

# **The role of alpha and beta oscillations in the human EEG during perception and memory processes**

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## **Abstract**

Traditionally alpha and beta oscillations have been viewed a passive phenomenon, being active only when our minds are idling. Empirical evidence over the last two decades challenged this classic view and suggests that alpha/beta play a much more active role during cognitive processes. In the human brain alpha oscillations influence processing of large neural ensembles by regulating the strength of synchronization within these ensembles and by providing discrete time windows for firing. With EEG recordings we can observe these two mechanisms via modulations of the signal strength (i.e. power) and modulations of phase, respectively. In this chapter we focus on these two signal properties of alpha/beta oscillations and review studies that investigated the relevance of alpha power and phase modulations in tasks involving perception and memory processes. These studies reveal a reduction in alpha/beta power when a stimulus is being perceived or mentally replayed. Furthermore, alpha phase reflects rhythmical sampling of stimulus information during perception, and the replay of that information during retrieval. Based on these findings, we argue that alpha oscillations play an active role in representing information-rich content in the brain. Importantly, alpha/beta oscillations perform this function regardless of whether the information is being presented externally, as is the case in perception, or whether it is being generated internally, as is the case in memory retrieval.

## 1. Alpha oscillations and their relation to cognition

In 1929 a German physician named Hans Berger recorded the first human EEG. The first thing he noticed was a regular oscillation with a frequency of 10 Hz (Berger, 1929), which he termed alpha oscillations. Many decades after Berger discovered these alpha oscillations researchers use them as a first quality check of their EEG signal. After attaching electrodes to the subject's head, the researcher would typically ask the subject to close their eyes and relax, and sure enough one can observe beautiful alpha waves with a frequency of around 10 Hz being maximal over posterior channels. When the subject then opens their eyes, alpha oscillations are largely reduced. This phenomenon is extremely reliable, such that not seeing the reduction in alpha amplitude when subjects open their eyes would typically indicate that something went wrong. Reductions in alpha amplitude occur in all ranges of cognitive tasks such as visual processing (E.D. Adrian, 1944), auditory processing (Krause et al., 1994; Obleser & Weisz, 2012), somatosensory processing (Crone et al., 1998), memory encoding (Hanslmayr, Spitzer, & Bauml, 2009; Klimesch et al., 1996), memory retrieval (Burgess & Gruzelier, 2000; Waldhauser, Braun, & Hanslmayr, 2016), working memory maintenance (Sauseng et al., 2009), decision making (Pornpattananangkul, Grogans, Yu, & Nusslock, 2019), motor preparation and execution (Pfurtscheller, Neuper, Andrew, & Edlinger, 1997). The exact frequency at which power reductions are maximal varies between tasks and often involves the faster beta oscillation around 15 Hz, which can be considered the 'fast' brother of alpha. In this chapter we therefore do not distinguish between alpha and beta oscillations and refer to these oscillations as alpha/beta from

hereon. Suppression of alpha/beta oscillations is not only observed in humans, but in a wide range of animals such as non-human primates (Haegens, Nacher, Luna, Romo, & Jensen, 2011), dogs (Lopes da Silva, Vos, Mooibroek, & Van Rotterdam, 1980), cats (von Stein, Chiang, & Konig, 2000), rodents (Wiest & Nicoletis, 2003) and even insects (Popov & Szyszka, 2019). This ubiquity of alpha/beta power suppression across cognitive domains and across the animal kingdom indicates that alpha/beta power reductions are a signature of an extremely general mechanism which is called upon in almost any cognitive task and has been retained over millions of years of evolution. What could this mechanism be? This is the question we try to answer in this book chapter.

Before delving into the different physiological interpretations of alpha oscillations it is worth pointing out a theoretical caveat that has become evident in cognitive neuroscience and the way we can avoid these problems. Historically the job description for a cognitive neuroscientist was to pick a cognitive phenomenon (i.e. Attention, Memory, etc.) and then find the “neural correlate” of that phenomenon. To demonstrate this approach let’s consider a short thought experiment involving two hypothetical cognitive neuroscientists AC and BD. Let’s assume researcher AC is interested in Attention. She runs several meticulously controlled experiments which all manipulate certain aspects of attention whilst she records EEG. Across this series of experiments, she finds that alpha oscillations are very consistently modulated by attention. She goes on a conference, presents her results and concludes, alpha oscillations are the neural correlate of attention. On that same conference, researcher BD who is interested in memory also presents his results. In a series of carefully controlled experiments he shows that alpha oscillations are reliably modulated by various memory processes. He concludes his talk with saying that alpha oscillations are the neural correlate of memory.

So, who is right? What cognitive function do alpha oscillations represent, memory or attention? The answer is both are wrong. The error that both scientists make is to assume that there is a one-to-one mapping between neural phenomena and cognitive functions. This error has become known under the term ‘reverse inference error’, i.e. observing neural signature X has no predictive value for cognitive process Y to occur (Poldrack, 2011). With respect to alpha oscillations, given their ubiquity in terms of cognitive tasks (from attention to decision making) and species (from human to honeybees) it is evident that the task of trying to attach one particular label from cognitive psychology (attention vs memory) to them is bound to fail. An alternative approach is needed if we want to truly understand what the function of alpha oscillations is. This alternative approach needs to be one that does not limit itself by definitions of cognitive processes. Instead, this approach needs to embrace the fact that a given neural phenomenon can be of service to many different cognitive processes in many different species. One such alternative is to assume that different oscillations implement canonical computations (Siegel, Donner, & Engel, 2012; Womelsdorf, Valiante, Sahin, Miller, & Tiesinga, 2014), which are basic neural operations that are called upon by different cognitive processes. Regulating the balance between Excitation and Inhibition, for instance, would be one such basic operation. Another basic operation is to enable the neural representation of information rich content. These operations arguably are required by almost any cognitive task and species. The difference from this approach to the traditional cognitive neuroscience approach is not in using different labels, but to try to understand the computational utility of a neural operation for a given cognitive process (see (Buzsaki, 2019) for a similar line of argument). Instead of asking what the neural correlate of attention is, we ask how can a decrease in alpha oscillations be of service for attention, memory, decision making, etc. In the following we give a brief overview of how we can describe the behaviour of alpha oscillations in terms of frequency, power and phase. It is critical to understand these terms first before we can consider the physiological interpretations of alpha oscillations in the following sections.

