Feature Review

Alpha-band oscillations, attention, and controlled access to stored information

Wolfgang Klimesch

Department of Physiological Psychology, University of Salzburg, A-5020 Salzburg, Austria

Alpha-band oscillations are the dominant oscillations in the human brain and recent evidence suggests that they have an inhibitory function. Nonetheless, there is little doubt that alpha-band oscillations also play an active role in information processing. In this article, I suggest that alpha-band oscillations have two roles (inhibition and timing) that are closely linked to two fundamental functions of attention (suppression and selection), which enable controlled knowledge access and semantic orientation (the ability to be consciously oriented in time, space, and context). As such, alpha-band oscillations reflect one of the most basic cognitive processes and can also be shown to play a key role in the coalescence of brain activity in different frequencies.

Oscillations and temporal structure in the brain

According to the traditional view, brain function is primarily described on the basis of functional anatomy. Anatomy and functional connectivity can be considered the spatial or geometrical dimension of the mind. However, for a more comprehensive understanding, an additional dimension must be considered: time. The brain generates its own temporal structure, which is largely organized by oscillations (e.g., [1]). This aspect has become an important issue in the investigation of perceptual and cognitive processes (for recent reviews see, for example, [2,3]). In this review, the focus is on alpha-band oscillations as the dominant oscillations in the human brain, with a mean frequency of approximately 10 Hz.

In the sections that follow, I will argue that alpha-band oscillations reflect the temporal structure of one of the most basic cognitive processes, which may be described as 'knowledge-based consciousness' and which enables 'semantic orientation' via controlled access to information stored in a complex knowledge system (KS; see Glossary).

Alpha-band oscillations and two types of event-related amplitude responses

Alpha-band activity is particularly interesting because it is the only frequency domain (with the exception of slow beta, a frequency higher than alpha, up to approximately 20 Hz) that responds to a stimulus and/or task demands either with a decrease or increase in amplitude/power, termed event-related desynchronization and synchronization, or ERD and ERS, respectively. The response of other frequencies (particularly in the delta, theta and gamma frequency

range) is 'simply' characterized by ERS (see [4,5]). This is interesting because one implicit assumption in EEG research is that oscillations have an impact on information processing that is proportional to their magnitude. In this sense, ERS, but not ERD, would have to be considered the 'active' task-relevant alpha-band response. This, however, is in contradiction with the classical view (e.g., [6]) which holds that suppression of alpha-band activity (ERD) is the

---

Glossary

Amplitude: the 'magnitude' of an oscillation, reflecting the distance between the maximal positive- and negative-going points (phase) of an oscillatory cycle.

Attentional blink (AB): the reduced ability to report a second target (T2) after identifying a first target (T1) in a rapid serial visual presentation (RSVP; see Figure 3a in main text) of stimuli. There are three preconditions for AB to be observed: (i) Stimulus presentation rate must be approximately 10 items per second. (ii) At least one distracter must follow T1 and T2. (iii) The second target, T2, must be presented between approximately 100 and 500 ms after T1 [42,97].

Attentional buffer: a 'pre-activated' region of the KS that keeps target information available. What region of the KS is pre-activated is determined by expectancy. The attentional buffer is not directly related to working memory (WM) and should not be confused with short-term memory or rehearsal. It is assumed that iconic memory is the bottom-up activated region of the KS, whereas the attentional buffer is the (overlapping) top-down activated region within iconic memory. One fundamental aspect of the proposal in this article is that WM and KS interact in such a way that (episodic) WM coding is based on the re-activation of information stored in the KS.

Cross frequency (CF) coupling: denotes the 'interplay' between two different frequencies (f1, f2). Here, the emphasis is on CF phase $\varphi_1(t)$ and $\varphi_2(t)$ synchronization.

Event-related desynchronization and synchronization (ERD and ERS): terms used to describe an event-related amplitude response (to a stimulus and/or task) within a selected frequency band that is quantified as the normalized difference in band power between a reference ('baseline') and a test period (see the original studies by Pfurtscheller and colleagues [9,98]). ERD reflects an amplitude decrease, whereas ERS reflects an increase. In the present article, as the focus is on alpha-band activity, ERD/ERS will be used synonymously with alpha ERD/ERS.

Golden mean: denotes a certain ratio between two quantities which equals 1.618.

Inhibitory filter: a process that blocks task-irrelevant, competing processes/neuronal structures and selectively increases the SNR in task-relevant processes/neuronal structures.

Knowledge system (KS): a storage system, comprising not only traditional long-term memory (LTM) – a system closely associated with the storage of declarative information – but any type of knowledge, including procedural and implicit-perceptual knowledge. In this article, the focus is on access to the KS, not on processes operating within the KS. Perception, encoding, and recognition are processes that are guided by attention [99,100] and are closely related to access of information in the KS. Early stages of encoding can be considered categorization processes that are based on global features. They operate to establish an 'access field', which is considered a necessary step for initiating a spreading activation process within the KS that underlies the retrieval of information.

Phase: indicates a particular time point within a single oscillatory cycle or period (for an example, see Figure 3b in main text) and is frequently measured in degrees (0-360°).

Power: a measure that estimates the magnitude of oscillatory amplitude within a defined time window.

'typical' event-related alpha response. This view comes from the basic observation that alpha amplitudes are large when the eyes are closed and become suppressed when eyes are opened. It has been known since the early days of EEG research that this type of alpha suppression is not due to visual stimulation because it can also be observed in a completely darkened room [7,8]. ERD can be observed in response to a variety of different tasks, and it was assumed that it reflects cortical activation, or more precisely, cortical excitation. More recently, however, it was recognized that under certain task demands ERS (instead of ERD) can be observed.

ERS reflects inhibition and ERD the release from inhibition

Numerous studies have meanwhile suggested that alpha ERS reflects inhibition. The most general observation is that brain regions that are activated during a task exhibit ERD, whereas regions associated with task irrelevant and potentially interfering processes exhibit ERS (see [9]). This has been observed for example, in tasks that vary stimulus modality, stimulus processing domain (e.g., related to the ventral vs dorsal processing stream) or stimulation side (e.g., stimulation of the right vs left visual hemifield). Findings show that alpha power is larger over visual cortices when attention is focused on the auditory part of a compound auditory-visual stimulus [10]. Alpha power is larger over parietal regions when a task engages the ventral stream [11]. In spatial cueing and hemifield tasks, alpha power is larger over the ipsilateral than the contralateral hemisphere (e.g., [12–15]). Most interestingly, this result is not simply a 'passive' effect of contralateral power suppression, due to stimulus processing. Even if both hemispheres are stimulated, the attentional focus is the critical factor that leads to ERD at the contralateral, but to ERS at the ipsilateral hemisphere (e.g., [15,16]). This important finding demonstrates that ERD is not an obligatory response to a stimulus (for a discussion, see [17]).

As a logical consequence, if an increase in amplitude (i.e., ERS) reflects inhibition, a decrease in amplitude (i.e., ERD) reflects release from inhibition. The latter interpretation is in agreement with the traditional view, which assumes that the magnitude of ERD reflects the degree of cortical activation (see the cortical activation model by Pfurtscheller [18]).

Alpha phase and the inhibition timing hypothesis

ERS and other measures of power are insensitive to phase. However, it is the very nature of an oscillation to reflect rhythmic changes. With respect to alpha oscillations, as inhibitory oscillations, this means that the change is between minimal and maximal inhibition (see [19] and Figure 1).

The two faces of inhibition: selective activation vs blocking of information processing

In an ideal situation, excitation and inhibition may influence each other in such a way that inhibition is silencing weakly excited cells, but operates to induce a pulsed pattern of action potentials (APs) in cells with a higher excitation level, as is illustrated in Case 2b of Figure 1a. Thus,

the time and direction of a change in inhibition – described by phase – is functionally related to the timing of neuronal activation processes. This interpretation can nicely explain the observation that inhibition is an active process for information processing that helps to increase the signal to noise ratio (SNR). In this sense, inhibition and excitation depend on and are 'tuned' by each other (e.g., [20,21]) to increase SNR.

It is important to note that this ideal situation cannot simply be explained by an increase in amplitude. Consider Case 1 and Case 2a in Figure 1a. An increase in amplitude induces 'timing', which is apparent in the pulsed AP pattern for Cell 1 and Cell 2. However, a further increase in amplitude would not lead to inhibition (in the sense of silencing less excitatory cells), but to even more precise timing. A hypothetical assumption to overcome this problem is to assume a baseline shift as is illustrated in Case 2b and 3 of Figure 1a, which means that the phase with minimal inhibition also exhibits an increase in the magnitude of inhibition. This could be a mechanism that enables the 'silencing' of those principal cells which have a comparatively low level of excitation (see Cell 1 in Case 2b).

