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# Instantaneous voltage of electroencephalographic oscillatory activity: an alternative to power and phase measurements

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# Abstract

Power and phase of low-frequency oscillations are the predominant measures of cortical excitability. These measures assume that oscillations are sinusoidal and symmetrical. However, studies have shown that this notion is not informed by physiological principles, and it has been suggested that the instantaneous amplitude of a biased alpha oscillation, which does not make these assumptions, is a better predictor of cortical excitability than either the power or the phase. The presented thesis characterizes and validates the instantaneous amplitude as predictor of cortical excitability.

For this purpose EEG signals were recorded from 64 locations in 34 human subjects while they responded to visual perception-threshold stimuli with a button press. The recorded signals were used to determine how oscillatory power, phase, and the instantaneous amplitude in the alpha band predicted the perception of the visual stimuli.

The results show that instantaneous amplitude explains 35% more of the behavioral variance than power or phase, and that it can also predict when the cortex is most receptive to perceptual input. The validation of instantaneous amplitude as a predictor of cortical excitability opens up new possibilities for scientific, clinical and consumer applications that use EEG.

Keywords: Electroencephalography (EEG), alpha, oscillations, phase, visual perception, instantaneous voltage

# Zusammenfassung

Leistung und Phase niederfrequenter Oszillationen sind die vorherrschenden Parameter zur Bestimmung kortikaler Erregbarkeit. Diese Maßnahmen setzen voraus, dass die auftretenden Schwingungen sinusförmig und symmetrisch sind. Studien haben jedoch gezeigt, dass diese Ansicht nicht durch physiologische Prinzipien informiert werden. Es wurde vorgeschlagen, die momentane Amplitude einer vorgespannten Alpha-Schwingung, welche keine Symmetrie annimmt, als einen besseren Prädiktor für kortikale Erregbarkeit zu verwenden. Die vorliegende Diplomarbeit validiert und charakterisiert die momentane Amplitude als Prädiktor der kortikalen Erregbarkeit.

Es wurden die EEG-Signale von 64 Elektroden in 34 menschlichen Probanden aufgezeichnet, während diese auf visuelle Wahrnehmungsschwellenreize mit einem Knopfdruck reagierten. Von diesen Signalen wurden die oszillatorische Leistung, Phase und die momentane Amplitude im alpha-Band extrahiert, um deren Einfluss auf die Wahrnehmung unserer visuellen Reize zu quantifizieren.

Die Ergebnisse zeigen, dass die momentane Amplitude 35% mehr Varianz im Verhalten erklären kann als Leistung oder Phase, und dass es auch voraussagen kann, wann der Kortex am empfänglichsten für deren Wahrnehmung ist. Die Validierung von momentaner Amplitude als Prädiktor für kortikale Erregbarkeit eröffnet neue Möglichkeiten für wissenschaftliche, klinische und Verbraucheranwendungen, die EEG verwenden.

Schlüsselwörter: Electroencephalography (EEG), Alpha, Oszillationen, Phase, visuelle Wahrnehmung, momentane Amplitude

# Contents

# Acronyms

| | |
|---|---|
| **fMRI** | functional Magnetic Resonance Imaging |
| **PET** | Positron Emission Tomography |
| **SPECT** | Single-Photon Emission Computerized Tomography |
| **LFP** | Local Field Potentials |
| **GBI** | Gating-by-Inhibition |
| **CTC** | Communication-through-Coherence |
| **FBO** | Function-through-Biased-Oscillations |
| **ECoG** | Electrocorticography |
| **EEG** | Electroencephalographic |
| **ERP** | Event Related Potential |
| **MEG** | Magnetoencephalography |

| | |
|---|---|
| **EMG** | Electromyography |
| **BCI** | Brain Computer Interface |
| **PSD** | Power Spectral Density |
| **IIR** | Infinite Impulse Response |
| **MEG** | Magnetoencephalography |
| **GABA** | Gamma-Aminobutyric Acid |
| **PAC** | Phase-Amplitude Coupling |
| **V1** | Primary Visual Cortex |
| **LGN** | Lateral Geniculate Nucleus |

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# 1 Introduction

Selective attention to external stimuli is a crucial ability to survive in the environment. Without the capability to weaken or enhance incoming sensory information (i.e., visual, auditory or tactile information) mundane seeming tasks like driving a car would be nearly impossible. For example, while driving, we pay attention to the road, regulate the car speed and most of the time we also listen to the radio, talk to a person or perform a various amount of different motor tasks. All this information is processed by the vast network of neurons in our brain. This ability, that allows us to pay more attention to one modality than to another, helps us to process only the information that is relevant for the task at hand. Let us illustrate this in our car example, if the complexity of the situation increases (i.e., at a busy intersection), our brain will reduce influences from irrelevant stimuli (e.g., the song in the radio) to avoid distractions from the more important task. These shifts in attention happen within seconds and it is therefore impossible that they are facilitated by structural changes in the anatomy of the brain, which leads to the conclusion that this capability is a fundamental property of the cortical activity that governs our brain.

The investigation of dynamic changes in cortical activity has a long history and different techniques have been developed. All these techniques have their unique advantages and disadvantages. They are reliant on the measurement of different physical and physiological properties that are affected by cortical activity. For example, active neuronal populations require an increased blood flow to meet metabolic requirements. This change in blood flow can be measured by techniques like functional magnetic resonance imaging (fMRI), positron emission tomography (PET) or single-photon emission computerized tomography (SPECT) [1]. These investigatory tools are able to provide information about metabolic changes with a high spatial resolution in a three dimensional structure. However, the equipment is expensive in acquisition and maintenance and the temporal resolution of these techniques is comparably low (i.e., in the range of seconds). Another approach to investigate cortical activity is the measurement of electrical signals caused by action potentials propagating along the axons of the nerve cells. The propagation of these action potentials causes transmembrane currents which can be measured in the extracellular medium. Although, synaptic transmembrane currents are the major contributor to extracellular signals, other signal sources do exist. These sources include $Na^{+}$ and $Ca^{2+}$ spikes, ionic fluxes caused by voltage- and ligand-gated channels and intrinsic membrane oscillations [2].

