implement states of increased arousal. As further discussed below and in the next section, specific coupling of such oscillations across neural populations seems required.

Anesthesia provides a highly interesting setting for studying physiological mechanisms underlying consciousness, albeit with the caveat that the mechanisms of drug-induced modulation of levels of consciousness may only partly correspond to those involved in state changes without medication. A substantial number of studies have addressed changes of oscillatory activity during anesthesia (for review, see e.g., Brown et al., 2010; McCarthy et al., 2012).

Using propofol-induced anesthesia as a model, a recent study has addressed the interplay between incoming sensory information and state-dependent intrinsic large-scale cortical dynamics (Supp et al., 2011). Intrinsic cortical dynamics modulates the processing of sensory information and therefore may be critical for conscious perception. In a recent study, this hypothesis was tested by EEG recording during stepwise drug-induced loss of consciousness in healthy human participants (Figure 3.1). It was observed that progressive loss of consciousness was tightly linked to the emergence of a hypersynchronous cortical rhythm in the alpha-frequency range (8–14 Hz). This drug-induced ongoing alpha activity was widely distributed across frontal cortex (Figure 3.1A and B). Stimulus-related responses to median nerve stimulation comprised an early component in primary somatosensory cortex and a late component also

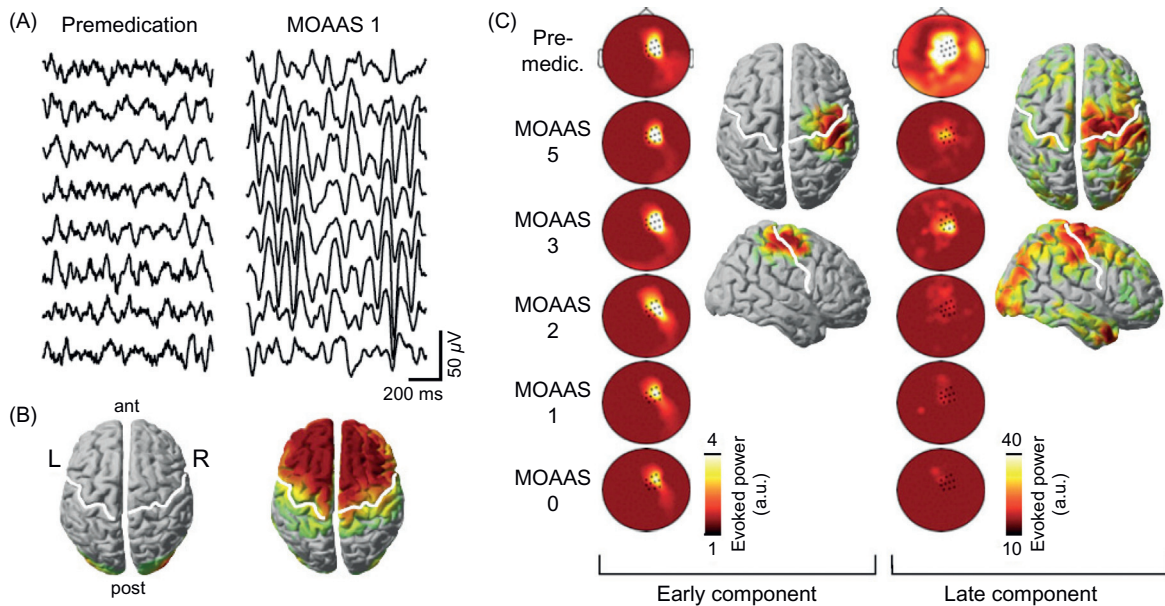


FIGURE 3.1 Impairment of conscious access by hypercoherent oscillations under propofol anesthesia. (A) EEG was recorded before drug application (premedication) and during intravenous administration of increasing levels of propofol. Shifts in the participant's state of sedation induced by a given drug level were quantified by a standardized rating scale (MOAAS) ranging from 5 (fully conscious) to 0 (unresponsive). Single participant's EEG traces exemplify the emergence of an alpha-frequency rhythm during loss of consciousness. (B) As compared to premedication (left), alpha power strongly increased in frontal brain areas during loss of consciousness (right, MOAAS 1). (C) During each block, participants received electrical median nerve stimuli at their left wrist. Source reconstruction revealed an early response component largely confined to contralateral primary somatosensory cortex. In addition, a late response component was observed that also involved right temporal and parietal brain areas. The topographies display the modulation of the early (left) and late (right) components with increasing sedation, showing a persistent early response across all sedation levels but a breakdown for the late component. *Source: Modified from Supp et al. (2011).*