For task irrelevant/competing structures yet another mechanism might be considered. The excitation level of principal cells will generally be low and an increase in amplitude will lead to precise timing, but without any systematic variation in the temporal AP pattern. The reason is that the excitation level of principal cells is not modulated (as they are – by definition – not involved in processing a task) and, thus, the AP firing pattern will not differ systematically between cells. Because information is most likely encoded by variations in interspike intervals and the number of spikes in bursts, a completely monotonous AP pattern as illustrated in Figure 1b will not allow information to be transmitted. Such a scenario might be consistent with the suggestion that oscillations play a role for phase coding, as suggested by Nadasdy [22] for fast frequencies in the gamma range. The central idea is that topographical phase differences in traveling waves code information. A stationary wave, characterized by a lack of topographical phase differences, will not be able to code information but may lead – via spatial summation – to a large amplitude at a scalp electrode. A lack of phase coding may be considered a state that blocks the processing of information. The finding that alpha hypersynchronization is associated with a loss of consciousness [23] is well in line with these considerations.

The physiology of brain oscillations is very well investigated, particularly in animal research, for certain types of oscillations, especially for theta, gamma, and sleep spindles (for reviews see, for example, [24,25]). Only a few studies have focused on alpha oscillations (Box 1). Although there is evidence that alpha-band oscillations have an inhibitory influence on the generation of action potentials as was demonstrated by Haegens [26] (Figure 2), the exact physiological mechanisms that generate alpha-band activity are not yet known.

The cognitive significance of alpha-band oscillations

When trying to evaluate the possible cognitive significance of alpha-band oscillations the following two questions should be considered. First, is the cognitive role of alpha
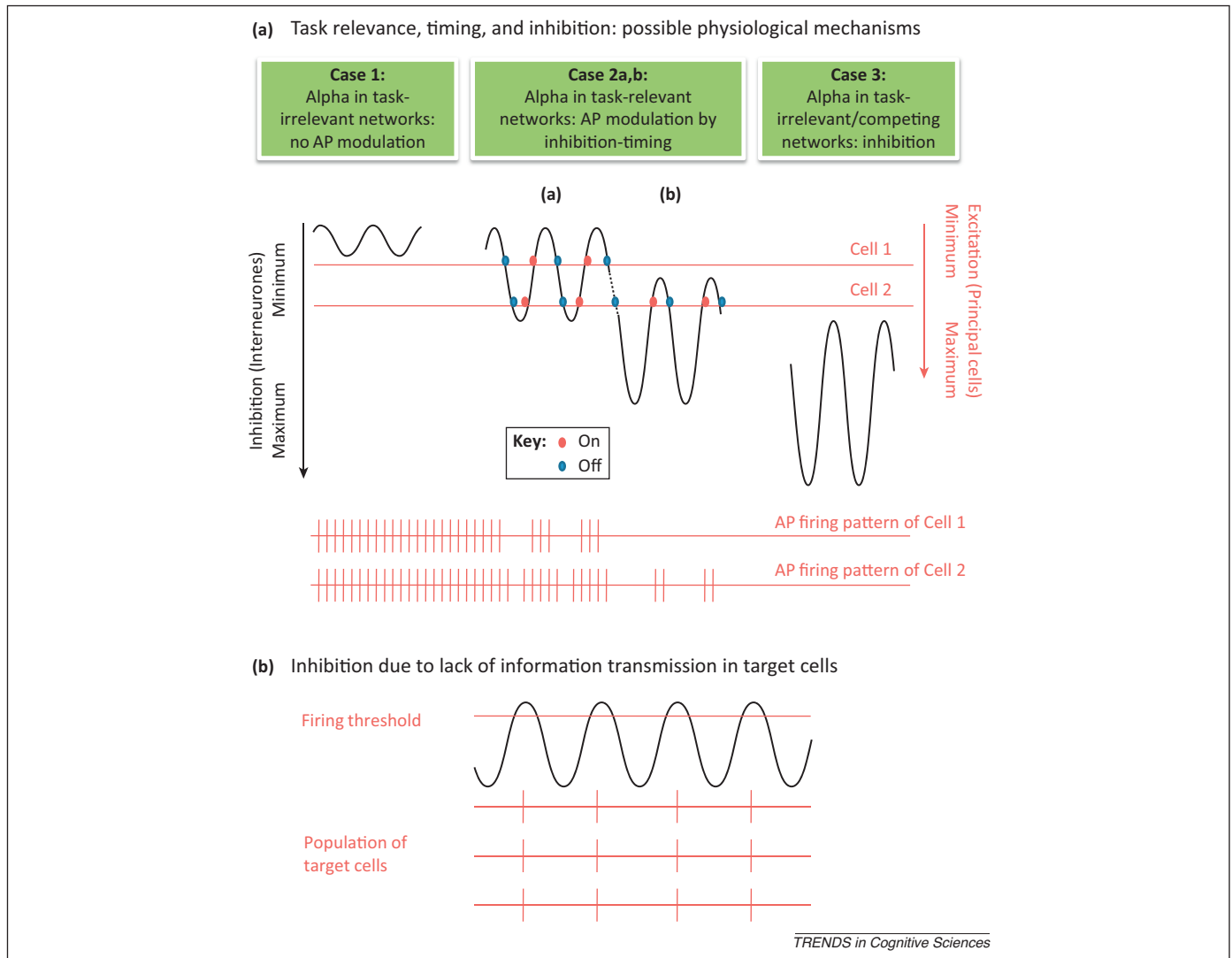
Figure 1. The inhibition timing hypothesis. **(a)** Illustration of the main assumption of the inhibition timing hypothesis. Three cases are distinguished. Case 1: In task-irrelevant networks, the amplitude of alpha oscillations is small and has no impact on cell firing rate, which is symbolized by short vertical lines representing action potentials (APs) in the lower panel. Case 2: In task-relevant networks, the amplitude of alpha oscillations increases and starts to inhibit the generation of APs in target cells during the inhibitory phase of the oscillation. Depending on the excitation level of target cells, the impact of the inhibitory oscillation is different (cf. Cell 1 and 2). With an increase in amplitudes, the inhibitory baseline increases, which means that inhibition increases not only during the phases with maximal inhibition (plotted here as troughs), but also during those with minimal inhibition (plotted here as peaks). Case 3: If inhibition increases further, all target cells are silenced. This case is assumed for neuronal structures that are potentially competing relative to the processing of a task. A good example is the inhibition of potentially competing regions in the ipsilateral hemisphere. Adapted, with permission, from [30]. **(b)** An alternative interpretation of Case 3. The increased alpha amplitudes during a state of inhibition may stem from spatial summation (at the level of scalp electrodes) of phase-coherent alpha sources that lead to a monotonous firing pattern in a population of target cells. If there is no variation in the AP firing pattern, no information can be transmitted. Such a case may emerge in task-irrelevant structures in which the excitation level of a population of principal cells is low and does not vary systematically.

oscillations related to a well described cognitive 'domain', such as perception, attention, working memory (WM), and long-term memory (LTM), or is it related to functions that are yet not well described or difficult to describe? I will argue for the latter. Second, in light of the fact that the inhibitory function of alpha oscillations appears well supported and elaborated [27], the question which cognitive processes are best compatible with the inhibition timing function must be asked.

The first question is complex and difficult to answer. The reason is that alpha oscillations appear to respond to almost all of the aforementioned cognitive domains. I will argue that alpha-band activity reflects a special class of processes – related to the controlled access to and retrieval from the KS – which are yet not well described. These processes are very basic and, thus, underlie many other

cognitive processes. Let us consider the traditional alpha response, ERD, as an example. ERD can be observed in response to a large variety of stimuli, but also to cognitive demands without stimulation (e.g., [28,29]). A first hint to a possibly specific function of alpha-band activity is the very reliable finding that during retrieval from LTM the magnitude of ERD varies as a function of the semantic content of the information that is retrieved. The more semantically integrated the retrieved information is, the larger the ERD magnitude is (at approximately 200 – 500 ms poststimulus; for reviews see [5,19,30,31]). Because ERD can be interpreted as release from inhibition, this finding simply means that retrieval of semantically well integrated information elicits more cortical excitation than less integrated information. This finding is interesting because of its cognitive selectivity.