There are multiple ways to measure the resulting electrical signals but their effectiveness varies in spatial, temporal and spectral resolution as well as signal quality. For example, the measurement of local field potentials

(LFP) is achieved by inserting microelectrodes, like the Utah array, in the extracellular space of brain tissue [3] which is a highly invasive procedure that can lead to inflammation or tissue damage on the target site [4]. These microelectrode arrays achieve a high spatial resolution with up to 128 electrode needles spaced in an area of around 13 $mm^2$. The electrodes allow the measurement of action potentials as well as local field potentials. The measured local field potentials reflect the activity of a small population of neurons. It is the result of transmembrane currents, located in the vicinity of the electrode [5].

Another approach in the acquisition of cortical activity are electrodes attached to the surface of the cerebral cortex. This method, termed electrocorticography (ECoG) is used for the localization of seizure foci in epilepsy patients prior to surgical resection [6]. Additionally, due to the proximity to the cerebral cortex, the signal-to-noise ratio and spatial resolution is much higher than what can be expected by noninvasive methods like electroencephalography (EEG).

One of the most prominent tools to investigate neuronal activity are noninvasive techniques, namely the electroencephalography (EEG) and magnetoencephalography (MEG). The magnetoencephalography allows the non invasive measurement of the magnetic field changes caused by neuronal currents in the brain. These extremely small changes (50fT - 500fT) in the magnetic field are measured by superconducting quantum interference devices [7]. Although, MEG is costly, its spatiotemporal properties make it an ideal candidate for research and clinical application.

Nevertheless, the most widespread noninvasive method to measure brain signals is the EEG, because it allows the measurement of cortical activity with comparatively low costs. The obtained signal can be seen as the spatiotemporally smoothed version of the local field potentials [2] integrated over a large cortical area of millions of neurons. Electroencephalography has a long history due to its non-invasiveness and comparably simple instrumentation requirements. In contrast to invasive methods, the measured potential differences are very small (1-100$\mu$V). Therefore, EEG measurements have a comparatively low signal-to-noise ratio and decreased spatial selectivity due to the volume conduction between the cortical sources and the electrode. Additionally, the recorded frequencies are limited as higher frequencies tend to be more locally specific and are more attenuated than lower frequencies [8]. Despite these limitations, EEG has become an important tool for research as well as for clinical and consumer applications.

The first humans EEG recordings were performed by Hans Berger in 1924. In 1929 he published his paper "On the Electroenephalogram of Man" [9] in which he demonstrated that it was possible to measure cortical activity from the scalp of humans. These investigations of cortical activity showed, that the signals recorded from the scalp, are composed of different types and frequencies. Two very prominent distinctions are the division of activity into stimulus locked responses and ongoing activity [10]. Stimulus locked respones, like event related potentials (ERP) are measurable responses that result from specific time locked sensory, cognitive or motor events. In contrast, ongoing activity describes rhythmic changes in the neural activity that are not the response to a specific event. One of these oscillations, the alpha wave (discovered by Hans Berger who termed it the Berger rhythm) has received a lot of attention since its discovery.

The oscillatory activity of the brain has been linked to different mental states. For example, relaxation typically induces oscillations in the alpha band ($8 - 12$ Hz). Alpha has also been associated with shifts in attention [11–13], thus enabling the dynamic cortical function within the static anatomy of the brain. For a long period of time, alpha activity has been interpreted as the result of cortical idling [14]. In principle, if a cortical area is inactive, its brainwaves are in a synchronous idle state, which causes alpha power to be high. If a cortical area is active, the brainwaves desynchronize due to the task demand which results in a decrease in alpha power. As an example, the power of the alpha wave in the occipital cortex increases when the eyes are closed and decreases when the eyes are open, reflecting changes in the workload of visual processing.

Investigations of working memory have challenged this view. In these experiments [15, 16] subjects had to remember items for a short period of time. As a result alpha power increased during the retention interval in which they had to memorize the presented items. This finding is contrary to the believe that high alpha power indicates cortical idling and lead to the theory that increased alpha power inhibits communication with other areas of the brain. Based on the observations that alpha power decreases in active areas, but increases during the retention time in memory experiments Klimesch et al. formulated the inhibition-timing hypothesis [17]. In their view, alpha is an active phenomenon that helps neurons in different networks to activate common target cells. They state that alpha could play an important role in the top-down control of cortical activity. Therefore, cyclic changes in cortical excitability in the alpha range, phase synchronization, alpha coherence and phase locking could be manifestations of a timing mechanism to guide information flow. A few years later, Jensen and Mazaheri formulated their theory, termed Gating-by-Inhibition [13], which is also based on the observation that alpha power decreases in task relevant areas, and increases in task irrelevant areas. Their central assumption is based on the idea that information is routed by inhibiting task-irrelevant pathways. This is supported by the discovery that task performance was better when alpha power increased in task irrelevant areas [18]. Another hypothesis, formulated by Fries, was termed Communication-through-Coherence [19, 20] and is based on cyclic changes in cortical excitability caused by phasic changes of the alpha cycle. His theory suggests that active neuronal groups engage in rhythmic synchronization. These synchronization patterns cause sequences of inhibition and excitation, creating windows for neuronal communication. This concept establishes that communication therefore requires coherence between the neuronal groups. This implies that if a neuronal group receives information from different presynaptic groups, it primarily responds to the group to which it has the highest phase coherence.

While the origin of this oscillatory activity is still under investigation, there is a growing body of evidence suggesting that oscillations in the alpha band originate from the thalamus [21, 22], modulate cortical excitability (i.e., the probability of neuronal firing), and cause variations in behavioral performance. These changes in cortical excitability are assumed to be a key mechanism to facilitate (or inhibit) information propagation between cortical structures and therefore modulate attention.