involving temporal and parietal regions. During progressive sedation, the early response was maintained, whereas the late response was reduced and eventually vanished (Figure 3.1C). The antagonistic relation between the late sensory response and ongoing alpha activity held for constant drug levels on the single-trial level. Specifically, the late response component was negatively correlated with the power and long-range coherence of ongoing frontal alpha activity. These results suggest that blocking of cortical communication by hypersynchronous ongoing activity may be a key mechanism for the loss of consciousness under anesthesia.

Other studies have also related altered oscillatory cross-frequency coupling to the loss of consciousness under anesthesia. Under propofol-induced anesthesia, the emerging alpha-range rhythm can show different modes of coupling to slow (<1 Hz) oscillations that seem to involve spatially different neuronal networks (Mukamel et al., 2014). In conclusion, consciousness may depend on a delicate balance between locally specific information processing and the coupling structure of intrinsic global cortical dynamics (Engel et al., 2013). Under anesthesia, abnormal low-frequency coupling seems to be one possible mechanism that prevents specific large-scale interactions needed for processing and selection of information. In the same vein, excessive

unspecific synchrony seems to relate to the loss of consciousness during epileptic seizures (Bartolomei and Naccache, 2011).

RELATION OF OSCILLATIONS AND COHERENCE TO CONTENTS OF CONSCIOUSNESS

A relation of oscillatory activity to changes in the contents of conscious states is suggested by studies that have applied bistable or ambiguous perceptual conditions while recording oscillatory coupling across neural assemblies. Early evidence was obtained in experiments in which activity was recorded from the visual cortex of awake cats under conditions of binocular rivalry (Fries et al., 1997, 2002). Binocular rivalry is a particularly interesting case of dynamic response selection that occurs when the images in the two eyes are incongruent and cannot be fused into a coherent percept. In this case, only signals from one of the two eyes are selected and perceived at any given time, whereas those from the other eye are suppressed. In normal subjects, perception alternates between the stimuli presented to left and right eye, respectively. Obviously, this experimental situation is particularly

suiting for studying the basis of consciousness, because neuronal responses to a given stimulus can be studied either with or without an accompanying awareness (Crick and Koch, 1990; Engel et al., 1999).

Fries and colleagues (1997, 2002) tested the hypothesis that response selection in early visual areas might be achieved by modulation of oscillatory neuronal coupling. These measurements were performed in awake strabismic cats with electrodes chronically implanted in primary and secondary visual cortex. The animals were subjected to dichoptic visual stimulation, that is, patterns moving in different directions were simultaneously presented to the left and the right eye, respectively. Due to the strabismus, one eye was dominant, that is, that eye's stimulus was perceived when equal contrast stimuli were given to both eyes. The results obtained with this experimental approach showed that visual cortical neurons driven by the dominant and the suppressed eye, respectively, did not differ in the strength of their firing rate response to visual stimulation. They showed, however, profound differences with respect to their synchronization. Neurons supporting the dominant percept increased their synchrony, whereas cells processing the suppressed visual pattern decreased their coupling. This effect was observed specifically in the gamma-frequency band (Fries et al., 1997, 2002). These studies clearly suggest that changes in the contents of consciousness, as evident during binocular rivalry, are associated with fluctuations in neural coupling. Studies on bistable perception in monkey visual cortex also support these conclusions (Wilke et al., 2006).