Box 1. The physiological basis of alpha-band oscillations in animal research

Early research [101] tried to relate alpha-band activity to spindle activity and to thalamo-cortico-thalamic re-entrant loops. Nevertheless, it is clear that alpha-band oscillations and spindle oscillations have a strikingly different physiological basis [102]. Alpha-band activity certainly plays an important role in thalamo-cortical structures [103–107]. Thalamic nuclei, particularly the lateral geniculate, are known to play an important role in driving alpha activity [108]. Recent findings suggest that the thalamic pulvinar nucleus modulates alpha synchrony between cortical areas as a function of attentional demands [109]. Nonetheless, the functional meaning of alpha-band oscillations appears closely associated with activity in cortico-cortical networks [110–112]. There is promising recent research about the cortical sources of alpha-band activity, showing that it is present at different cortical layers and is capable of driving multi-unit activity in a task dependent manner [26,112]. Most importantly, Haegens *et al.* [26] were also able to demonstrate that during periods of increased alpha activity, multi-unit activity decreases (see Figure 2 in main text). This is probably the first physiological evidence for an inhibitory role of alpha-band activity. Up to the present, there is only indirect evidence that alpha-band oscillations may stem from rhythmic GABAergic activity. For example, Lörincz *et al.* [105] demonstrated that a subtype of excitatory thalamo-cortical neurons burst in alpha frequency and are driving inhibitory interneurons.
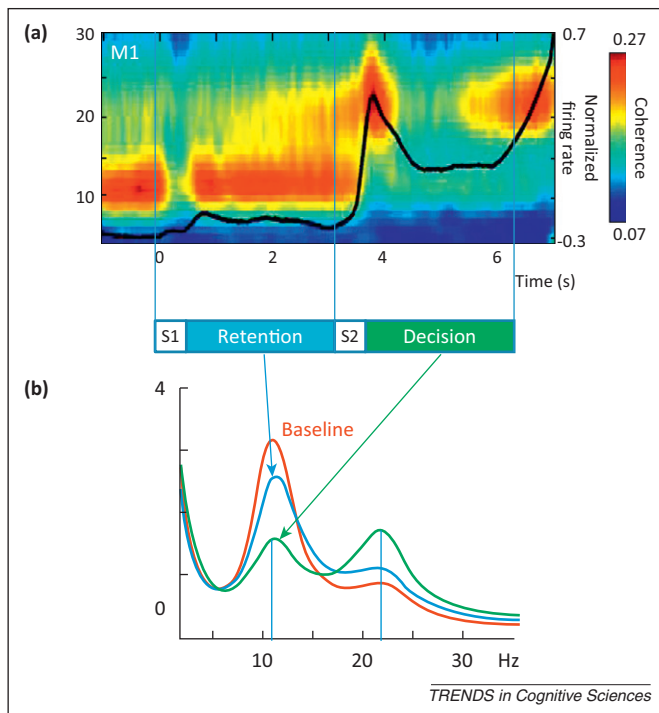

Figure 2. A recent animal study by Haegens *et al.* [26] demonstrates nicely that alpha activity drives spiking and that the power of alpha oscillations is associated with the rate of spiking. Monkeys were trained to perform a vibrotactile discrimination task between two stimuli S1 and S2. Local field potentials and spikes were recorded simultaneously. **(a)** Spike field coherence in M1 (contralateral to the responding hand) is most pronounced in the alpha frequency range. This indicates that alpha-band activity drives action potentials. The black line represents the spiking rate during task performance. **(b)** Power spectra for a baseline, the retention period, and the decision period exhibit a clear alpha peak at approximately 11 Hz. During the decision period, a harmonic peak at approximately 22 Hz emerges, probably reflecting the preparation of the motor response. Note that spiking rate is negatively associated with alpha power. Large alpha power during retention is associated with reduced spiking, whereas a decrease in alpha power during decision is associated with enhanced spiking. Reproduced, with permission, from [26].

The second question is easier to answer. If alpha-band activity is indeed inhibitory, then it should underlie a cognitive process that reflects the two aspects of inhibition, timing and blocking information processing as described above. One of the most promising candidates is attention, because one of its central functions is to enhance and 'sharpen' processes within the attentional focus and to block processing outside the focus. When focused on external information, attention is usually under top-down control and operates as an 'interface' with the external world. In this way, attention interacts closely with perception and is subject to capacity limits of the 'attentional buffer' (which may be considered a 'sub-buffer' of iconic memory, closely related to the KS, but not to WM). In the internal and external processing mode, attention is anticipatory with a focus on the type of information that is conveyed by a stimulus and the time point of its appearance. These two aspects of attentional selection are referred to as anticipatory and temporal attention and are suggested to be closely associated with alpha-band oscillations.

For a long time the alpha-band frequency range has been associated with attention [7]. However, attention is a very complex concept comprising very different functions. Here, I will argue that the two fundamental functions of attention as filter (suppression and selection) enable selective access to the KS and operate according to the proposed inhibition timing function of alpha-band activity [19,30]. Brain processes related to the enhancing function within the attentional focus are characterized by a phase response (reflecting the 'timing' aspect of alpha-band oscillations; see also [32]) and a subsequent ERD. On the other hand, brain processes related to the suppressing function of attention are primarily associated with an increase in alpha amplitude (ERS), reflecting the inhibitory aspect of alpha-band oscillations (see also [32,33]). A good example for this antagonistic ERD/ERS response is the concept of focal ERD/surround ERS, suggested by Suffczynski *et al.* [34] to emphasize that cortical activation (reflected by ERD) may be more focused when surrounded by inhibition (reflected by ERS).

Alpha-band activity is associated with certain types of attention only

In support of the notion that alpha-band activity reflects a specific aspect of attention – and not attention in general – is the fact that monitoring new information reliably elicits a strong task- and event-related increase in the theta frequency band (approximately 6 Hz). A good example is the frontal midline theta-band activity that can be observed in response to increased WM demands (e.g., [35] and Figure 4b) reflecting sustained attention to the processing of new information. It should be mentioned that in these tasks, alpha-band activity responds with ERS, most likely reflecting the suppression of task-irrelevant structures and not the enhancing aspect of attentional selection.

Anticipatory attention and prestimulus ERD

The traditional argument for an involvement of alpha-band activity in attention is provided by findings showing that alpha-band activity desynchronizes in response to anticipatory attention and in the absence of stimulation

(e.g., [36]). This type of ERD will be termed 'prestimulus, anticipatory ERD' and is well documented in discrimination tasks with well defined targets under difficult presentation conditions.

It is interesting that the anticipatory ERD is related to good discrimination performance. In discrimination tasks, requiring the identification of a visual target (e.g., the letter 'p' or 'q') under difficult perceptual conditions (a very short target exposure time and an immediately following mask), a large prestimulus ERD is related to good detection performance ([37,38]; for related findings, see [39,40]). This type of prestimulus ERD reflects anticipatory attention, which may be interpreted to reflect the maintenance of target information in an attentional buffer that is not part of WM, but is understood as a selectively activated part of the KS. Thus, anticipatory attention is focused attention on information stored in the KS. This means that the respective (target-) information does not need to be retrieved when the target is presented. Because there is good evidence that the onset of ERD reflects the onset of the retrieval process [41], the prediction is that in discrimination tasks with well defined targets no ERD should develop. This is indeed the case as, for instance, the results in Hanslmayr *et al.* [38] have shown. In other words, in this type of tasks, there is a lack of ERD, despite visual stimulation. It should also be noted that, in memory tasks, the relationship between pre- and post-stimulus power is reversed (for a review see [5]): large pre-stimulus power is indicative of good memory performance. This may reflect an attentional mode of suppressing or blocking the processing of distracting information in memory tasks, which means blocking access to the KS in the pre-stimulus period, in order to enable selective access during the post-stimulus period.

Temporal attention and alpha phase
The relationship between alpha-band activity and attention is not restricted to task-related changes in amplitude; it also comprises phase. As the findings in Hanslmayr *et al.* [38] suggest, focused attention elicits large phase locking during the processing of a target stimulus without a concomitant amplitude change. This phase response may be interpreted to reflect temporal attention. Thus, alpha phase should also play a crucial role for the attentional blink (AB) phenomenon, which is one of the most important experimental examples of temporal attention. The AB represents reduced ability to report a second target (T2) after identifying a first target (T1) in a rapid serial visual presentation (RSVP; Figure 3a) of stimuli. The explanations of the phenomenon proposed so far have focused primarily on cognitive aspects, such as attentional filter, capacity limitation, and retrieval failure processes (for reviews see [42,43]). More recently, the role of brain oscillations has also started to be considered (for a review see [44]).