Several studies have shown that cortical excitability is modulated by power and phase of oscillatory activity [23–27]. Frequency decomposition (i.e., Fast Fourier Transform), as the prevalent investigatory tool for oscillatory activity, assumes that the measured oscillations are sinusoidal and symmetrical. However, studies have shown that this notion is not informed by physiological principles, and that the shape of oscillatory activity is actually non-sinusoidal [9, 28, 29] and asymmetric [30–32]. For example, the *mu*-rhythm (a 10Hz rhythm in the motor area) can be better described as an arch, comb or wicket shape [33]. This is especially important for methods like phase-amplitude-coupling (PAC), which quantifies the correlation between the phase of one oscillator and the amplitude of a higher-frequency oscillator. A recent investigation has shown that failing to consider the non-sinusoidal shape of oscillations can lead to confounding biases in PAC investigations [34].

Recently, Function-through-Biased-Oscillations [FBO; 35] has emerged as a new theory that describes an alternative to power or phase-based measurements. In this theory, a special emphasis is placed on the bias of alpha oscillations as the driving force behind rhythmic inhibition. This theory is based on physiological considerations and tries to reconcile the previously established Gating-by-Inhibition (GBI) and Communication-through-Coherence (CTC) theories. Function-through-Biased-Oscillations (FBO) combines ideas from GBI and CTC by considering the physiological principles of the ongoing oscillation. Specifically, the introduction of asymmetry creates a bias in the oscillation that facilitates information transfer between cortical areas when the instantaneous voltage amplitude of a biased alpha oscillation is low. With this, FBO can now reconcile the role of alpha power and alpha phase in information transfer. In other words, low instantaneous peak-to-peak voltage corresponds to low alpha power which facilitates information transfer. Similarly, the trough of the instantaneous voltage corresponds to a specific phase. The operating principles of how GBI, CTC and FBO are thought to modulate cortical excitability and therefore gate the flow of information throughout the cortex is illustrated in Figure 1.1.

Recent experimental work in electrocorticography (ECoG) has already demonstrated that the instantaneous amplitude is a better predictor for cortical excitability than power or phase alone [36]. In this thesis, I investigated whether these findings extended to the much more prevalent electroencephalographic (EEG) recordings from the scalp. While ECoG has numerous advantages including high spatiotemporal resolution, signal fidelity, resistance to noise and robustness for continued recordings [37] its usage in research is limited. To record signals, ECoG electrodes need to be implanted which requires intracranial surgery. Additionally, the electrode grid placement is done solely by clinical indication without consideration for research needs. Therefore, EEG constitutes a much more prevalent tool for scientific investigations because it is inexpensive, readily available and

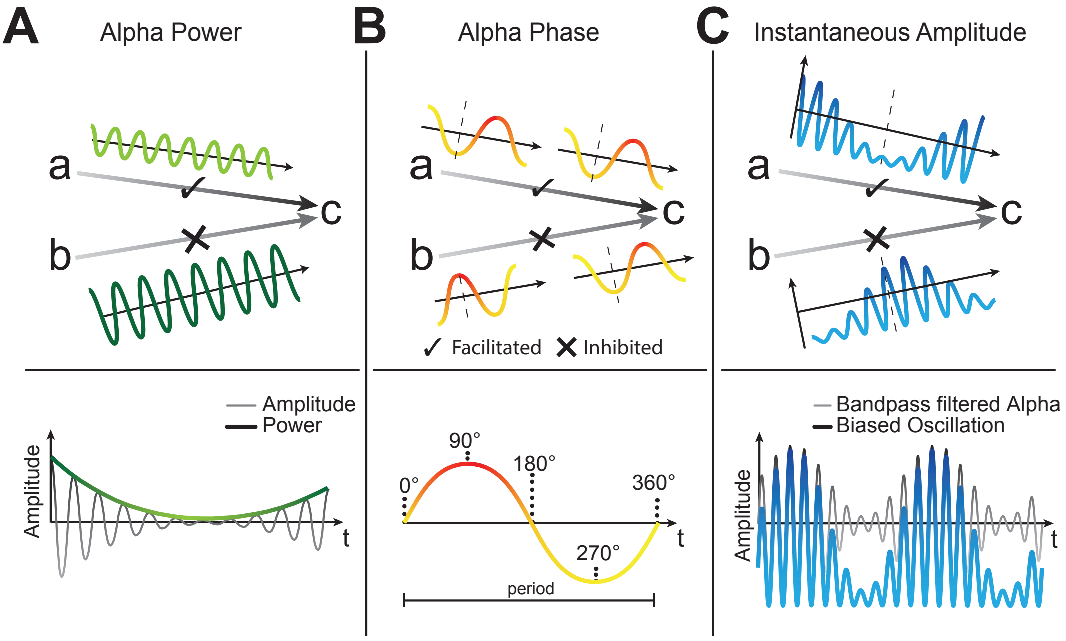

Figure 1.1: Gating mechanisms. **Top Row:** Illustration of gating mechanisms between cortical areas (a→c and b→c) for alpha power, alpha phase and instantaneous amplitude. **(A)** Inhibitory effect of alpha power. Information is only gated through the network if alpha power is low. **(B)** Excitatory effect of phase synchronization. Information is only gated through the network if phase is synchronized. **(C)** Inhibitory effect of instantaneous amplitude. Information is only gated through the network if the instantaneous amplitude of the biased oscillation is low. **Bottom Row:** Illustration of alpha power, alpha phase and instantaneous amplitude. **(A)** Alpha power as the envelope of the ongoing oscillation. **(B)** Alpha phase as the cyclic variation in amplitude of the ongoing oscillation. **(C)** Instantaneous amplitude as the biased asymmetric oscillation.

provides data with a high temporal resolution. It is of course not without its limitation, especially considering its limited spatial resolution and comparably low signal-to-noise ratio.

To investigate the instantaneous amplitude as a neural correlate with EEG recordings, a cortical structure with a good projection onto the electrodes had to be chosen. The visual cortex represents an ideal candidate for such an experiment and it has been shown that variability in the behavioral response to a visual perception threshold stimulus can be used as a proxy for cortical excitability[38]. I therefore decided to investigate whether the instantaneous amplitude could be used as an informative neural correlate of behavioral performance in a visual near-threshold experiment.