In humans, studies using ambiguous stimulus settings also suggest a clear relation between intrinsic fluctuations of dynamic coupling and changes in the perceptual state. Doesburg and coworkers (2005) recorded EEG during binocular rivalry and reported that increases in gamma-band coupling preceded the subjects' perceptual switches. Using a dynamic apparent motion stimulus, Rose and Büchel (2005) showed that perceptual changes were associated with fluctuations of gamma-band coupling across the cerebral hemispheres. In a similar vein, fluctuations in beta-band coupling have been shown to predict the perceptual state in an ambiguous audio-visual paradigm (Hipp et al., 2011) (Figure 3.2). Neuronal activity was reconstructed from the EEG of human subjects presented with two moving bars that could be perceived either as bouncing or passing (Figure 3.2A). Long-range beta-band coherence between frontoparietal and visual cortex was observed during the processing of the ambiguous motion stimulus, which was enhanced for about 1 s around the time of bar overlap (Figure 3.2B). Coherence was enhanced in a widespread cortical network including bilateral frontal eye fields, posterior parietal cortex and motion-sensitive

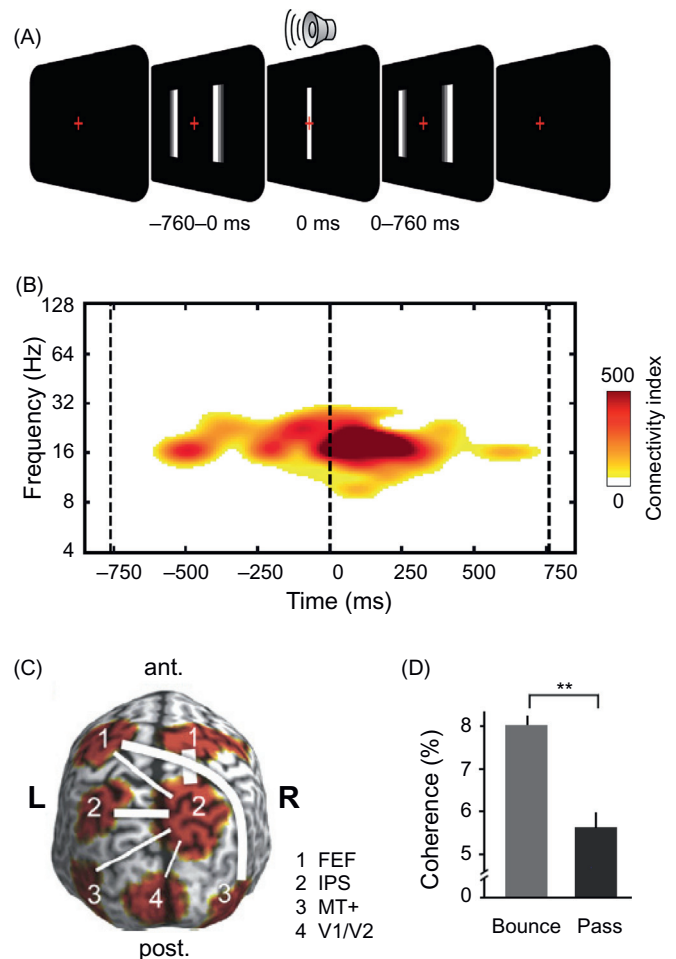


FIGURE 3.2 Selection of conscious contents by coherent oscillations in bistable perception. (A) While EEG was recorded, participants watched a screen on which two bars approached, briefly overlapped, and moved apart again. At the time of overlap of the bars, a brief click sound was played. Participants perceived this stimulus either as two bouncing or passing bars, with the percept spontaneously changing across trials. (B) Around the time when the stimulus became perceptually ambiguous, beta-band coherence (15–30 Hz) was enhanced. (C) Beta-band coupling (white lines indicate coherence strength) occurred in a large-scale cortical network including bilateral frontal eye fields (FEF), posterior parietal cortex (IPS), visual areas involved in motion processing (MT+) as well as early visual cortex (V1/V2). (D) The strength of beta-band coupling predicted the subjects' percept: stronger beta-band coherence predicted perceiving the bars as bouncing, whereas weaker coherence predicted the percept of passing bars. Source: Modified from Hipp et al. (2011).

visual areas (Figure 3.2C). Importantly, the beta-band coherence within this network was found to predict whether the subjects perceived the bars as bouncing or passing (Figure 3.2D). Taken together, these studies strongly suggest that intrinsically generated fluctuations in neural coupling during the processing of ambiguous stimuli are relevant for controlling changes in the subjects' conscious perceptual contents.

Evidence for a relation between oscillations and conscious processing has also been obtained in studies using masking paradigms. In a study comparing the processing of visible and invisible word stimuli in a delayed match-to-sample task, stimulus visibility was found to be associated with enhanced long-range synchronization in the gamma-band (Melloni et al., 2007). Combining a similar paradigm with intracranial recordings in epilepsy patients, another study has observed enhanced beta-band coherence for visible compared to invisible stimuli (Gaillard et al., 2009). A recent MEG study has reported that conscious word-form perception correlates with alpha-band suppression in occipito-temporal cortex (Levy et al., 2013).