The central issue here is that the AB depends on a stimulation frequency of approximately 10 items per second, which equals a mean alpha frequency of approximately 10 Hz. The interesting point here is that a fast visual stimulation frequency changes the event-related potential in the sense that the appearance of the typical P1/N1 waveform (consisting of a positive wave at approximately 100 ms and a negative wave at approximately 160 ms post-stimulus; [45]) disappears and a steady state visual evoked potential (SSVEP) emerges (e.g., [46,47]). The properties of driven EEG activity are well documented (e.g., [46,48,49]; for a recent review see [50]) and show in general that the alpha frequency range is the most responsive. The hypothesis here is that entrainment of alpha phase at a certain phase angle, which is associated with the inhibitory phase, is responsible for the AB (Figure 3b). This assumption rests on findings suggesting that the phase angle of alpha-band activity at stimulus onset predicts target detection performance. As an example, Mathewson *et al.* [51] found that, for undetected trials, the phase at stimulus onset was different from that of detected trials (for similar results, see [52]). When the target could not be detected, a prominent negative peak at stimulus onset was associated with significantly reduced P1 amplitude. As illustrated in Figure 3b, this may suggest that, in trials where the phase of alpha-band activity at stimulus onset interferes with the generation of the P1, the stimulus will not be detected. The crucial consideration then is that ongoing alpha-band activity at 10 Hz (and a period of 100 ms) exhibiting a negative peak at stimulus onset will develop a negative peak at 100 ms post-stimulus. This would lead to suppression of P1 amplitude and failure to detect the target stimulus, because there is evidence that the P1 reflects early processes of stimulus categorization (e.g., [30,53]). A recent study by Zauner *et al.* [54] tested whether failure to detect T2 (in AB trials) is associated with alpha phase-locking and an entrainment at a phase angle that approximates the negative alpha peak. The findings clearly supported this hypothesis (Figure 3c-e). In the time window around T1 and T2, significant phase-locking (as measured by the phase locking index, PLI) was observed for AB trials only. Most importantly, the phase angles during the onset of T1 (detected) and T2 (undetected) stimuli were different. For T1 stimuli, mean phase angle was at 245°, which is beyond the positive peak in the negative-going slope. For undetected T2 items, the mean phase angle of 161° is close to the 'unfavorable' negative peak of 180°. Thus, the critical difference between T1 and T2 is a combination of phase-locking and phase angle (Figure 3). In general, these findings are well in line with the notion that perception is discrete and not continuous (e.g., [55,56]).

During the AB task, the attention-related alpha response is restricted to phase and does not comprise amplitude. There are, however, also changes in amplitude – preceding the RSVP – that are associated with AB magnitude (ABm). For example, McLean *et al.* [57] observed a complex interaction between alpha ERD (measured in a foreperiod of 2 sec before the RSVP started), ABm, and lag [57]. At short lags (351 ms after T1), a large ERD was associated with low T2 accuracy (high ABm), but at long lags (936 ms after T1), a large ERD was associated with high T2 accuracy. The authors interpreted this finding in terms of an attentional over-investment [58,59] that leads to an increase in ERD in a foreperiod preceding the RSVP, which in turn leads to an increased ABm at short lags. In addition, they observed that resting alpha power is positively associated with ABm [60].
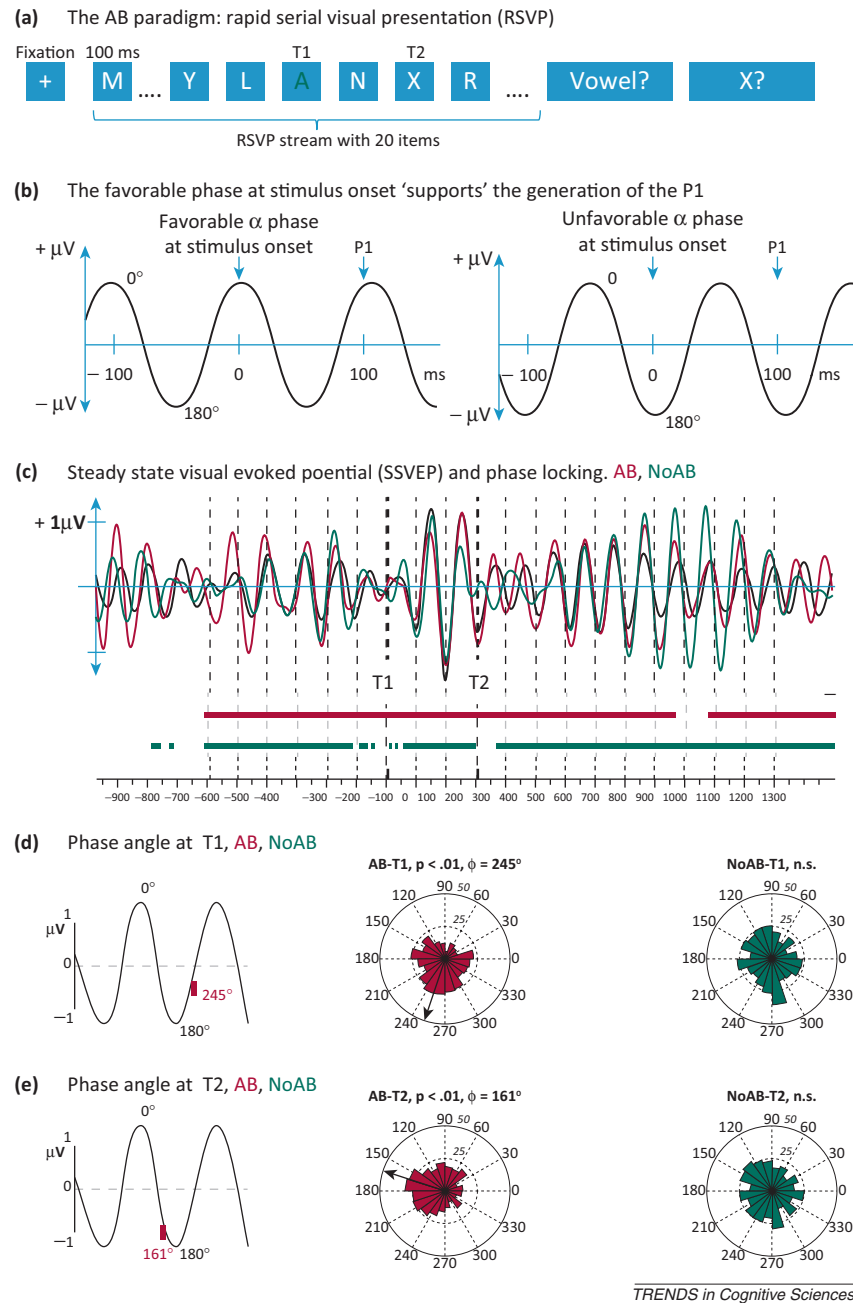
Figure 3. The influence of temporal expectation on alpha phase. **(a)** Single trial structure of an attentional blink (AB) task. The rapid serial visual presentation (RSVP) of stimuli is typically at a rate of approximately 10 items per second. Two targets, T1 and T2, have to be reported after the RSVP. An AB trial is characterized by failure to report T2 after T1 has been detected. **(b)** For a mean alpha frequency of 10 Hz, phase at stimulus onset around the positive peak (coded as 0°) represents a favorable phase. The idea is that, in this case, alpha-band activity will also exhibit a positive peak at 100 ms post-stimulus that coincides with the appearance of the P1. **(c)** The rapid presentation rate leads to an occurrence of a steady state visual evoked potential (SSVEP). The evoked potential shown here is filtered in the broad alpha range (8–12 Hz). Broken vertical lines indicate stimulus onset. Note the appearance of a pronounced SSVEP with phase entrainment at the negative alpha peak (approximately 180°) after the appearance of T1. The horizontal red and green lines below the SSVEP indicate time windows of significant phase locking. Note that AB and NoAB trials differ around the appearance of both targets, T1 and T2. **(d)** and **(e)** Mean phase angle for the 8-12 Hz filtered data. AB single trials showed significant deviation from uniform distribution, with a mean phase angle of 245° for T1 (d) and 161° for T2 (e) onset. NoAB trials were uniformly distributed (right column). Parts of the Figure are adapted, with permission, from [54].