In visual near-threshold experiments, subjects respond to a very faint visual stimulus. Psychophysiological investigations of contrast sensitivity have shown that the perceived intensity depends on different factors like the position in respect to the field of vision, temporal properties, the intensity of the background on which the stimulus is presented or the orientation of the presented stimulus [39, 40]. In near-threshold experiments, the stimulus intensity will be decreased until the response to the stimulus changes to a probabilistic function, the so-called psychometric function. This function establishes the connection between stimulus intensity and the probability that the stimulus is perceived. Since the physical properties of the stimulus are fixed, the variability in the detection rate results from fluctuations in the cortical excitability of the brain[38].

Numerous studies have applied near-threshold stimuli to investigate the parameters influencing visual perception. It has been shown that alpha power [38, 41–46] and alpha phase [47, 48] influence visual perception. Their results show that a decrease in alpha power is associated with an increase in perception rate. This is in line with the idea that the perception of a stimulus is connected to cortical excitability. Similarly, investigations with alpha phase report that the perception of a near-threshold stimulus is more likely if alpha is in a certain phase. Research has also shown that the influence of visual perception can be extended to the confidence with which the stimulus is perceived [49, 50]. This finding, that alpha power modulates confidence can also be extended to other modalities [51]. This suggests that alpha power therefore changes the likelihood that a stimulus is reported as perceived which is thought to be influenced by cortical excitability.

It also has been hypothesized that the alpha voltage itself influences perception [52, 53]. The results of this thesis demonstrate that this is indeed the case.

# 2 Methods

## 2.1 Subjects and data collection

In this thesis, 34 healthy subjects (12 females, 22 males, $18 - 69$ years old, normal or corrected to normal vision) participated in a visual perception-threshold task. All subjects provided written consent for participating in the study, which was approved by the Institutional Review Board of the New York State Department of Health.

EEG signals, eye movements, visual stimulus onset and the behavioral response were recorded using the general-purpose BCI2000 (brain-computer interface) software [54, 55] interfaced with four 16-channel g.USBamp bio-signal amplifiers (g.tec, Graz, Austria), a Tobii X30 eye tracker (Tobii, Stockholm, Sweden), and a g.TrigBox (g.tec, Graz, Austria). The bio-signal amplifiers acquired EEG signals from 64 scalp locations using the standard 10/10 montage with the amplifier ground and reference placed on the right mastoid and ear lobe, respectively. An additional ground cable, fixed onto the subjects forearm was connected to the ground of the amplifier casing, to further reduce the influence of line noise. Throughout the experiment electrode impedances were kept below 40kΩ and the resulting EEG, eye-gaze, visual stimulus onset and button response signals was sampled at 512 Hz. This technique also allowed for an accurate measurement of subject reaction times.

Since I was interested in the relationship between visual stimulus onset, behavioral response and the EEG, hardware triggers were used to avoid any temporal uncertainty (i.e., jitter) between these measures. Specifically, the onset of the visual stimulus was recorded with an optical sensor (i.e., photodiode) mounted on the presenting screen, and the behavioral response with a push button digitized simultaneously with the EEG signals.

## 2.2 Behavioral task

Subjects performed the visual perception task in a dark room in front of a 42-inch LCD screen that spanned their entire visual field (65 cm distance, $\pm 36^\circ$ horizontal, $\pm 22^\circ$ vertical). Throughout the experiment this screen presented a dimmed white noise background (2.0 cd/m$^2$).

The stimuli in this task were large-scale Gabor wavelets presented on top of the noise background at one of four positions within the foveal field of vision (i.e., $1^\circ$ of the visual field, see Figure 2.1A). The intensity granularity was limited by the presenting screen which allowed only 255 different gray-scale values for the full scale from black to white.

First, the subject's visual perception threshold for these stimuli was determined. For this, subjects responded to a visual staircase procedure in which visual stimuli at alternating positions within foveal vision were presented with increasing intensity (21 steps, 10 repetitions, 1.6 sec per step). To report a visual change the subjects pressed a button as soon as they perceived the stimulus. This yielded an estimate of the visual perception threshold. To accurately determine the perceptual threshold, subjects were presented stimuli at five different intensities, centered around the estimated perception-threshold in a block randomized sequence (16 repetitions per intensity). This yielded the parameters of the psychometric function of visual perception (i.e., the sigmoid function in Figure 2.1B). For the main experiment, the stimulus with the intensity closest to the visual perception threshold (i.e., 50% in the psychometric function) was used.

Each trial started with a 2-sec long inter-stimulus interval, during which a bright masking stimulus was presented to prevent retinal adaptation (11.2 cd/m$^2$). After a subsequent randomized waiting period (1.625 to 3 sec), the stimulus appeared in one of the four quadrants within the foveal field of vision. The visual stimulus disappeared after the subject responded with a button press, or after a 1.6-sec long time out. Figure 2.1A illustrates this sequence. A trial was considered as perceived if the button was pressed between 200ms and 1.6-sec after the stimulus onset. Button presses outside of this time window were considered erroneous and triggered a repeat of the trial. Similarly, if the subject responded during the prestimulus period the trial was repeated to maximize the number of trials available for analysis.

Each subject performed 600 trials, structured into 10 blocks. Inbetween blocks, subjects were allowed to rest for up to five minutes. In total, the experiment was conducted over a period of one hour and thirty minutes (including breaks and calibration) and yielded 150 trials for each stimulus orientation. Throughout the experiment, an additional 60 catch trials with no stimulus, and 60 catch trials with a high intensity stimulus were presented, to control for the subject's task compliance. Each block contained an equal amount of randomly distributed catch trials.