As stated above, we assume that conscious awareness requires a mechanism that selects relevant information and enhances its impact on subsequent processing stages. Evidently, attention is of particular importance for the selection of signals and top-down modulation of sensory processing. Therefore, investigation of attentional mechanisms seems highly relevant for understanding consciousness (Engel and Singer, 2001; Dehaene et al., 2006). Strong evidence for attentional modulation of neural synchrony is provided by experiments in behaving monkeys. One of the earliest studies (Steinmetz et al., 2000) investigated cross-modal attentional shifts in monkeys that had to direct attention to either visual or tactile stimuli that were presented simultaneously. Synchrony among neurons in somatosensory cortex depended strongly on the monkey's attention. If the monkey shifted attention to the visual task, temporal correlations typically decreased among somatosensory cells, as compared to task epochs during which attention was not distracted from the somatosensory stimuli.

In the visual system of monkeys, attentional effects on oscillatory synchrony were first investigated by recordings from area V4 (Fries et al., 2001). In this study, two stimuli were presented simultaneously on a screen, one inside the receptive fields of the recorded neurons and the other nearby. The animals had to detect subtle changes in one or the other stimulus. If attention was shifted towards the stimulus processed by the recorded cells, there was a marked increase in local synchronization. This finding was confirmed by Taylor and coworkers (2005) using a demanding visual task that required monkeys to track changes in an object's shape over time. In both studies, the attentional effects were observed specifically in the gamma-frequency band. A recent study has provided evidence that this attentional enhancement of synchrony in local populations in area V4 strongly involves the locking of putative inhibitory interneurons (Vinck et al., 2013). Recent studies in monkeys have also demonstrated an attention-specific enhancement of long-range gamma-band coupling between V4 and V1 (Figure 3.3)

(Bosman et al., 2012; Grothe et al., 2012) and between V4 and the frontal eye field (Gregoriou et al., 2009, 2012). These data clearly demonstrate that gamma-band coupling is not only relevant for local processing, but also for long-range functional communication (Fries, 2005, 2009).

Buschman and Miller (2007) provided evidence that beta-band activity can also be associated with attentional selection. The authors trained monkeys to detect a target amongst a set of distractors in either a pop-out or a serial search regime. Analysis of coherence between frontal and parietal signals revealed that interactions occurred predominantly in the beta-band during search, that is, in the condition involving a strong endogenous top-down processing component. In contrast, coupling was more prominent in the gamma-band in the pop-out condition, where performance primarily depended on the saliency of the target stimulus. These data support the hypothesis that endogenously driven top-down attention may be associated with large-scale communication in lower frequency bands, whereas coupling may occur at higher frequencies when bottom-up signals need to be conveyed (Engel and Fries, 2010).

A relation between attention and modulation of synchronized oscillations is also well established for the human brain. Evidence from EEG and MEG studies shows that high-frequency oscillations are enhanced by attention in the human visual system (e.g., Tallon-Baudry et al., 2005; Kranczioch et al., 2006, 2007; Vidal et al., 2006; Engell and McCarthy, 2010; Müsch et al., 2014). Similar evidence is available for the auditory system (e.g., Tiitinen et al., 1993; Debener et al., 2003) and the tactile system (e.g., Bauer et al., 2006). In all these studies, attention was observed to specifically enhance gamma-band activity. An MEG study also demonstrated that attention selectively modulates large-scale coupling of oscillatory signals in the human brain (Siegel et al., 2008). Subjects were simultaneously presented with two weak motion stimuli in the left and right visual hemifield. At the beginning of each trial, a cue instructed subjects to attend to one of the two stimuli and to assess its motion direction. The authors combined MEG with source reconstruction to characterize the phase coherence between motion-sensitive visual areas, the posterior parietal cortex and the frontal eye fields. Attention selectively enhanced gamma-band phase coherence between these regions in the hemisphere that processed the attended stimulus. This enhancement in the gamma-band was accompanied by a reduction of coherence in the alpha- and beta-range. Other findings also suggest an important role for lower frequencies. One MEG study (Gross et al., 2004) investigated the neuronal basis of the attentional blink, that is, a transient reduction of