The attentional buffer, anticipatory ERD, and resting alpha power

These findings are well in line with the hypothesis that alpha-band activity reflects an inhibitory filter [19,30]. Large resting power may reflect a person's ability to build up a highly efficient filter [60]. In target detection and discrimination tasks, the filter operates as anticipatory attention, which can be understood as an 'attentional buffer' that keeps target information activated. The ability to activate the attentional buffer selectively - already in the foreperiod of the RSVP – will lead to a pronounced anticipatory ERD. If it is assumed that the buffer lasts for a few 100 ms (e.g., up to 350 or 450 ms), then the re-orientation to a new target – within (but not beyond) the duration of the buffer – results in interference, as suggested, for instance, by Di Lollo *et al.* [61]. The findings by Zauner *et al.* [54] suggest that the attentional filter is 'paced' by alpha oscillations and becomes entrained by stimulation
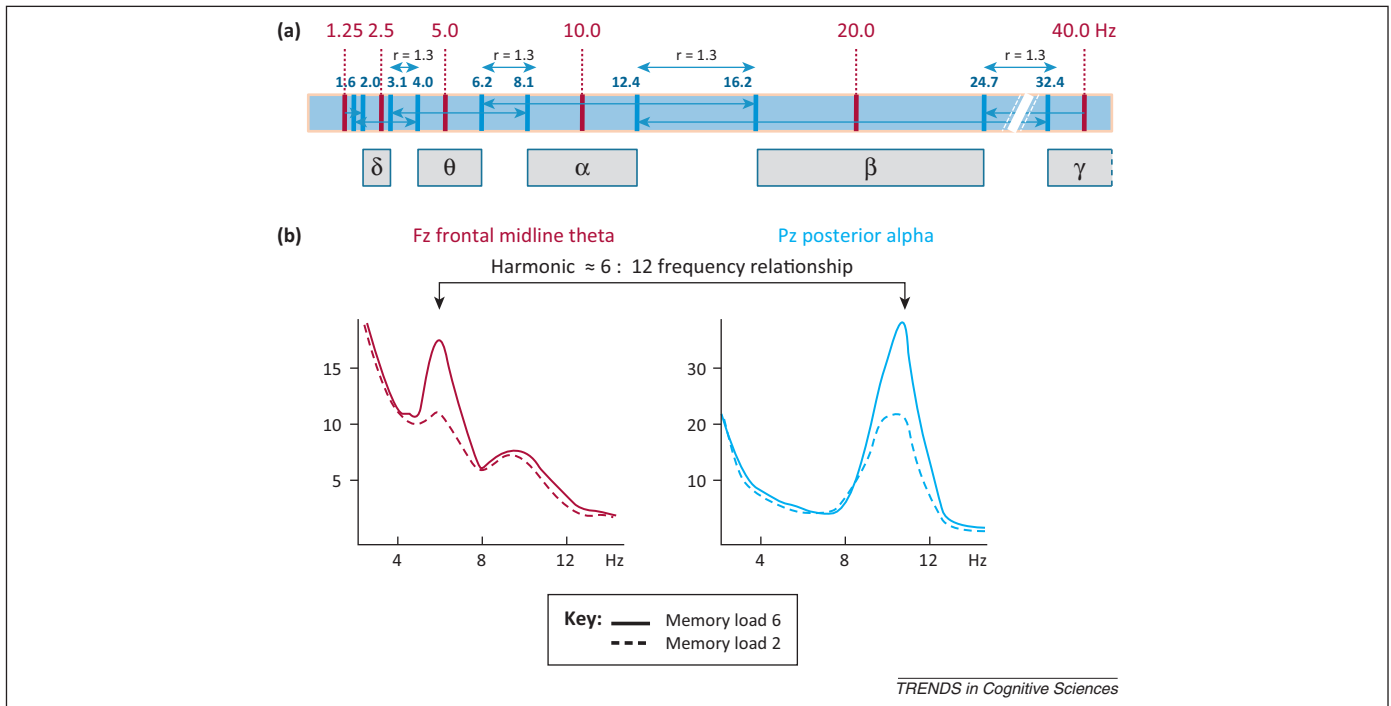
Figure 4. The harmonic/golden mean frequency architecture around the alpha frequency range. **(a)** Traditional frequency bands can be 'reconstructed' on the basis of three assumptions. (i) The alpha band has a mean center frequency of approximately 10 Hz. (ii) The center frequencies of all neighboring frequency bands are harmonics of the alpha frequency band (see red vertical bars). (iii) The bandwidth is calculated on the basis of golden mean (g = 1.618) frequency relationships to ensure minimal interference between bands. For example, $10 \times g \approx 16$. 2 Hz is a frequency maximally separated from the alpha band and marks the lower end of the beta band. The golden mean relationships are indicated by blue bars. **(b)** Harmonic relationships are frequently observed. An interesting example is the appearance of frontal midline theta-band activity at approximately 6 Hz and posterior alpha-band activity at approximately 12 Hz during the retention period of a demanding working memory task. Adapted, with permission, from [35]. Another example of a harmonic relationship with alpha is shown in Figure 2b.

frequency (see also [62]). If entrainment is at a phase angle that interferes with the generation of the P1, then processing of T2 becomes suppressed.

It is worth noting that there is a complex association between resting alpha power and ABm [60], on the one hand, and between ABm, attentional investment, and personality trait dimensions (such as trait affect or the tendency to focus on local vs., global information; see [63,64]), on the other hand. This may suggest that different properties of the attentional filter [65,66] are associated with personality trait rather than state differences.

Alpha-band oscillations, semantic orientation, access to the knowledge system (KS), and the P1

Access to the KS may be an event-related or a continuous process. In the latter sense, the alpha-band frequency range reflects continuous 'semantic orientation', which represents the ability to be consciously oriented in time, space, and with respect to the meaning of all entities surrounding the individual (note the similarity with the proposed function of a default mode system [67]). This ability requires a certain kind of attention (see above) and is 'knowledge based', which means that semantic orientation provides individuals with the ability to selectively access stored information that represents the meaning of sensory information and 'higher order information', such as language, mathematics, and geography.

It is interesting to note that the suggested association between semantic information as integrated knowledge [68] and a knowledge based consciousness plays a key role

in Tononi's integrated information theory of consciousness [69,70]. The central idea is that 'consciousness is integrated knowledge and that its quality is given by informational relationships [71].

Selective access to the KS is thought to depend largely on inhibiting task-irrelevant memory entries. Thus, periods of prolonged access should be associated with ERS, reflecting increased alpha-band activity. A nice anecdote to illustrate this idea is a report by Penfield and Jasper ([8], p. 189) about EEG recordings from Albert Einstein. Einstein produced continuous alpha waves during the solution of complex mathematical tasks which he was skilled and trained to solve. When his alpha-band activity suddenly disappeared, he was asked what had happened because he appeared nervous. He replied that he had just become aware of a mistake in the calculations he had recently done. Another nice example that can be observed under controlled experimental conditions is the increase in alpha-band activity during divergent thinking which requires top down-controlled [72] and prolonged access attempts to long-term memories (see [28,29]).

Event-related access to the KS can be easily studied by using object recognition paradigms. The early event-related EEG response reflects sensory processes and it is not obvious when access to memory begins. One empirical approach to de-confound memory access from sensory processes is to present distorted objects, starting with a high level of distortion and ending with the undistorted presentation of the object. This approach was used in a study by Freunberger *et al.* [41]. On each trial, four items

(representing the same object at decreasing levels of distortion) were presented one after the other. The interesting finding was that the first item – which could never be recognized – elicited neither a P1 nor ERD. Thus, neither the P1 nor ERD can be considered EEG responses that are stimulus evoked or stimulus induced (for reviews, see [17,30]). The working hypothesis is that the P1 reflects early stimulus categorization and the onset of ERD retrieval.

The P1, access to the KS, and traveling alpha waves
The P1 may be considered the event-related phase response of alpha-band activity that reflects an inhibitory filter during access to the KS (for an extensive review, see [30]). The relation between the P1 and alpha-band oscillations is documented by a variety of findings. The frequency characteristic of the P1 is in the alpha band and its peak latency of approximately 100 ms corresponds to the length of an alpha period. The functional responsiveness of the P1 is also similar to alpha oscillations. Its amplitude increases in response to stimuli that must be ignored [73]. Moreover, in spatial cueing tasks, the P1 tends to be larger over the task irrelevant ipsilateral hemisphere [30]. The hypothesis is that the P1 reflects a transient inhibitory filter that modulates the SNR during access to the KS [30]. Depending on tasks demands, the SNR increases with processing complexity in task-relevant networks, whereas inhibition increases in task-irrelevant networks. Both factors operate to increase P1 amplitude.

Probably the most convincing evidence for the hypothesis that the P1 is generated (at least in part) by alpha oscillations are findings showing that the degree of phase alignment in the alpha band predicts P1 amplitude [74] and that topographical P1 peak latency differences can be described as a manifestation of traveling alpha waves [17]. In a recently performed semantic categorization task [75], it was found that the speed of the P1-traveling alpha wave was significantly and negatively correlated with reaction time, indicating that slow traveling speed was associated with fast picture-categorization. Slow-, as compared to fast-, traveling waves may reflect a more intensive and more complex memory search during early access that enables – because of a more precise categorization – a faster categorization response.

Alpha-band oscillations and the frequency architecture of the brain

Some researchers have criticized the traditional approach of investigating strictly defined frequency bands while ignoring the functional interplay between frequencies [25]. This critical view is well justified, because there is hardly any doubt that different frequencies interact in some way and represent different aspects of brain processes. However, so far, there is no global brain theory in sight. Nonetheless, such an approach may be possible if one considers fundamental aspects of between-frequency interactions and the possibility that a certain frequency architecture enables a balanced coupling and de-coupling between oscillations.