## 2.3 Data processing

For the analysis, a notch filter was used to remove line noise at 60 Hz, and then the EEG signals between 1 and 40Hz were extracted using a 4th-order Butterworth IIR bandpass filter. Next, the continuous EEG signal was divided into 4-sec long trials centered around stimulus onset. To remove the influence of eye-blinks on the analysis, all trials for which the amplitude during the period of ±300 ms around the stimulus onset exceeded $50\mu$V at location Fpz were rejected. The signal was further inspected visually to remove any trials that exhibited EMG- or movement-related contamination. In the course of this visual inspection, 3 out of 34 subjects were discarded, as the contamination affected occipital scalp locations (i.e., the area of interest

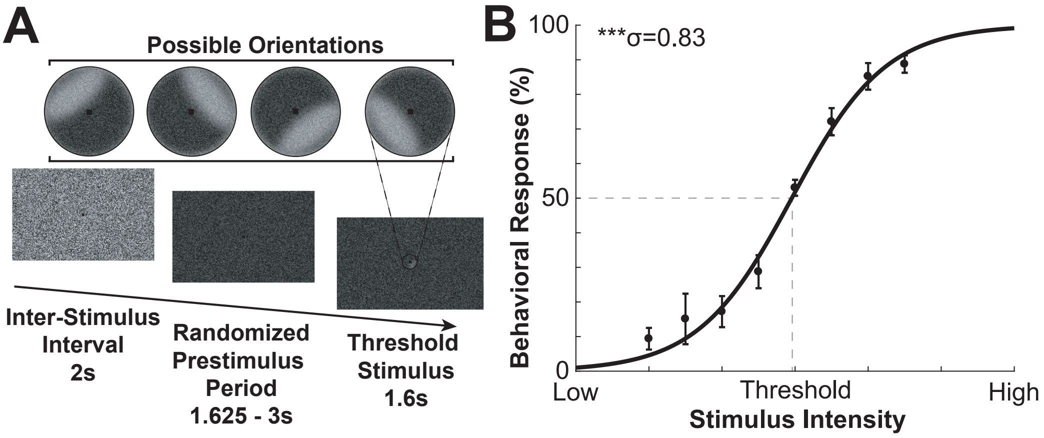

Figure 2.1: Experimental Design and Calibration. Subjects performed a visual perception-threshold task in a dark room, calibrated for a 50% behavioral response rate. **(A)** At the beginning of each trial, a 2-sec long bright masking stimulus prevented retinal adaptation. Following a 1.625 to 3-sec long pre-stimulus period, the visual perception-threshold stimulus appeared at one of the four quadrants within the foveal vision (i.e., $1^\circ$ of the visual field). The visual stimulus disappeared when the subject responded with a button press, or after a 1.6-sec long time out. **(B)** Calibrated psychometric function averaged across all subjects and aligned to the perception threshold (monotonic function, $^{***}p \ll 0.01$ , Spearman's rank-order correlation). Throughout the experiment, stimulus intensity was set to the perception threshold.

in this thesis). For the remaining subjects, between 0 and 70 trials (i.e., less than 10% of all trials; median: 5 trials) were removed. As the focus of this thesis were changes in cortical activity in the occipital areas, a Laplacian filter was applied to increase spatial selectivity as described in section 2.4.

Next, the dominant alpha band frequency was determined by applying a power spectral density (PSD) estimation on the EEG signals acquired while the subjects closed their eyes for one minute. Afterwards, a 2 Hz-wide 4th order Butterworth bandpass filter centered around the dominant alpha band frequency was used to extract the alpha oscillations from the EEG signals of the main experiment. From these alpha oscillation signals, alpha power and alpha phase was extracted by using a Hilbert transform, and the instantaneous amplitude using the procedure described in section 2.5. To ensure that the temporal relationship between stimulus onset and the features in the EEG remained constant throughout the analysis, all filters were implemented with the filtfilt function in MATLAB for zero phase-lag filtering.

## 2.4 Calculation of the surface Laplacian

Electroencephalographic measurements on the scalp are potential measurements in respect to a reference electrode, in this case mounted on the right earlobe. These measurements are highly correlated due to volume conduction effects between the cortical sources and the position of the electrode

[56]. The electrical activity of these neuronal populations is measured with a sensor through biological tissue which causes a superposition of the different sources at the sensor. To reduce the effect of this volume conduction and therefore increase spatial selectivity, a spatial filter was applied to the data [57]. This spatial filter, called a surface Laplacian, has the advantage that it does not require a volume conduction model of the head or specific information about the cortical sources. To estimate the surface Laplacian a variation of the finite difference method introduced by Hjorth [58] was used. The Laplacian estimate for each electrode was calculated according to Equation 2.1 where $V^i_{laplace}$ refers to the Laplacian estimation for i$^{\text{th}}$ scalp electrode. The estimation was calculated by subtracting the mean of the measured voltage of the surrounding electrodes ($V^n_e$) from the voltage of the electrode ($V^i_e$). To decide which electrode surrounds a certain electrode, the three dimensional positions of all sensors was measured and the euclidean distance between the electrodes was calculated. An electrode was considered as a surrounding electrode if the euclidean distance was smaller than 30mm.

$$V^i_{laplace} = V^i_e - \frac{\sum_{n=0}^{N} V^n_e}{N} \tag{2.1}$$

## 2.5 Extraction of instantaneous amplitude

A central assumption of the FBO hypothesis is that the troughs of the oscillatory alpha activity are always aligned at the same low voltage level, creating a biased oscillation (illustrated in Figure 1.1C). The described procedure for the extraction of this biased oscillation is identical to the one previously described by Schalk et al. [36]. The unbiased, zero-mean alpha wave ($S_{AA}$) was extracted by bandpassing the recorded signals with the identical filters used for the extraction of alpha power and alpha phase. The voltage bias (i.e., the minimum voltage value for the troughs of the oscillation, $offset_{bias}$) was determined individually for each electrode as the 5th percentile of the voltage values in the bandpass filtered alpha activity. To calculate the bias corrected alpha activity (i.e., the instantaneous amplitude, $S'_{AA}$) from the alpha oscillation, the difference between the negative voltage envelope ($S_{AE}$) and the bias offset ($offset_{bias}$) was subtracted from each time-point, following equation Equation 2.2.

$$S'_{AA} = S_{AA} - (-S_{AE} - offset_{bias}) \tag{2.2}$$

With this procedure, it was possible to reintroduce the bias which would otherwise be lost due to the bandpass filter.