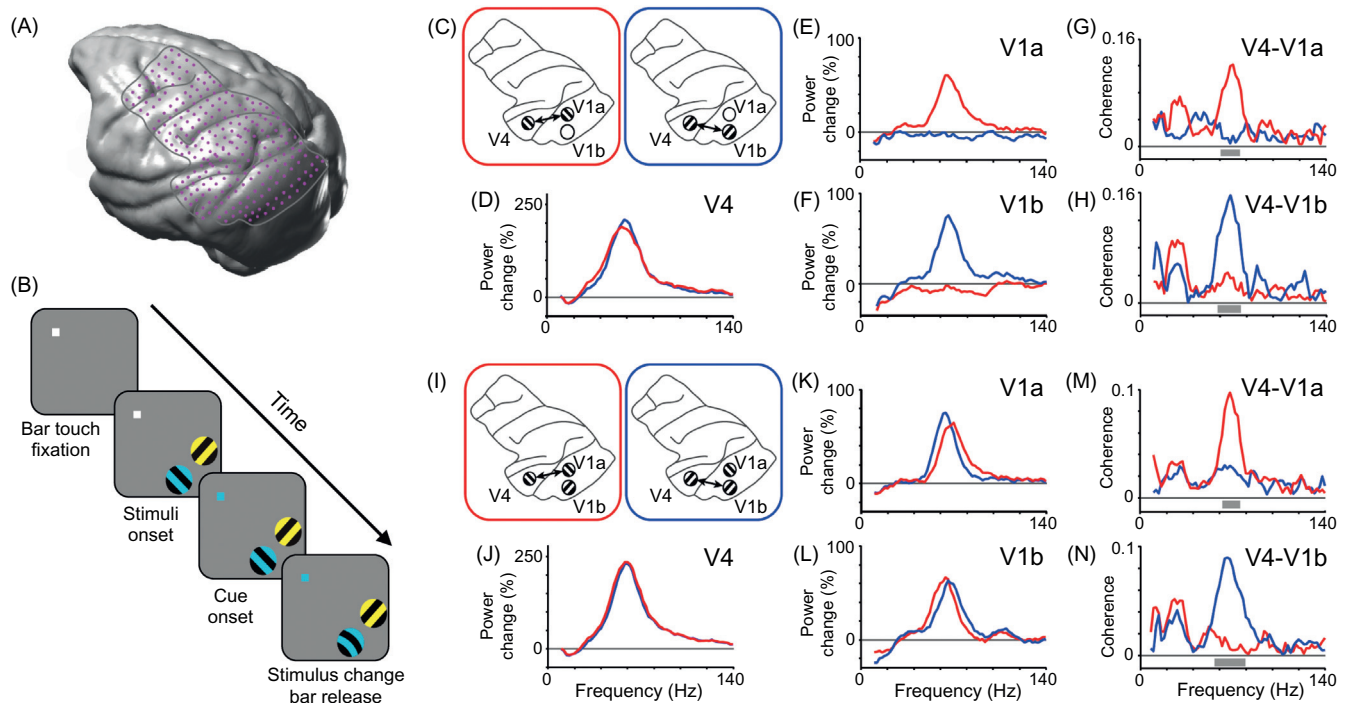


FIGURE 3.3 Attentional selection through specific inter-areal gamma-band synchronization. (A) Rendering of a monkey brain with the locations of 252 electrodes in an electrocorticographic grid. (B) Selective attention task. A yellow and a blue tinted grating were presented, with random color assignment. The fixation point assumed the color of one of the stimuli, thereby cueing this stimulus to be behaviorally relevant (target) and the other to be irrelevant (distractor). Up to several seconds later, either the target or the distractor transiently changed shape, and the monkey was rewarded for releasing the bar upon target changes. (C–N) Example triplet recording of one V4 and two V1 sites, using data between cue presentation and stimulus change. (C) Illustration of the two single-stimulus conditions, corresponding to the red/blue lines in (D–H). Both conditions induced gamma-band activity in V4, but only the condition labeled red (blue) activated site V1a (V1b). The double arrow illustrates the presumed pattern of interaction between neuronal groups for the indicated sites. (D–F) Spectral power changes (relative to pre-stimulus baseline) for the indicated sites. (G–H) Coherence spectra for the indicated site pairs. Gray bars indicate frequencies with a significant effect. Note that there was a specific interaction, as reflected in enhanced gamma-band coherence, between the V4 site and the respective site driven in V1. (I) Illustration of the two attention conditions with simultaneous presentation of both stimuli and attentional selection of one or the other stimulus, corresponding to the red/blue lines in (J–N). The arrows indicate the selective interaction of the V4 site with the behaviorally relevant V1 site. (J–L) Spectral power changes (relative to pre-stimulus baseline) for the indicated sites. (M–N) Coherence spectra for the indicated site pairs. Importantly, there was a specific attention-related enhancement of gamma-band coherence between the V4 site and the attended site in V1. *Source: Modified from Bosman et al. (2012).*