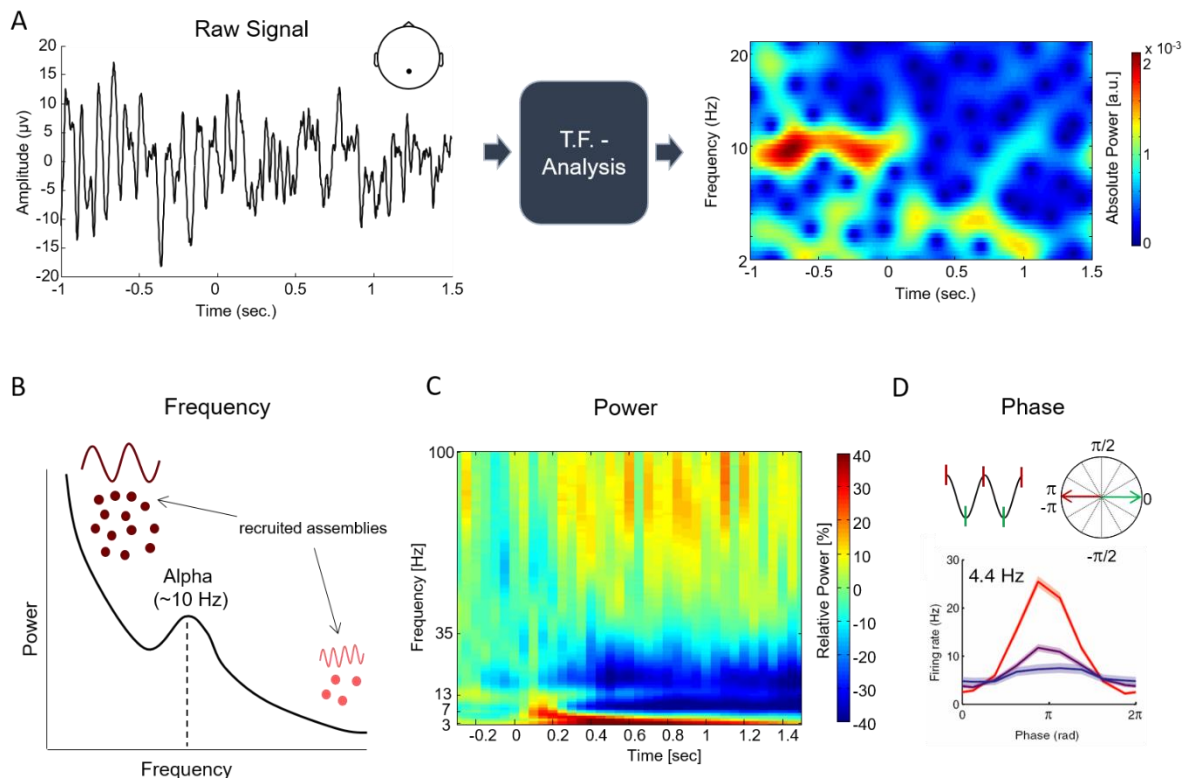
## 2. Signal properties of alpha: Frequency, Power and Phase

Frequency: Analysing alpha oscillations typically involves transforming an EEG signal into time-frequency space (see (Mike X. Cohen, 2014) for an excellent overview of the different methods and hands-on tutorials). Figure 1A shows a typical example of a raw EEG trace in a healthy human subject. It is easy to spot the decrease in alpha amplitudes at time 0 (when a stimulus was presented). Brain oscillations are defined by three physical properties: (i) frequency (Figure 1B), (ii) amplitude (Figure 1C) and (iii) phase (Figure 1D). Different brain networks are hypothesized to oscillate at different frequencies (Keitel & Gross, 2016), with small networks oscillating at fast frequencies ( $>40$  Hz) and large networks oscillating at slower frequencies ( $<20$  Hz) (von Stein & Sarnthein, 2000). Small and large here refers to the number of neurons involved in generating the signal. This anatomical property is reflected in the  $1/F$  power ratio of EEG signals, which refers to the exponential drop in signal power with increasing frequency. Alpha oscillations are remarkable because they stand out from the  $1/F$  pattern (Figure 1B) which shows that they are a particularly strong oscillation recruiting large pools of neurons. Frequencies are typically used to distinguish between different types of oscillations, i.e. theta  $\sim 4$  Hz, Beta  $\sim 15$  Hz, Gamma  $\sim 40$  Hz, etc. The frequency within an oscillation has been shown to be linked to interindividual variability in memory processes (Cohen, 2011) or intelligence (Anokhin & Vogel, 1996). Recent work has demonstrated that the frequency of alpha can also change within a subject, from trial-to-trial (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014) and may reflect cortical excitability (M. X. Cohen, 2014). Therefore, it is important to consider that the frequency of alpha may vary from individual to individual and even from trial to trial within a participant. Sometimes it can even be challenging to distinguish a 'fast theta' from a 'slow alpha'.