Research on brain oscillations suggests that different frequency domains are associated with different classes of cognitive processes. As an example, theta oscillations appear to be related to the processing of new (episodic) information, whereas alpha-band activity is associated with access to information that represents knowledge of the environment (for reviews, see, for example, [5,30,31,76]). Beta-band activity (approximately 20 Hz) may reflect the cognitive control of motor activity and gamma (approximately 40 Hz and higher frequencies) is probably associated with a variety of perceptual and cognitive processes in more localized cortical networks. It is important to note that frequency is related to the size of neural networks in a way that smaller networks oscillate with a higher frequency than larger networks [1,77–80]. A crucial implication is that different frequency domains interact in terms of cross-frequency (CF) coupling [80]. The problem, however, is that spurious ('unwanted', 'erroneous') CF synchronization may cause considerable interference between oscillatory processing domains. Depending on their numerical ratio, the excitatory phases of two frequencies, f1 and f2, will either meet frequently and regularly, as is the case for harmonic frequency relationships, or infrequently and irregularly, as is the case for non-harmonic relationships. Harmonic coupling provides an optimal basis for a functional interchange between two oscillatory systems and is frequently observed (e.g., [81,82] and the examples shown in Figure 2b and 4b). Most importantly, Palva and Palva

---

Box 2. The alpha frequency range and the frequency structure of oscillatory activity in the brain

The traditional EEG frequency bands can be determined as a specific frequency structure around the alpha band, when proceeding from the following three assumptions: (i) Alpha-band activity at approximately 10 Hz is the dominant – and most resonant – frequency in the awake, conscious brain and the main factor in the coalescence of oscillations. (ii) Harmonic frequencies (relative to $f\alpha = 10$ Hz) allow optimal between-frequency communication with the alpha band and they define the center frequencies of traditional frequency bands. For frequencies slower than alpha, the respective values are $f\alpha/2 = 5$ Hz for theta, and $f\alpha/4 = 2.5$ Hz for delta. For faster frequencies, the respective values are $f\alpha*2 = 20$ for beta and $f\alpha*4 = 40$ for gamma. (iii) Golden mean frequencies (relative to alpha) allow one to define the frequency separation between frequency domains, as well as the width of each band. Let us assume that the border frequencies of each domain can still interact with the center frequency (i.e., they are part of the domain), but do not overlap with neighboring domains. For example, for a separation between the theta band and the alpha band one may calculate the borders by dividing alpha by g ($f\alpha/g = 6.2$) and multiplying theta by g ($f\theta*g = 8.1$). Thus, the lower frequency border for alpha is 8.1 (a frequency maximally separated from theta, but still within alpha), whereas the upper frequency border for theta is 6.2 (a frequency maximally separated from alpha, but still within theta). If this simple rule is applied to the four neighboring harmonics of alpha, the following bandwidths are obtained: 2-3 Hz for delta, 4–6 Hz for theta, 8–12 Hz for alpha, 16–25 Hz for beta and 32 Hz (and higher frequencies) for gamma (see Figure 4a in main text for a graphical illustration). Within a frequency band, the center frequency may shift to guarantee either maximal decoupling or coupling with neighboring frequency domains. For instance, the alpha band may shift from 10 to 8 Hz, to obtain separation from theta (8/1.618 = 5 Hz), or may stay at 10 Hz to enable optimal coupling with theta. On the basis of this approach, a possible explanation for the traditional EEG frequency bands can be provided. More importantly, different frequency domains may be understood as elements of a global frequency structure.

Box 3. Alpha-band oscillations, consciousness, and changes in the global frequency structure

Conscious mentation may be considered a state of continuous, dynamic change between a harmonic and a golden mean relationship between neighboring frequencies that either enables or blocks co-activation of neuronal assemblies. This kind of dynamic change appears to be absent in slow wave sleep (SWS). The gradual loss of conscious daytime mentation is characterized by a transition from stage I to stage II sleep. This process starts with a slowing and cessation of alpha, and is fully established with the onset of sleep spindles in the range of 12–15 Hz. Most interestingly, the sleep spindle range lies exactly in the 'gap' between alpha-band and beta-band activity, as illustrated in Figure 4a in main text. In humans, SWS is dominated by three frequencies, spindles (12–15 Hz), delta and slow oscillations (at and below 1 Hz). Thus, lack of (daytime) consciousness is associated with a change in the global frequency structure from a harmonic/non-harmonic relationship centered around alpha-band activity to a 'nested' structure where slow oscillations (with spindles riding on their hyperpolarizing slope) are the main factor for the coalescence of brain rhythms [25]. It should also be noted that a task-related involvement of alpha is not an unequivocal sign of consciousness, because several studies show that alpha-band activity plays a role in dream recall [113] and reactivity to disturbing noise to sleep [114]. Thus, the role of alpha-band activity in the coalescence of frequencies may be considered the critical factor.

have demonstrated that phase-coupling between alpha-band (at approximately 10 Hz) and beta-band (at approximately 20 Hz) oscillations changes in a task dependent manner ([83,84]; for reviews, see [71,85]). Non-harmonic coupling blocks an interchange only to some extent because of spurious CF synchronization. Pletzer *et al.* [86] demonstrated that, in a mathematical sense, two frequencies f1 and f2 will never synchronize if the frequency relationship for f1, f2 (f2 > f1) equals the golden mean (g = 1.618) and that there is no other frequency relationship that is better capable of avoiding spurious CF synchronization (see also [87], for empirical findings).

The interesting point is that the traditional EEG frequency bands can be explained by a frequency architecture that is centered around alpha-band activity (Box 2 and Figure 4). The assumption is that the alpha frequency domain, as a basic process of the conscious brain, interacts best with those frequency domains that have a harmonic relationship with the alpha domain and that the separation between frequency domains is obtained with frequency ratios equaling the golden mean. It is a consequence of this assumption to expect that the frequency architecture changes when consciousness changes. For example, in slow wave sleep a frequency structure is expected that is not centered around alpha-band activity (Box 3).

Concluding remarks and suggestions for future research

Controlled access to the KS, operating under anticipatory and temporal attention, represents the class of cognitive processes that are reflected by alpha-band activity. If this is a valid conclusion, future research on the alpha frequency domain will shed new light on a cognitive domain that has not been well described yet. Access is associated with an inhibitory filter that is reflected in synchronized alpha activity (a phase response and/or ERS) that is followed by ERD (approximately 250 to 400 ms post-stimulus). In

traditional research, ERD was considered the 'typical' alpha response. The interpretation suggested here is that ERD reflects release from inhibition and, thus, is only part of a more complex alpha process that also comprises inhibition and timing that precedes ERD.

Access to the KS is not only an event-related, but also a continuous process. For adult humans, it is a basic and also largely automatic process that may in everyday language be described as 'knowing'. One probably could also use the term 'knowledge-based consciousness' and contrast it to a 'WM- or emotion-based consciousness'. Over the life span, alpha activity becomes dominant during early adulthood [88–90], probably reflecting the emergence of an established KS. In childhood, slower frequencies in the broad theta frequency range dominate. They probably reflect the dominance of a WM-based consciousness, because these slower frequencies are closely associated with the encoding and retrieval of new information [5]. These considerations may also explain why for some people alpha-band activity is not dominant (e.g., [88]). Possibly, their consciousness is more WM- or emotion- and less knowledge-based. Another implication is that individual differences in alpha-band activity could reflect trait differences related to the (dominant) cognitive processing mode and personality. Trait differences related to ABm and alpha-band activity are a good example (see the section on resting alpha power and the attentional buffer).

The considerations presented here have a variety of implications, which offer promising avenues for future research. For example, because alpha-band activity is associated with access to the KS, the question which processes underlie WM and the encoding of new information arises. The basic idea here is that the KS and WM interact in a way that traces stored in the KS are used for short-term storage (see [91,92]). The implication is that CF coupling between alpha, theta, and gamma oscillations is expected to reflect the interaction between WM and the KS (cf. [15,93]). Another interesting question is which processes reflect spreading activation within the KS. Furthermore, the predicted baseline shift of alpha activity during increases of inhibition in task-relevant networks (Figure 1a) may also be an interesting phenomenon for future research. This shift appears to bear a close resemblance to findings revealing an asymmetric amplitude fluctuation of alpha activity that possibly explains the generation of slow event-related potentials [94,95].

Further implications are related to the hypothesis that early ERP components are generated (at least in part) by oscillations in different frequency domains and to the investigation of traveling waves. All available evidence suggests that the EEG is not stationary. However, neither EEG nor MEG is well suited to study this question, because the folding (gyrification) of the cortex leads to the emergence of radial and tangential dipoles. The first type of dipole underlies the EEG signal, the second the MEG signal. The simultaneous recording of both signals and new software technology make it possible to observe complex traveling waves as they spread over the 'flattened' cortex [96] and allow fascinating new insight in the temporal dynamics of the brain.