## 2.6 Statistical analysis

For the statistical analysis, the single trial correlations of alpha power, alpha phase and instantaneous voltage with the behavioral response (i.e., button press or no button press) were calculated using a Spearman's correlation for alpha power and instantaneous voltage. To take into account the circular nature of alpha phase the correlation between phase and behavioral response was calculated with the circular linear correlation implemented in the CircStat[59] toolbox. This calculation is used to correlate a circular variable ($\alpha$) with a linear variable ($x$), in this case the subjects response to the stimulus. The value is obtained by calculating the multiple correlation coefficient $r$ between the correlation of the sine of phase with the linear variable ($r_{sx}$), the cosine of phase with linear variable ($r_{cw}$) and the correlation between sine and cosine of the phase ($r_{cs}$) as described in Equation 2.3. As implemented in the CircStat toolbox, the function $c(x, y)$ is defined as the Pearsons correlation coefficient. The result of this computation is a multiple correlation coefficient $r$ which is limited between 0 and 1 and therefore no information about direction can be obtained.

$$\begin{aligned}
r_{sx} &= c(sin\alpha, x) \\
r_{cx} &= c(cos\alpha, x) \\
r_{cs} &= c(sin\alpha, cos\alpha) \\
r &= \sqrt{\frac{r_{cx}^2 + r_{sx}^2 - 2r_{cx}r_{sx}r_{cs}}{1 - r_{cs}^2}}
\end{aligned} \tag{2.3}$$

In the analysis, I was interested in quantifying the variance in the behavioral task that was explained by alpha power, alpha phase and instantaneous amplitude. This entailed determining *where* (i.e., for which scalp location) and *when* (i.e., relative to stimulus onset) this quantification should be performed. To accomplish this, the most prominent difference in alpha power between responded and non-responded trials (Figure 3.1A) was identified (i.e., at which scalp location). To validate the results of this single-trial analysis, a control analysis was performed, in which alpha power was divided into four equally spaced bins, which were used to calculate the perception ratio (i.e., percentage of responded trials) for each bin, as suggested by others [46, 49, 50]. To prevent the influence of variations across subjects, the results for each bin was normalized by the subject's overall perception ratio. For each subject and each stimulus orientation, this yielded one normalized perception ratio value per binned alpha power level. Finally, across all subjects and all orientations, the Spearman's correlation between the binned alpha power levels and the normalized perception ratio was calculated. The p-value was calculated with a randomization test according to section section 2.7.

To determine *when* after stimulus onset the variance in the behavioral task, that was explained by alpha power, alpha phase and instantaneous amplitude, should be compared the time when the correlation between instantaneous amplitude and behavioral response reached its maximum after stimulus onset was used. In the final step, a paired Wilcoxon Signed Rank test was used to statistically compare the amounts of variance in the behavioral task that were explained by alpha power, alpha phase and instantaneous amplitude at that time point. The p-value was calculated according to 2.7.

## 2.7 Randomization Test

In statistical tests, the p-value signifies the probability that an obtained correlation is due to chance, or in more a more general term signifies the probability that under the null hypothesis a result is equal or more extreme than the actually observed result. It is therefore important to calculate these values correctly. For different statistical tests, an approximation of the p-value can be performed, but only if the underlying data adheres to certain statistical properties, which include independence and a certain a priory distribution of the correlated values. It is not always possible to know if these criteria are met. To avoid this problem, a randomization test, although computational costly, was applied to determine the significance of the presented results. In this test the data and labels are shuffled multiple times to create a distribution of correlation values. Since data and label are shuffled, the obtained distribution of correlation values can be seen as the probability that a certain correlation value is obtained by chance. With this distribution it is possible to determine the real p-value by calculating the probability, that the calculated correlation value was created at random.

# 3 Results

## 3.1 Verification of behavioral compliance

To verify the subjects compliance to the behavioral task, the response to the catch trials was analyzed. The results of this verification show that the subjects responded to almost all of the high-intensity catch trials (median: 100%) and almost none of the non-stimulus catch trials (median: 0%), which confirms that the subjects performed the task with high accuracy. Further analysis revealed that the detection for stimuli presented in different quadrants is significantly different ($p \ll 0.01$, One-Way ANOVA). To account for this, all subsequent analysis were performed for each quadrant individually. The analysis revealed that the lower half of the visual field was more receptive to visual inputs than the upper half, and that the lower right quadrant showed a significantly higher perception rate than lower left quadrant.

## 3.2 Location identification

In the first analysis, the scalp locations which exhibit the most stimulus-induced changes in alpha power were determined. For this purpose, the correlation between behavioral response and the alpha power at stimulus onset was calculated. This calculation was performed for each of the four stimulus orientations, and the resulting correlation averaged across all subjects (Figure 3.1A). The result of this analysis shows that the location Oz exhibits the highest stimulus-induced changes in alpha power. This location (Oz) was therefore used for all subsequent analyses. A control analysis also shows that the relationship between alpha power and perception ratio is linear and statistically significant (Figure 3.1B, Spearman's correlation, Bonferroni-corrected for 64 channels, $^{***}p \ll 0.01$, binned alpha power, across all trials and all subjects).

## 3.3 Comparison

Next, I was interested in quantifying the extent to which alpha power, alpha phase and instantaneous amplitude are informative of visual perception. For this, the portion of the behavioral variance that can be explained by alpha power, alpha phase and instantaneous amplitude was compared. Single trial correlation between each of these three features and behavioral response were calculated, individually for each orientation. For each feature, this