Power: The power of an oscillation refers to its signal strength. It is usually calculated by taking the square of the signal. In human EEG, a signal is generated by the summation of several millions of postsynaptic potentials (inhibitory and excitatory) over an area of some  $\text{cm}^2$  (Pfurtscheller, Stancak, & Neuper, 1996). Importantly, the current changes induced by postsynaptic potentials are tiny and we record these potentials with an electrode that is attached to the scalp, separated by various layers of bone, Cerebrospinal fluid, skin, etc. from the brain. Therefore, in order to detect a signal that is large enough to be visible in the EEG tens of thousands of post-synaptic potentials must come together in time. To give analogy, recording EEG is a bit like recording the noise in a football stadium with one big microphone hanging from the ceiling. Using this coarse signal we cannot stand the chance to tune in onto an individual conversation between two fans, but surely we can use the signal to tell whether a goal was scored (because thousands of fans start shouting at the same time). Accordingly, the strength of an oscillation is assumed to reflect the degree of synchrony between inhibitory or excitatory postsynaptic potentials to an underlying neural assembly. Power increases indicate increased local synchrony whereas power decreases indicate de-synchronized local activity. This idea is reflected in the classic work of Pfurtscheller & Aranibar (Pfurtscheller & Aranibar, 1977) who coined the terms event-related synchronization and de-synchronization (ERS/ERD), which denotes power increases and decreases in response to an event or stimulus, respectively. In EEG experiments absolute power is usually transformed into power changes in response to a baseline (e.g. prestimulus interval). Figure 1C shows a typical example of such data with stimulus driven power increases in the lower (1-8 Hz: delta/theta) and higher (40 – 100 Hz; gamma) frequency ranges, and power decreases in the middle frequency ranges (8-35 Hz; alpha/beta).

Phase: The phase of an oscillation specifies the current position in a given cycle (Figure 1D), that is whether the oscillation exhibits a peak, trough or zero crossing. Because the EEG reflects the sum of postsynaptic input to a given neuron, we can assume that it impinges on the neuron's probability to fire an action potential. This is demonstrated in figure 1D, which shows a single neuron recorded in the human brain. The figure shows that the neuron is more likely to fire in the trough of the oscillation, which indeed resembles the time point of maximally coinciding excitatory input (note that the LFP in this case is measured in the extracellular space; therefore, negativity indexes excitation). This same figure also shows that the modulation of firing rate is stronger for trials of high power (red)

and lower for trials of low power (blue). We can therefore assume that the phase of alpha oscillations (or any other oscillation for that matter) represent discrete time windows for neural firing, and that this synchronizing effect scales with power. This is a very useful computational property as it gives alpha oscillations the power to control the timing of neural firing in large groups of neurons. Like the conductor of an orchestra, which tells individual instruments when to play a particular note (and when to not play note), alpha oscillations can synchronize large groups of neurons to temporally structure neural processing. This aspect will become particularly important in section 5 of this chapter when we talk about the role of alpha phase for sampling information and replaying this information from memory.



**Figure 1.** Alpha oscillations and their parameters. (A) An example of a raw signal as recorded with a parietal EEG electrode is shown on the left. A stimulus was presented at time 0. The plot on the right shows the results of a time-frequency analysis in which power is depicted for each time-point (x-axis) and frequency band (y-axis; a.u. = arbitrary units). (B) A schematic of a typical EEG power spectrum is shown, with frequency on the x-axis and power on the y-axis. The inverse relationship between the size of neural assemblies and power is depicted. Note the peak at the alpha frequency which violates the 1/F relation between power and frequency. (C) A typical time-frequency plot showing event related power increases (hot colours) and decreases (cold colours) during processing of verbal information. Note the power increases in theta (3-7 Hz) and gamma (35-100 Hz) and the power decreases in alpha (8 – 12 Hz) and beta (13 – 35 Hz). (D) The relationship between EEG phase (top) and firing rates (bottom) is shown. The differently coloured lines show phase modulations in trials with high (red), medium (purple) or low (blue) power. [A is reprinted with permission from Hanslmayr et al. (2011a), C is modified and reprinted with permission from Hanslmayr et al. (2012); and D modified and reprinted with permission from Jacobs et al. (2007).

### 3. Alpha Oscillations: Passive idling versus active inhibition

Alpha oscillations decrease in amplitude when a subject is engaged in a task as opposed to when a subject is resting (especially with eyes closed). This goes against intuition as one would usually expect to see an increase in brain signal strength when a subject performs a challenging task, not a decrease. How can we functionally interpret this negative relationship between alpha power and

cognitive processing? Up until the early 2000s the prevailing view was that alpha oscillations reflect a state of “idling” or rest. In their article (Pfurtscheller et al., 1996) give the example of the motor cortex, in particular the hand area and the visual cortex during a reading task or a motor task requiring finger movements. During reading, the visual cortex displays profound alpha power decreases, whereas the hand motor area shows an increase in alpha power. This picture switches when the subject engages in a motor task requiring finger movement. Within the idling hypothesis, one would interpret the increased alpha power over areas that are not required by the task as ‘nil work’, i.e. a passive resonance phenomenon of a part of cortex that has ‘nothing to do’ (E. D. Adrian & Matthews, 1934). Since almost any cognitive task always involves specific activation of some regions and de-activation of other regions (Fox et al., 2005) the EEG would always reflect some areas that show alpha power decreases (or desynchronization) and some areas that show alpha power increases (or synchronization). The important emphasis of the idling hypothesis is on the passive aspect of alpha synchronization which has no functional role per se.