References

1 Buzsaki, G. and Draguhn, A. (2004) Neuronal oscillations in cortical networks. *Science* 304, 1926–1929

2 Arnal, L.H. and Giraud, A.L. (2012) Cortical oscillations and sensory predictions. *Trends Cogn. Sci.* 16, 390–398

3 Chakravarthi, R. and VanRullen, R. (2012) Conscious updating is a rhythmic process. *Proc. Natl. Acad. Sci. U.S.A.* 109, 10599–10604

4 Klimesch, W. *et al.* (1994) Episodic and semantic memory: an analysis in the EEG-theta and alpha band. *Electroencephalogr. Clin. Neurophysiol.* 91, 428–441

5 Klimesch, W. (1997) EEG-alpha rhythms and memory processes. *Int. J. Psychophysiol.* 26, 319–340

6 Pfurtscheller, G. *et al.* (1996) Event-related synchronization (ERS) in the alpha band – an electrophysiological correlate of cortical idling: a review. *Int. J. Psychophysiol.* 24, 39–46

7 Adrian, E. and Matthews, B. (1934) The Berger rhythm: potential changes from the occipital lobes in man. *Brain* 4, 355–385

8 Penfield, W. and Jasper, H. (1954) *Epilepsy and the functional anatomy of the brain*, Little, Brown & Co

9 Pfurtscheller, G. and Lopes da Silva, F.H.,eds(1999)In *Event-Related Desynchronization. Handbook of Electroencephalography and Clinical Neurophysiology* (Vol. 6), Elsevier

10 Foxe, J. *et al.* (1998) Parieto-occipital approximately 10 Hz activity reflects anticipatory stat of visual attention mechanisms. *Neuroreport* 9, 3929–3933

11 Jokisch, D. and Jensen, O. (2007) Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J. Neurosci.* 27, 3244–3251

12 Thut, G. *et al.* (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502

13 Worden, M.S. *et al.* (2000) Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalographic increases over occipital cortex. *J. Neurosci.* 20, 1–6

14 Medendorp, W.P. *et al.* (2007) Oscillatory activity in human parietal and occipital cortex shows hemispheric lateralization and memory effects in a delayed double-step saccade task. *Cereb. Cortex* 17, 2364–2374

15 Sauseng, P. *et al.* (2009) Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* 19, 1846–1852

16 Kelly, S.P. *et al.* (2006) Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J. Neurophysiol.* 95, 3844–3851

17 Klimesch, W. *et al.* (2011) Alpha oscillations and early stages of visual encoding. *Front. Psychol.* 2, 118

18 Pfurtscheller, G. (2006) The cortical activation model (CAM). In *Progress in Brain Research* (Vol. 159). *Event-Related Dynamics of Brain Oscillations* (Neuper, C. and Klimesch, W., eds), pp. 19–27, Elsevier

19 Klimesch, W. *et al.* (2007) EEG alpha oscillations: the inhibition timing hypothesis. *Brain Res. Rev.* 53, 63–88

20 Shen, W. *et al.* (2011) Inhibition to excitation ratio regulates visual system responses and behavior in vivo. *J. Neurophysiol.* 106, 2285–2302

21 Yizhar, O. *et al.* (2011) Neocortical excitation/inhibition balance in information processing and social dysfunction. *Nature* 477, 171–178

22 Nadasdy, Z. (2010) Binding by asynchrony: the neuronal phase code. *Front. Neurosci.* 4, 51

23 Supp, G. *et al.* (2011) Cortical hypersynchrony predicts breakdown of sensory processing during loss of consciousness. *Curr. Biol.* 21, 1988–1993

24 Buzsaki, G. (2006) *Rhythms of the Brain*, Oxford University Press

25 Steriade, M. (2006) Grouping of brain rhythms in corticothalamic systems. *Neuroscience* 137, 1087–1106

26 Haegens, S. *et al.* (2011) α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. U.S.A.* 108, 19377–19382

27 Jensen, O. and Mazaheri, A. (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186

28 Benedek, M. *et al.* (2011) EEG alpha synchronization is related to top-down processing in convergent and divergent thinking. *Neuropsychologia* 49, 3505–3511

29 Jauk, E. *et al.* (2012) Tackling creativity at its roots: evidence for different patterns of EEG alpha activity related to convergent and divergent modes of task processing. *Int. J. Psychophysiol.* 84, 219–225

30 Klimesch, W. (2011) Evoked alpha and early access to the knowledge system: the P1 inhibition timing hypothesis. *Brain Res.* 1408, 52–71

31 Klimesch, W. (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res. Rev.* 29, 169–195

32 Jensen, O. *et al.* (2012) An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends Cogn. Sci.* 16, 200–206

33 Händel, B.F. *et al.* (2011) Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J. Cogn. Neurosci.* 23, 2494–2502

34 Suffczynski, P. *et al.* (2001) Computational model of thalamo-cortical networks: dynamic control of alpha rhythms in relation to focal attention. *Int. J. Psychophysiol.* 43, 25–40

35 Jensen, O. *et al.* (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb. Cortex* 12, 877–882

36 Klimesch, W. *et al.* (1992) Pre- and poststimulus processes in category judgement tasks as measured by event-related desynchronization (ERD). *J. Psychophysiol.* 6, 186–203

37 Ergenoglu, T. *et al.* (2004) Alpha rhythm of the EEG modulates visual detection performance in humans. *Brain Res. Cogn. Brain Res.* 20, 376–383

38 Hanslmayr, S. *et al.* (2005) Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neurosci. Lett.* 375, 64–68

39 Hanslmayr, S. *et al.* (2007) Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage* 37, 1465–1473

40 Romei, V. *et al.* (2010) On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *J. Neurosci.* 30, 8692–8697

41 Freunberger, R. *et al.* (2008) Alpha phase coupling reflects object recognition. *NeuroImage* 42, 928–935

42 Shapiro, K.L. *et al.* (1997) The attentional blink. *Trends Cogn. Sci.* 1, 291–296

43 Martin, E.W. *et al.* (2011) Turning the attentional blink on and off: opposing effects of spatial and temporal noise. *Psychon. Bull. Rev.* 18, 295–301

44 Hanslmayr, S. *et al.* (2011) The role of alpha oscillations in temporal attention. *Brain Res. Rev.* 67, 331–343

45 Hillyard, S.A. and Anllo-Vento, L. (1998) Event-related brain potentials in the study of visual selective attention. *Proc. Natl. Acad. Sci. U.S.A.* 95, 781–787

46 Silberstein, R.B. *et al.* (1995) Steady-state visually evoked potential topography during the Wisconsin card sorting test. *Electroencephalogr. Clin. Neurophysiol.* 96, 24–35

47 Vialatte, F-B. *et al.* (2010) Steady-state visually evoked potentials: focus on essential paradigms and future perspectives. *Prog. Neurobiol.* 90, 418–438

48 Herrmann, C.S. (2001) Human EEG responses to 1-100 Hz flicker: resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Exp. Brain Res.* 137, 346–353

49 Thut, G. *et al.* (2011) Rhythmic TMS causes local entrainment of natural oscillatory signatures. *Curr. Biol.* 21, 1176–1185

50 Thut, G. *et al.* (2011) Entrainment of perceptually relevant brain oscillations by non-invasive rhythmic stimulation of the human brain. *Front. Psychol.* 2, 170

51 Mathewson, K.E. *et al.* (2009) To see or not to see: prestimulus α phase predicts visual awareness. *J. Neurosci.* 29, 2725–2732

52 Busch, N.A. *et al.* (2009) The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci.* 29, 7869–7876

53 Ossandon, J.P. *et al.* (2010) Superposition model predicts EEG occipital activity during free viewing of natural scenes. *J. Neurosci.* 30, 4787–4795

54 Zauner, A. *et al.* (2012) Alpha entrainment is responsible for the attentional blink phenomenon. *NeuroImage* 63, 674–686

55 VanRullen, R. and Koch, C. (2003) Is perception discrete or continuous? *Trends Cogn. Sci.* 7, 207–213

56 Landau, A.N. and Fries, P. (2012) Attention Samples Stimuli Rhythmically. *Curr. Biol.* 22, 1000–1004

57 MacLean, M.H. and Arnell, K.M. (2011) Greater attentional blink magnitude is associated with higher levels of anticipatory attention as measured by alpha event-related desynchronization (ERD). *Brain Res.* 1387, 99–107

58 Olivers, C.N.L. and Nieuwenhuis, S. (2005) The beneficial effect of concurrent task-irrelevant mental activity on temporal attention. *Psychol. Sci.* 16, 265–269

59 Olivers, C.N.L. and Nieuwenhuis, S. (2006) The beneficial effects of additional task load, positive affect, and instruction on the attentional blink. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 364–379