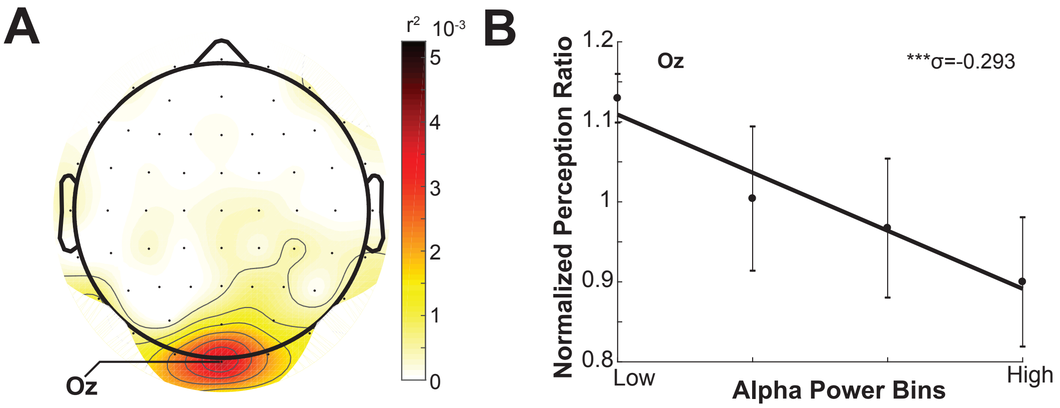

Figure 3.1: Relationship between alpha power and visual stimulus perception. **(A)** Portion of the variance in the perception of the visual stimulus that is explained by alpha power. The topography shows that this effect is most dominant at location Oz (single trials, Spearman's correlation). **(B)** Across all subjects and all trials, alpha power has a significant inhibitory effect on the perception of the visual stimulus at location Oz (Spearman's correlation, Bonferroni-corrected for 64 channels, $^{***}p \ll 0.01$, binned alpha power, across all trials and all subjects).

yields 124 correlation values (i.e., 31 subjects x 4 stimuli locations). The results in Figure 3.2 show that the instantaneous amplitude is indeed a significantly better neural correlate of visual perception than either power or phase ($p < 0.05$, paired Wilcoxon Signed Rank test).

This is further illustrated in Figure 3.3 for single trials in a representative subject. At the time of the arrival in the visual cortex, either alpha power (Figure 3.3A) or alpha phase (Figure 3.3B), but not both, can explain the detection of visual stimuli. In contrast, instantaneous voltage provides a reconciled explanation for the detection of visual stimuli in both cases (Figure 3.3A and Figure 3.3B).

The correlation between behavior and alpha power or alpha phase does not

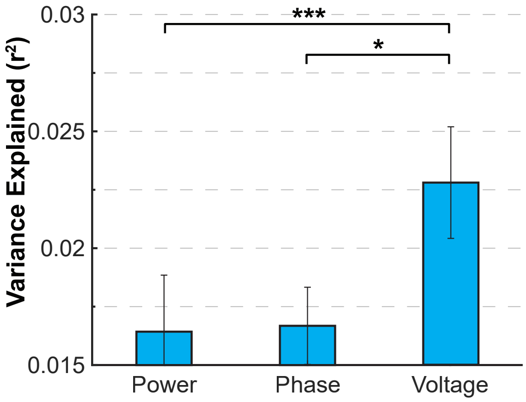

Figure 3.2: Portion of the variance in the perception of the visual stimulus that is explained by alpha power, alpha phase and instantaneous voltage. Overall, instantaneous amplitude is a better predictor for visual perception than either power or phase (Error bars show SEM, $^*p < 0.05$, $^{***}p \ll 0.01$, paired Wilcoxon Signed Rank test, N = 124).

change markedly within the first 150 ms of the post-stimulus period. In contrast, across all subjects, and when temporally aligned to the maximum, the correlation between behavior and instantaneous amplitude peaks 62.5 ms after stimulus onset (Figure 3.4). The temporal distribution of this alignment reveals a standard deviation of 28.5 ms (Figure 3.4B) for the maximum correlation across all subjects.

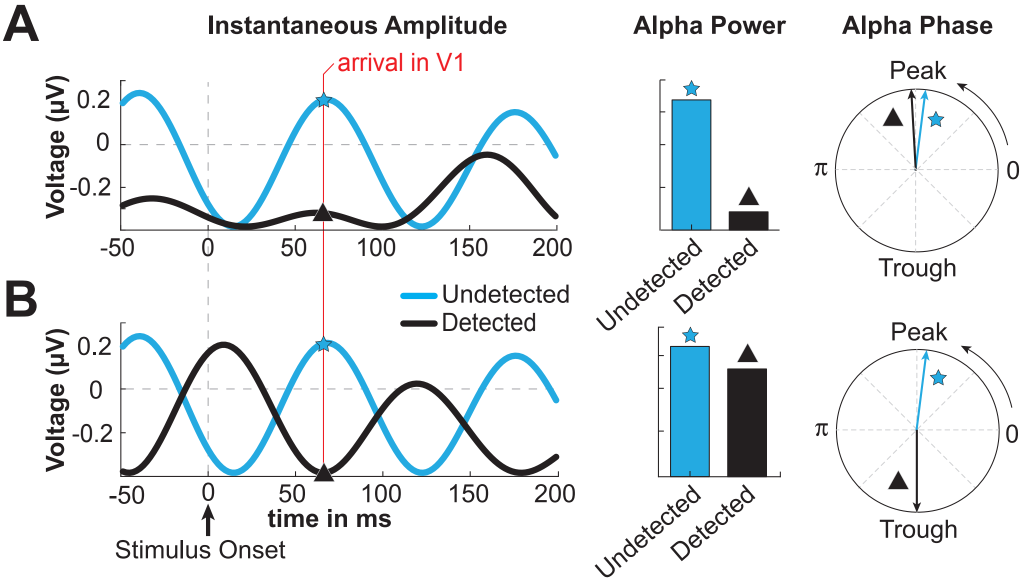

Figure 3.3: Single trial examples of how instantaneous amplitude, power, and phase influence the detection of visual stimuli at the time when they arrive in primary visual cortex (V1). **(A)** Difference in alpha power influences the detection of visual stimuli. **(B)** Difference in alpha phase influences the detection of visual stimuli. **(A&B)** While the examples in A and B can be explained by either alpha power or alpha phase, only instantaneous amplitude can explain both cases. Hence, only the function-through-biased-oscillations (FBO) hypothesis can provide a reconciled explanation for the detection of visual stimuli.