attention which often occurs if more than one target has to be processed in a series of rapidly presented stimuli. When subjects successfully detected target letters in a rapid visual stream of letters, coherent beta-band oscillations were enhanced between MEG sensors overlying the temporal cortex, prefrontal cortex and posterior parietal cortex. Thus, fluctuations in the strength of large-scale beta-band coherence may reflect fluctuations in visual attention that, in turn, cause fluctuations in behavioral performance.

Taken together, the studies reviewed above clearly suggest that neural oscillations and local as well as long-range coupling of oscillatory signals are highly relevant for attentional selection. Hence, it can be argued that these mechanisms may be highly relevant for regulating the access of signals to the conscious workspace. However, it should be mentioned that the relation

between attention and consciousness is controversial (Tallon-Baudry, 2011). While some authors argue that attention (at least in many cases) may be a prerequisite for access of signals to consciousness (Newman and Baars, 1993; Engel and Singer, 2001; Dehaene et al., 2006), others have proposed that processes underlying attention and consciousness may operate in a more parallel fashion (Lamme, 2003; Koch and Tsuchiya, 2007; Tallon-Baudry, 2011; see also Chapter 5). This is supported by experiments that have attempted to dissociate attentional selection and conscious access. In recent studies by Wyart and Tallon-Baudry (2008, 2009), subjects were cued to attend to the left or to the right hemifield, and were then presented with a faint oriented grating, either on the attended or unattended side. On each trial, subjects were asked whether they had consciously experienced the stimulus or not. Each stimulus can therefore be classified,

on the one hand, as attended or unattended and, on the other hand, as consciously perceived or not. Interestingly, these two cognitive functions were expressed separately in distinct sub-frequency ranges within the gamma range.

Apparently, further work will be needed to clarify the relation between attention and consciousness. The data on bistable perception and on stimulus masking discussed above suggest that selection of contents for access to awareness is also possible without strong involvement of attentional control. Thus, communication by specific coupling of oscillatory signals may provide a rather generic mechanism which may come into play in both attentional and non-attentional forms of signal selection.

Most accounts on the neural mechanisms of consciousness assume that awareness is necessarily associated with some form of short-term memory and that conscious contents need to be maintained in working memory (Crick and Koch, 1990; Tononi and Edelman, 1998; Engel and Singer, 2001; Lamme, 2003; Baars et al., 2013). It had been postulated early on that coupled oscillations might not only serve for selecting relevant signals, but that the same mechanism might support working memory by transiently stabilizing, through synchrony, the relevant neuronal population (Crick and Koch, 1990). The relationship between oscillations and working memory has been the subject of a large number of studies, which have been reviewed comprehensively by other authors (see Fell and Axmacher, 2011; Lisman and Jensen, 2013; Roux and Uhlhaas, 2013). These studies demonstrate the relevance of oscillatory signals in multiple frequency ranges for working memory processes. In particular, theta-band oscillations and gamma-band oscillations have been shown to be relevant for temporally structuring and maintaining working memory contents (Jensen and Lisman, 2005; Lisman and Jensen, 2013).