A contrasting view to the idling hypothesis was put forward by (Klimesch, Sauseng, & Hanslmayr, 2007) and (Jensen & Mazaheri, 2010), which stated that alpha oscillations play a critical role in cognitive processing. The seminal findings which led up to this interpretation were studies which showed that alpha power *increased* with increasing cognitive load in a working memory task (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). This alpha power increase with cognitive load is difficult to reconcile with the idling hypothesis and led to the Active Inhibition Hypothesis (Jensen & Mazaheri, 2010; Klimesch et al., 2007). Within the active inhibition hypothesis an increase in alpha power reflects an active inhibition process which serves to silence a particular region that is task-irrelevant. This silencing of task irrelevant areas ensures that information is processed selectively in task relevant areas and protects the processing of this information from interference or noise. A critical prediction that the inhibition account made was that an increase in alpha oscillations narrows the time windows for neurons to fire (see red vs blue lines in Figure 1D) and therefore reduces neural firing. Thus, periods of high alpha power should coincide with low neural firing, whereas periods of low alpha power should coincide with high neural firing. This prediction was confirmed in a non-human primate study (Haegens et al., 2011). These findings suggest that an increase in alpha power in a given area acts as a ‘silencing mechanism’, which puts a muffler on neural assemblies that otherwise might interfere.

Coming back to the example above, alpha synchronization of the hand area whilst reading this chapter ensures that you can focus on the text instead of moving around (or thinking about movements). The more challenging a task is, the more we need to tune out task irrelevant activity. The inhibition account has gained considerable support over the last decades because it can accommodate the findings in the literature better than the idling hypothesis. To give two examples, if subjects maintain visual content in working memory that was presented in the left hemifield, therefore being processed in the right occipital cortex, alpha power increases over the left occipital cortex (Sauseng et al., 2009). Externally enhancing alpha power with repetitive transcranial magnetic stimulation over the irrelevant hemisphere then increases working memory performance. Similar evidence comes from (Bonnefond & Jensen, 2012) who demonstrated that subjects actively increase their alpha power in anticipation of a task-irrelevant distractor that is being presented during working memory maintenance. The more the subjects upregulated alpha power the better the performance was on the working memory task. These results rule out a passive perspective of alpha oscillations and instead suggest that alpha oscillations are very much an active process, which regulates neural activity to ensure selective information processing. Within this perspective, alpha oscillations serve the function of a filter that tunes out task irrelevant information in order to render the task relevant signal more salient.

#### 4. Alpha power Decreases and the Representation of Information

The active inhibition account has been extremely useful in interpreting the role of alpha power increases, or alpha synchronization during cognitive processing. This is because any cognitive process requires selective information processing; alpha oscillations, by inhibiting task irrelevant neural assemblies, ensure such selective information processing. This functional interpretation of alpha oscillations is broad enough to accommodate the fact that modulations of alpha oscillations are observed in a variety of cognitive tasks and species. Returning to the thought experiment from above, the attention scientist AC and memory scientist BD would interpret their findings to show that both memory and attention crucially rely on an active filtering mechanism. Indeed, alpha power increases over areas that hold the representation of *task-irrelevant* information, regardless of whether this information is currently perceived (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000), held in working memory (Sauseng et al., 2009), or stored in long-term memory (Waldhauser, Johansson, & Hanslmayr, 2012). The emphasis of the active inhibition hypothesis is on alpha synchronization and its computational utility in terms of providing a filter mechanism for selective information processing. What is less clear from this perspective, however, is what the computational utility of alpha power decreases are for information processing (other than allowing for increased neural spike rates through less inhibition). We therefore proposed an additional theory, which is complementary to the inhibition account. Within this framework we put emphasis on the role of alpha power decreases in allowing for high fidelity information to be represented in neural assemblies. A key assumption of this account rests on the fact the alpha/beta power decreases represent periods of de-correlated neural firing (see (Murthy & Fetz, 1996) for such a demonstration for beta oscillations in the motor cortex).