60 MacLean, M.H. *et al.* (2012) Resting EEG in alpha and beta bands predicts individual differences in attentional blink magnitude. *Brain Cogn.* 78, 218–229

61 Di Lollo, V. *et al.* (2005) The attentional blink: resource depletion or temporary loss of control? *Psychol. Res.* 69, 191–200

62 VanRullen, R. and Macdonald, J. (2012) Perceptual echoes at 10 Hz in the human brain. *Curr. Biol.* 22, 995–999

63 MacLean, M.H. *et al.* (2010) Dispositional affect predicts temporal attention costs in the attentional blink paradigm. *Cogn. Emotion* 24, 1431–1438

64 MacLean, M.H. and Arnell, K.M. (2010) Personality predicts temporal attention costs in the attentional blink paradigm. *Psychon. Bull. Rev.* 17, 556–562

65 Martens, S. and Valchev, N. (2009) Individual differences in the attentional blink: the important role of irrelevant information. *Exp. Psychol.* 56, 18–26

66 Arnell, K.M. and Stubitz, S.M. (2010) Attentional blink magnitude is predicted by the ability to keep irrelevant material out of working memory. *Psychol. Res.* 5, 457–467

67 Raichle, M.E. *et al.* (2001) A default mode of brain function. *Proc. Natl. Acad. Sci. U.S.A.* 98, 676–682

68 Klimesch, W. (1994) *The structure of long-term memory: a connectivity model of semantic processing*, Lawrence Erlbaum

69 Tononi, G. (2004) An information integration theory of consciousness. *BMC Neurosci.* 5, 42

70 Tononi, G. (2008) Consciousness as integrated information: a provisional manifesto. *Biol. Bull.* 215, 216–242

71 Palva, S. and Palva, J.M. (2011) The functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Front. Psychol.* 2, 204

72 Zanto, T.P. *et al.* (2011) Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nat. Neurosci.* 14, 656–661

73 Freunberger, R. *et al.* (2008) Functional similarities between the P1 component and alpha oscillations. *Eur. J. Neurosci.* 27, 2330–2340

74 Gruber, W.R. *et al.* (2005) Alpha phase synchronization predicts P1 end N1 latency and amplitude size. *Cereb. Cortex* 15, 371–377

75 Fellinger, R. *et al.* (2011) Evoked traveling alpha waves predict visual-semantic categorization-speed. *NeuroImage* 59, 3379–3388

76 Klimesch, W. *et al.* (2007) The P1 and traveling alpha waves: evidence for evoked oscillations. *J. Neurophysiol.* 97, 1311–1318

77 Lakatos, P. *et al.* (2005) An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *J. Neurophysiol.* 94, 1904–1911

78 Lakatos, P. *et al.* (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320, 110–113

79 von Stein, A. and Sarnthein, J. (2000) Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *Int. J. Psychophysiol.* 38, 301–313

80 Varela, F. *et al.* (2001) The brainweb: phase synchronization and large-scale integration. *Nature Neurosci.* 2, 229–238

81 Nikulin, V.V. and Brismar, T. (2006) Phase synchronization between alpha and beta oscillations in the human electroencephalogram. *Neuroscience* 137, 647–657

82 Nikulin, V.V. *et al.* (2012) Cross-frequency decomposition: a novel technique for studying interactions between neuronal oscillations with different frequencies. *Clin. Neurophysiol.* 123, 1353–1360

83 Palva, J.M. *et al.* (2005) Phase synchrony among neuronal oscillations in the human cortex. *J. Neurosci.* 25, 3962–3972

84 Palva, J.M. *et al.* (2010) Neuronal synchrony reveals working memory networks and predicts individual memory capacity. *Proc. Natl. Acad. Sci. U.S.A.* 107, 7580–7585

85 Palva, S. and Palva, J.M. (2007) New vistas for alpha-frequency band oscillations. *Trends Neurosci.* 30, 150–158

86 Pletzer, B. *et al.* (2010) When frequencies never synchronize: the golden mean and the resting EEG. *Brain Res.* 1335, 91–102

87 Roopun, A.K. *et al.* (2008) Period concatenation underlies interactions between gamma and beta rhythms in neocortex. *Front. Cell. Neurosci.* 2, 1

88 Köpruner, V. *et al.* (1984) Quantitative EEG in normals and in patients with cerebral ischemia. In *Brain Ischemia: Quantitative EEG and Imaging Techniques, Progress in Brain Research* (Vol. 62) (Pfurtscheller, G. *et al.*, eds), In pp. 29–50, Elsevier

89 Markand, O.N. (1990) Alpha rhythms. *J. Clin. Neurophysiol.* 7, 163–189

90 Somsen, R.J.M. *et al.* (1997) Growth spurts in brain maturation during middle childhood as indexed by EEG power spectra. *Biol. Psychol.* 44, 187–209

91 Ruchkin, D. *et al.* (2003) Working memory retention systems: a state of activated long-term memory. *Behav. Brain Sci.* 26, 709–728

92 Klimesch, W. and Schack, B. (2003) Activation of long-term memory by alpha oscillations in a working memory task? *Behav. Brain Sci.* 26, 743

93 Sauseng, P. *et al.* (2002) The interplay between theta and alpha oscillations in the human electroencephalogram reflects the transfer of information between memory systems. *Neurosci. Lett.* 324, 121–124

94 Mazaheri, A. and Jensen, O. (2008) Asymmetric amplitude modulations of brain oscillations generate slow evoked responses. *J. Neurosci.* 28, 7781–7787

95 Nikulin, V. *et al.* (2007) A novel mechanism for evoked responses in the human brain. *Eur. J. Neurosci.* 25, 3146–3154

96 Palva, S. *et al.* (2011) Localization of cortical phase and amplitude dynamics during visual working memory encoding and retention. *J. Neurosci.* 31, 5013–5025

97 Raymond, J.E. *et al.* (1992) Temporary suppression of visual processing in an RSVP task: an attentional blink? *J. Exp. Psychol. Hum. Percept. Perform.* 18, 849–860

98 Pfurtscheller, G. and Aranibar, A. (1977) Event-related cortical desynchronization detected by power measurement of scalp EEG. *Electroenceph. Clin. Neurophysiol.* 42, 817–826

99 Summerfield, C. and Egner, T. (2009) Expectation (and attention) in visual cognition. *Trends Cogn. Sci.* 13, 403–409

100 Friston, K. (2009) The free-energy principle: a rough guide to the brain? *Trends Cogn. Sci.* 13, 293–301

101 Andersen, P. and Andersson, S.A., eds (1968) *Physiological Basis of the Alpha Rhythm*, Appleton-Century-Crofts

102 Steriade, M. *et al.* (1990) Basic mechanisms of cerebral rhythmic activities. *Electroencephalogr. Clin. Neurophysiol.* 76, 481–508

103 Lopes da Silva, F.H. *et al.* (1973) Organisation of thalamic and cortical alpha rhythms: spectra and coherences. *Electroencaphalogr. Clin. Neurophysiol.* 35, 627–639

104 Nicolelis, M.A.L. and Fanselow, E.E. (2002) Thalamcortical optimization of tactile processing according to behavioural state. *Nat. Neurosci.* 5, 517–523

105 Lörincz, M. *et al.* (2009) Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. *Neuron* 63, 683–696

106 Hughes, S. *et al.* (2011) Thalamic gap junctions control local neuronal synchrony and influence macroscopic oscillation amplitude during EEG alpha rhythms. *Front. Psychol.* 2, 193

107 Schmid, M.C. *et al.* (2012) Thalamic coordination of cortical communication. *Neuron* 75, 551–552

108 Hughes, S.W. and Crunelli, V. (2005) Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *Neuroscientist* 11, 357–372

109 Saalmann, Y.B. *et al.* (2012) The pulvinar regulates information transmission between cortical areas based on attention demands. *Science* 337, 753–756

110 Lopes da Silva, F.H. *et al.* (1980) Partial coherence analysis of thalamic and cortical alpha rhythms in dog – a contribution towards a general model of the cortical organization of rhythmic activity. In *Rhythmic EEG activities and cortical functioning* (Pfurtscheller, G., ed.), pp. 33–59, Elsevier

111 Lopes da Silva, F.H. *et al.* (1980) Relative contribution of intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by partial coherence analysis. *Electroencephalogr. Clin. Neurophysiol.* 50, 449–456

112 Bollimunta, A. *et al.* (2008) Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *J. Neurosci.* 28, 9976–9988

113 Marzano, C. *et al.* (2011) Recalling and forgetting dreams: theta and alpha oscillations during sleep predict subsequent dream recall. *J. Neurosci.* 31, 6674–6683

114 McKinney, S.M. *et al.* (2011) Covert waking brain activity reveals instantaneous sleep depth. *PLoS ONE* 6, e17351