Taken together, these data demonstrate that processes relevant to selecting and maintaining the contents of conscious mental states can be associated with specific changes in neural synchrony, thus supporting the proposal that coherence in neuronal assemblies may be a necessary condition for the occurrence of awareness (Crick and Koch, 1990; Engel et al., 1999; Engel and Singer, 2001). The data suggest that the selection of signals for access to awareness is not only dependent on bottom-up factors, but also strongly constrained by intrinsically generated large-scale dynamic patterns, which result from reentrant interactions of prefrontal, premotor, memory, and limbic regions with sensory brain areas. As suggested by Tononi and Edelman (1998), large-scale assemblies activated by such interactions may constitute a “dynamic core” that could control the access of signals to awareness and provide the substrate for a global workspace (Newman and Baars, 1993; Dehaene et al., 2006; Dehaene and Changeux, 2011).

CONCLUSIONS: COHERENCE AND CONSCIOUSNESS

The studies reviewed above strongly suggest that the temporal dynamics in neuronal activity may be critical for the emergence of conscious mental states. As discussed above, specific changes in oscillatory signals and in coherence of population activity may relate to regulation of the *level* of consciousness. Moreover, coherence may serve for the integration, structuring, selection, and communication of relevant signals. Therefore, changes in the pattern of neuronal coherence, both locally and across regions, may lead to changes in the *contents* of consciousness.

According to our view, both aspects of consciousness critically depend on dynamic coupling modes that are intrinsically generated in large-scale networks supporting consciousness and not driven by external events (Engel et al., 2013). An important point to be mentioned is that large-scale coherence is not equivalent to uniform synchrony. Indeed, global synchronization is associated with a low complexity of neural interactions which, as observed in deep sleep or epilepsy, is counterproductive to consciousness. As discussed above, drug-induced anesthesia seems associated with excessive unspecific coupling in low-frequency ranges that prevents specific large-scale interactions and, thus, presumably leads to a breakdown of the global workspace. Our proposal is summarized in the remainder of this section.

As mentioned above, arousal is characterized by an enhanced precision of neuronal synchrony and a shift to higher oscillation frequencies, indicating that thalamocortical systems change from large-scale synchrony into states with more specific, regionalized temporal patterning. We propose that central activating systems may act to modify, in a task- and context-dependent manner, the efficacy of dynamic integration mechanisms. Arousal may lead to enhanced readiness of thalamocortical circuits for specific coupling. By changing both the spatial range and the specificity of neuronal interactions arousal mechanisms, thus, contribute to more specific information processing.

As an additional prerequisite, consciousness requires the completion of basic sensory processing steps, including detection and binding of object features. These processes seem critical for structuring the contents of conscious states. We suggest that this may be implemented in the temporal domain. Synchrony as an integrative mechanism allows establishing specific relationships between neural discharges which are, in principle, independent of spatial proximity or direct neuronal connections. Synchrony is not only determined by the stimulus, but is modulated in a context- and task-dependent way by cooperative interactions within the cortical network.

Current awareness theories assume that not all results of sensory processing contribute to consciousness. Rather, as an additional step, part of the information is subjected to a selection process that gates access to awareness. We propose that selection can be mediated by neural synchronization, as temporally coincident signals are more easily detected by other neural assemblies than temporally dispersed signals. Only activity patterns carrying a strong temporal signature may be functionally efficacious and globally available and, therefore, such a signature may be a fundamental prerequisite for making information available to other brain centers. The selection is controlled both by bottom-up (e.g., stimulus novelty) and top-down (e.g., attention, expectancy, memory contents) influences, which can lead to competition among different assemblies and result in changes of synchrony. It should be emphasized that the notion of selection, as we have employed it here, is broader than the notion of attention.

Furthermore, coherence in neural populations may be ideally suited to promote maintenance of selected contents in working memory. Synchronized assemblies may transiently stabilize in some reverberatory state, endowing them with competitive advantage over temporally disorganized activity. This may provide the basis for working memory necessary to achieve the holding of situational context in the respective processing areas. The information carried by such assemblies during working memory states may become conscious.

Moreover, the mechanism advocated here may account for the global availability (Newman and Baars, 1993; von der Malsburg, 1997; Tononi and Edelman, 1998; Dehaene et al., 2006) of conscious information, because temporal signatures that reliably propagate across systems may be suited to establish patterns of large-scale coherence, thus enabling specific communication across different modules or systems. By the same token, our proposal could have implications for higher-order consciousness which seems to require the activation of motivation and action planning systems, episodic memory and, eventually, symbol processing capacities. With all likelihood, these faculties will require cross-system interactions that could also be mediated by coherent neural oscillations.

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