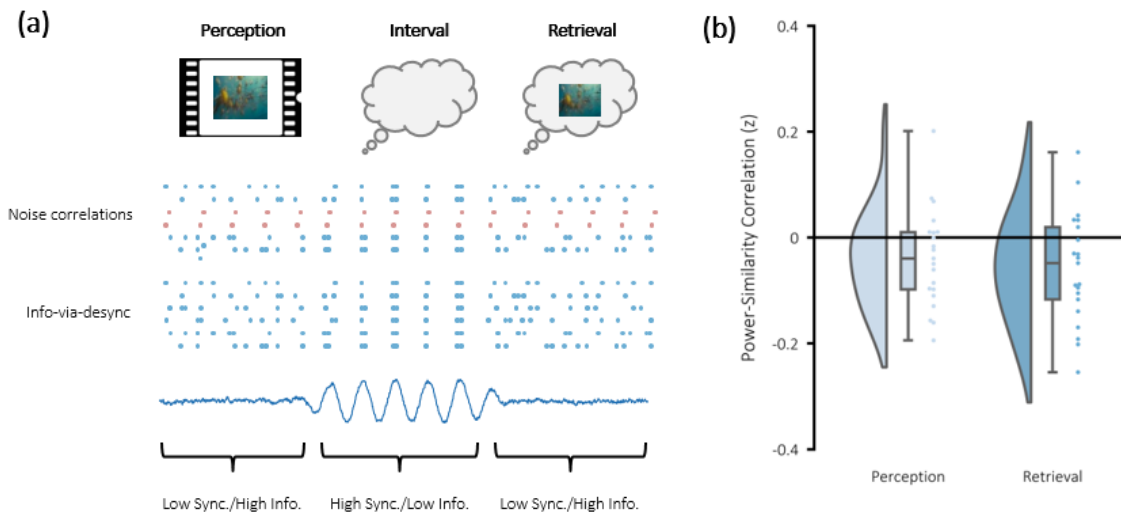
One way of interpreting the functional utility of de-correlated firing in alpha for cognitive processing applies tenets of information theory (Shannon & Weaver, 1949) to neural oscillations. This framework is known as the “information-via-desynchronisation hypothesis” (Hanslmayr, Staudigl, & Fellner, 2012) which proposes that synchronised alpha/beta states are inherently bad for information representation as neuronal activity is highly redundant. Take the simplified instance of two presynaptic neurons that act upon the same postsynaptic neuron: If one presynaptic neuron fires in perfect synchrony with another, what can this neuron add to the neuronal code that its synchronous partner does not already (Schneidman et al., 2011)? If we expand this principle to networks of neurons, we can postulate that highly synchronous networks are detrimental to information processing, because they only represent redundancies. To overcome this limitation therefore, the networks must desynchronise. Through desynchronisation, the underlying neural code can be more complex and hence convey a more detailed representation of information. The event-related desynchronisation so commonly seen in alpha oscillation may be a prime example of this phenomenon.

Numerous studies support the idea that alpha/beta power decreases reflect the representation of information within the cortex. One of the most direct lines of support comes from a recent simultaneous EEG-fMRI experiment (Griffiths et al., 2019). Griffiths and colleagues asked participants to associate video clips with words, and to later recall the clips using the words as a cue (Figure 2). For each trial, the researchers quantified the amount of visual information present in the cortex by conducting representational similarity analysis (RSA) on the fMRI data (Kriegeskorte, Mur, & Bandettini, 2008). RSA is based on correlations of neural patterns and reasons that representations of the same content, should elicit neural patterns that are more alike, than the patterns elicited by representations of different content (Kriegeskorte et al., 2008). The researchers then asked whether the power of the alpha and beta frequencies (8-30Hz) correlated with the quantity of information (calculated via RSA) represented on a given trial. Indeed, they found evidence to suggest a parametric link between alpha/beta power and information: as power decreased, information increased (see figure 2b). A similar study (Hanslmayr et al., 2009) presented participants with words and asked them to engage in semantic processing (i.e. does this word represent a living entity or a non-living entity?) or shallow processing (i.e. does the first letter of the word precede the last in the alphabet?). As semantic

processing involves much greater levels of information processing (you must not only process the letters, but also what those letters mean), the researchers hypothesised that alpha/beta power decreases would be greater during this type of processing. Their results revealed just that, suggesting that alpha/beta power decreases scale with the depth of information processing (see (Fellner et al., 2018) for similar results contrasting familiar and unfamiliar stimuli). In conjunction with a number of other studies, these results strongly implicate alpha/beta power reductions in information processing (Hanslmayr et al., 2012).

While the idling theory of alpha assumed that synchronous alpha oscillations mark a default state in which the cortex does nothing (Pfurtscheller et al., 1996), the inhibition theory of alpha highlights the active role of alpha synchronization in the suppression of task irrelevant information (Jensen & Mazaheri, 2010; Klimesch et al., 2007). It therefore attributes an operative function to alpha synchrony. The information via desynchronization hypothesis goes beyond the inhibition theory, in that it highlights the active role of power decreases for the processing of information. Therein, power decreases are not a mere absence of inhibition, but rather functionally involved in neural computations. The crucial insight is that in order to process complex information or represent information rich content, synchronous neural activity does not provide enough coding space. Desynchronous neural activity on the other hand, which is marked by power decreases in the alpha/beta band, provides the required coding space through locally decoupled neural assemblies. The information via desynchronization theory therefore stresses that, in order to perform cognitive operations that work on complex and information-rich content, alpha/beta power must go down.

Another way to interpret the inverse relation between alpha power and information representation, is offered by studies investigating so-called “Noise-Correlations”. Noise correlations refer to correlated firing of task-irrelevant neurons which can be detrimental to information representation (Mitchell, Sundberg, & Reynolds, 2009). If two task-irrelevant neurons fire together, their noise is amplified. Expand this principle to hundreds or thousands of neurons and their noise becomes deafening. In such quantities, these noise correlations mask the signal generated by neurons critical to the task at hand (Averbeck, Latham, & Pouget, 2006) (see figure 2a), leading to an impaired ability in processing and representing information. To rectify this situation, the magnitude of noise correlations needs to be attenuated. How, though, do noise correlations relate to alpha oscillations? Given that the summed electric potential of the correlated neurons creates a spike in the amplitude of local field potential (Averbeck et al., 2006), repeated and rhythmic patterns of noise correlations would create repeated and rhythmic increases in the amplitude of local field potential (LFP). As alpha oscillations dominate the neocortex, one may speculate that the rhythmic noise correlations may resonate within this frequency band. Under this assumption, periods of high-amplitude alpha oscillations would reflect periods of numerous noise correlations where information processing is inhibited. This interpretation conforms with the Active Inhibition Account because it would allow alpha power increases to suppress task-irrelevant information. Periods of alpha desynchrony, in contrast, would reflect periods of limited noise correlations, where there is a greatest potential for information representation.



**Figure 2.** Alpha power and information processing. (a) infographic depicting theories behind alpha and information processing. Perception and memory retrieval involve the processing of large quantities of information. The noise correlation account proposes that when task irrelevant neurons (in blue) synchronise (e.g. during the interval), they mask the signal generated by task-relevant neurons (in red). When the task-irrelevant neurons desynchronise however (i.e. during perception/retrieval), the signal can be detected above the background noise. The information-via-desynchronisation account proposes that oscillatory desynchronisation allows a more complex neural code to be generated. Such a complex code is necessary to process the highly complex information encountered in daily life. In both instances, oscillatory desynchronisation benefits information processing (b) reproduction of the results by Griffiths and colleagues. Power decreases during both perception and retrieval negatively correlate with the amount of stimulus specific information present on that trial.

In summary, there are two theoretical arguments that implicate alpha power decreases in the representation of stimulus-specific information. The information-via-desynchronisation account suggests that alpha power reductions allow for more complex neural codes to evolve, allowing for the representation of high-fidelity information in the cortex. The noise correlation account suggests that alpha power decreases reduce the background noise in the cortex, allowing for key signals to be more clearly communicated. Currently, empirical evidence supports both ideas by demonstrating that alpha power decreases scale with the quantity of information present in the cortex.

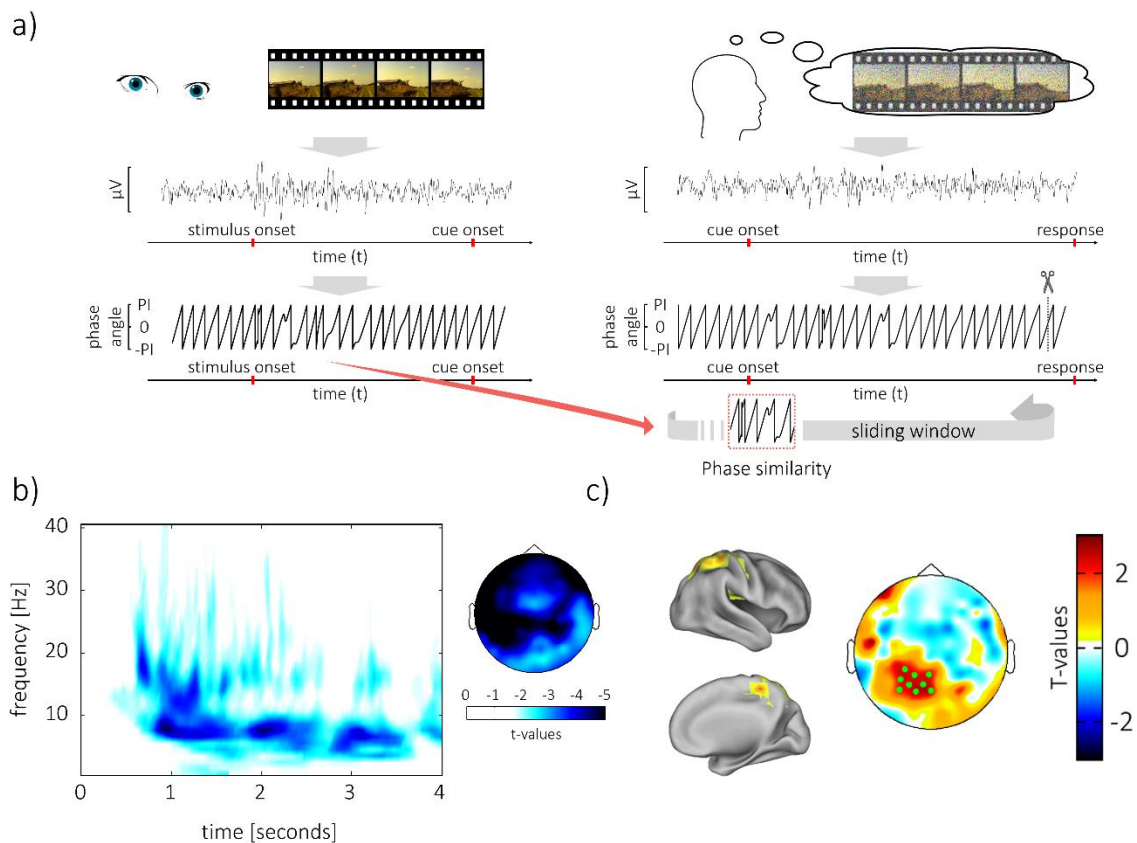
## 5. Alpha Phase: Information Sampling and Replay

Recent evidence suggests that the continuous input that our brain receives from the outside world is not sampled continuously, but in discrete rhythmic steps around the alpha frequency (VanRullen, 2016). These studies show that the probability of detecting a briefly presented visual stimulus fluctuates rhythmically (VanRullen, Carlson, & Cavanagh, 2007). This attentional sampling process has been suggested to operate at a frequency of roughly 8 Hz (Landau & Fries, 2012), even when sustained attention to the same object is maintained (Fiebelkorn & Kastner, 2019; Fiebelkorn, Saalman, & Kastner, 2013). Overall there appears to be an intimate relation between the phase of an oscillation in the lower alpha band (around 8 Hz) and the perception of an incoming stimulus. In the perception of continuous and dynamic stimuli, the stimulus identity can be reliably decoded from the ongoing phase of neural oscillations. Therein, an individual continuous stimulus is associated with a unique time course of neural activity. Specifically, the stimulus entrains the cortical rhythm in a content specific way that organizes neural firing (Ng, Logothetis, & Kayser, 2013). Interestingly, the phase of the ongoing oscillation has been shown to contain more information about stimulus identity than its power (Schyns, Thut, & Gross, 2011).



Considering this information sampling role of alpha phase in perception, an imminent question is, whether the reinstatement of information from memory, relies on the replay of that information sampled in the alpha frequency. To this end, alpha phase could index similar mechanisms during attention and memory, just like alpha power decreases as described above. But how can we measure the information sampling and the replay thereof in the phase of a recorded EEG?

Similar to assessing the similarity of neural patterns in space, as is usually done in fMRI, one can assess the similarity of neural patterns in phase (over time), via the use of RSA methods (see above). To quantify the similarity of neural patterns in the phase of the alpha frequency band, established measures of connectivity can be used (Greenblatt, Pflieger, & Ossadtchi, 2012). Connectivity measures usually assess the similarity between different channels in their time course of activity. This typically measures shared information between regions. Yet, measures of connectivity will lend themselves perfectly to quantify representational similarity between encoding and retrieval (see Figure 3a for an illustration).



**Figure 3.** Alpha power decreases during memory retrieval code stimulus-specific information. A, Subjects first encoded a video (left). They later retrieved a vivid representation of that video from memory (right). The phase time course was extracted from the EEG during encoding and retrieval in order to calculate a similarity measure between encoding and retrieval. B, During retrieval, strong and sustained alpha power decreases were observed. C, Reactivation of stimulus-specific information, as measured with phase similarity, could be detected in the alpha frequency band with a maximum in parietal regions. Reproduced from Michelmann, Bowman, and Hanslmayr (2016). This reactivation was localized in parietal cortex (C, left).

In a first study we applied such similarity measures of phase in a human EEG experiment where subjects were instructed to encode and replay dynamic visual (short movie clips) or auditory stimuli (short melodies played by different instruments). Indeed, content specific patterns of oscillatory phase

in the lower alpha band during perception represent the identity of the visual or auditory stimuli in the visual and auditory cortex, respectively. Strikingly, these phase patterns reappear, when representations of short video-clips and short sound-clips are replayed from memory (Michelmann, Bowman, & Hanslmayr, 2016). Importantly this replay takes place in the absence of the dynamic stimulus itself and can be localized in sensory specific areas (Figure 3c). A recent study replicated this effect in the visual domain and demonstrated that the reinstatement of temporal patterns is only observed when content is successfully recalled, i.e. temporal pattern reinstatement is implicated in successful memory (Michelmann, Staresina, Bowman, & Hanslmayr, 2019). Another study replicated this effect during sleep, indicating that replay of stimulus specific phase patterns supports memory consolidation (Schreiner, Doeller, Jensen, Rasch, & Staudigl, 2018). Further evidence documents that such content specific phase patterns are also replayed, when an association with a previously shown dynamic stimulus is formed (Michelmann, Bowman, & Hanslmayr, 2018).

Interestingly, the reinstatement of temporal patterns is not always beneficial for memory but can in some cases interfere with memory. This was demonstrated in studies where the contextual overlap between encoding and retrieval was manipulated. For instance, (Staudigl, Vollmar, Noachtar, & Hanslmayr, 2015) manipulated the context in which a word is learned and remembered, playing the same video-clip in the background behind the word, at encoding and at retrieval (context match); or playing a different video-clip in the background at encoding and at retrieval (context mismatch). The importance of reinstatement of contextual information was observed via temporal and spatial pattern similarity in the beta frequency band. Specifically, higher pattern similarity was associated with better memory performance when contexts were matching. Non-overlapping contexts on the other hand, were characterized by more dissimilar patterns for remembered vs. forgotten words. These findings were recently replicated in a study using sensory modality (i.e. presenting a word visually or aurally) as a context match/mismatch manipulation (Staudigl & Hanslmayr, 2019). The results of these studies are in line with the notion that context reinstatement is only helpful when the context has not changed and substantiate the importance of temporal patterns for content representation.

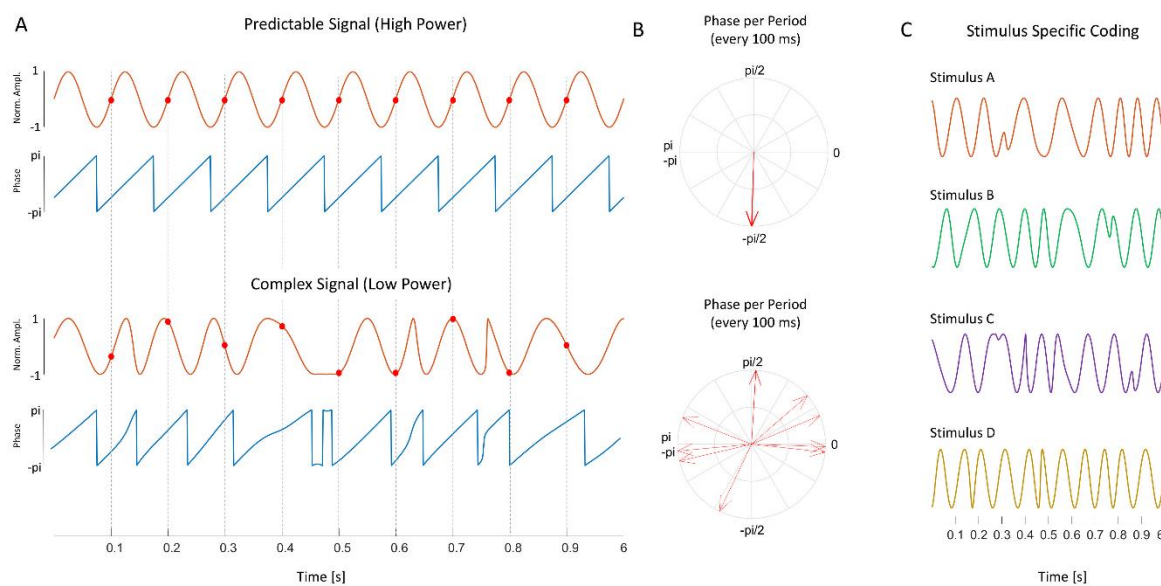
Most studies reported above found that stimulus specific information was coded in the phase of the lower alpha band, around 8 Hz (Michelmann et al., 2016, 2018; Michelmann et al., 2019; Staudigl & Hanslmayr, 2019). Corroborating evidence for a special role of 8 Hz in the sampling of memories comes from a recent study that decoded content specific representations in memory, from spatial patterns of activity (Kerren, Linde-Domingo, Hanslmayr, & Wimber, 2018). The authors show that these patterns fluctuate at a frequency of 8 Hz. The sampling of information at an 8 Hz rhythm therefore seems to underlie both, rhythmic sampling of information during perception (VanRullen et al., 2007) and the replay of that information during memory reinstatement.

## 6. Linking alpha phase and power

A crucial result from (Michelmann et al., 2016) is that the frequency band that contains content specific temporal patterns is also the one that displays the most prominent power decreases during retrieval (Figure 3b). Furthermore, in (Michelmann et al., 2016) an interaction was observed, such that sensory areas that were involved in the reinstatement of auditory and visual temporal patterns also expressed stronger power decreases in the respective condition. This suggests that power decreases and the representation of information in oscillatory phase are not two separate processes but are rather intertwined. This raises the question as to how the two signal properties of alpha, power and phase interact in the service of information representation.

We suggest that a decrease of power in an ongoing oscillation renders a signal less stationary (and therefore also less predictable) and thereby allows for a flexible adjustment of phase (Hanslmayr, Staresina, & Bowman, 2016). These phase adjustments, or deviations from stationarity, make it

possible that time courses in phase can represent stimulus specific patterns, and to replay these patterns from memory (see Figure 4C). From an information theoretic view, a stationary oscillation without phase adjustments, wouldn't be able to represent much information in its phase. This is because the time course of a stationary signal is perfectly predictable once the phase at one time point is known. The signal in the top-row of Figure 4A for instance visits the same phase every 100 ms (to row in Figure 4B). Since information theory quantifies information as the inverse of the predictability (i.e. negative logarithm in the case of Shannon's Entropy; (Shannon & Weaver, 1949)) we can infer that this signal has little potential to carry information. Indeed, if we were to code the identity of a stimulus in such a perfectly predictable signal, we would not be able to distinguish between different stimuli. In contrast, a non-stationary signal, illustrated in the lower row of Figure 4A, which has phase modulations can carry much more information. In this case, the phase cannot be predicted from previous time points (lower panel in Figure 4B). This allows us to code different stimuli by assigning a phase time course to each stimulus (Figure 4C). This simple relationship between the power of a signal and predictability of phase time courses elegantly unifies the findings described in this chapter. To this end, a signal with high alpha power leads to a more stationary time course and thus inhibits information coding. In contrast, a signal with lower alpha power allows for a less stationary time course and therefore the coding of information. Importantly, this idea is in line with the general notion of an inhibitory role of alpha power increases, but goes beyond the previous work in ascribing specific computational roles to power and phase in the service of representing information.



**Figure 4.** Information coding properties for stationary and non-stationary signals is illustrated. (A) A stationary (high power) signal (orange) is shown together with its phase (blue) in the upper row. The lower row shows a less stationary signal. (B) Phases for each signal are shown every 100 ms (indicated by ticks in A). (C) Non-stationary signals allow for stimulus specific coding by assigning a different time course to each stimulus.

## Concluding Remarks

In this chapter we have shown that alpha oscillations are ubiquitous as they are modulated by almost any task, and can be observed in almost any animal. It therefore follows that alpha oscillations must perform a basic neural operation, which is of service for many cognitive operations. After giving an overview of the idling vs inhibition hypothesis we then focused on the computational utility of alpha power reductions for information representation. We reviewed studies which demonstrated that alpha power reductions are intimately linked to information coding. In particular, these studies showed that stimulus specific information is coded in the phase of alpha. Importantly, several studies demonstrated

that this phase information is replayed when a reminder to that stimulus is presented. Finally, we illustrated how power decreases allow for less stationary phase time courses and consequently for information representation. Together, we can conclude that alpha power decreases do play an important role for information representation, a neural operation which is needed in almost any task and in almost any animal.

An important crucial future question refers to the nature of the relationship between alpha power decreases and its role for coding information. If indeed, as we here suggest, alpha power decreases are mechanism for representing information we should be able to manipulate perception, maintenance and retrieval of information by directly manipulating alpha oscillations via brain stimulation techniques (Hanslmayr, Axmacher, & Inman, 2019). Such a demonstration of a causal relationship between alpha power decreases and the representation of information is crucial in order to show that alpha oscillations are indeed a mechanism for information representation instead of a mere epiphenomenon.

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