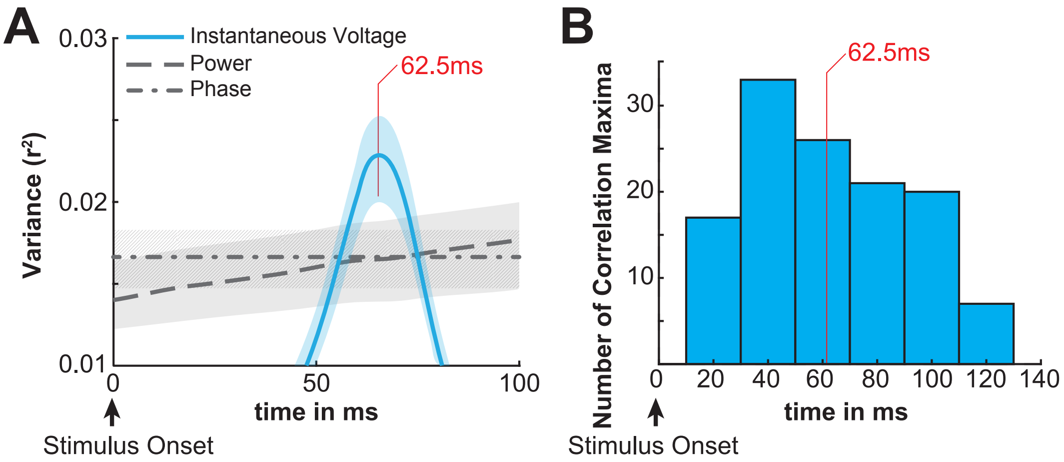

Figure 3.4: Temporal fidelity of power, phase and instantaneous amplitude as predictor of visual perception. **(A)** Correlation between power, phase and instantaneous voltage, with visual perception, as a function of time. The defined peak, 62.5 ms after stimulus onset, makes instantaneous voltage a more reliable predictor of whether and when visual information is gated and consequently will result in the corresponding behavior. **(B)** Distribution for time of maximum correlation with the instantaneous amplitude shows a mean latency of 62.5 ms (standard deviation: 28.5 ms).

# 4 Discussion

In this thesis, I investigated the role of oscillatory alpha activity in a visual near-threshold experiment. Specifically, I quantified the variability of the response to a visual near-threshold detection task explained by alpha power, alpha phase and instantaneous amplitude. The results unequivocally show that the instantaneous voltage explains variability in visual perception better and at a higher temporal fidelity than alpha power or alpha phase.

Since the early days of EEG, researchers have reported on the role of low-frequency oscillations in behavior, injury and disease [9, 28, 60–62]. The earliest reports described low-frequency oscillations as both non-sinusoidal and asymmetric in nature [9, 28]. However, since the advent of Fourier-based methods, which are based on the assumption that oscillatory activity is symmetrically distributed, the non-sinusoidal and asymmetric features of low-frequency oscillations have been largely ignored. This has led to the predominant use of power and phase in the investigation of oscillatory brain activity. For example, power changes in low-frequency oscillations have been associated with alertness [63], motor activity [14] and different mental disorders [64–66]. More specifically, changes in alpha power (i.e., 8-14 Hz) have been associated with shifts in attention [11–13] and cortical excitability [44, 67, 68]. Experiments have also shown that changes in alpha power modulates decision confidence [49–51]. These experiments show, that a decrease in alpha power increases the likelihood that a stimulus is reported as perceived. Additionally, the usage of transcranial magnetic stimulation [45] suggests that alpha power indeed causes changes in visual perception. By stimulating areas of the visual cortex it was possible to modulate the perception rate in a visual near-threshold paradigm.

Similarly, it has been shown that alpha phase correlates with the probability of neural firing [47, 48, 69]. Alpha phase has also been shown to represent cortical connectivity throughout the cortex [70–72]. There has also been evidence for phasic influences in the alpha band causes perceptual differences in phosphenes induced by single transcranial magnetic stimulation pulses [73].

These investigations of alpha power and alpha phase have culminated in two theories about how information transfer is facilitated within the static anatomy of the brain. The first theory, Gating-by-Inhibition [GBI; 13], is based on observations that alpha power decreases in task relevant areas while alpha power increases in task irrelevant areas. Therefore alpha power gates information by inhibiting irrelevant pathways. The second theory, Communication-through-Coherence [CTC; 19, 20] is based on observations that cortical excitability coincides with certain periods of the alpha phase.

Evidence shows that information transfer is facilitated when the oscillations between cortical areas are synchronized.

Interestingly, both GBI (i.e., alpha power), and CTC (i.e., alpha phase) theories are required to explain variability in perception and behavior [12, 26, 47, 48]. Recently, the reemerging evidence that oscillatory activity is asymmetric and non-sinusoidal [30, 32, 33] has led to the Function-through-Biased-Oscillations theory [FBO; 35], which reconciles the GBI and CTC theories. In the FBO theory, the increase of the instantaneous voltage amplitude of the biased oscillation reduces cortical excitability. Changes in alpha power are therefore a measure of the modulation of in the peak-to-peak voltage of the instantaneous voltage. This would allow communication between cortical areas when it would not be probable if only the GBI hypothesis is considered. Mathewson et al. formulated a similar conclusion [48] during the investigation of phasic influences on visual perception which they labeled the "$\alpha$ breaking system". In their framework they suggested that inhibition is not equal across the alpha cycle but manifests itself as pulsed inhibition. This pulsed inhibition would only occur if alpha power is high (i.e., alpha oscillation is present). They therefore proposed two different mechanisms that influence perception, based on the suppression state of alpha power. This view is consistent with the single trial results illustrated in Figure 3.3, if the instantaneous amplitude would not be considered. In conclusion, only the Function-through-Biased-Oscillations model is able to explain both cases with a unified theory.

Therefore, the presented results do not only validate the FBO theory in

EEG signals, but give a different perspective on the modulation of cortical excitability. As previously discussed, if alpha power does indeed modulate subject confidence, this should also hold true for the instantaneous amplitude. These findings open up new possibilities for scientific, clinical and consumer applications. This is because instantaneous amplitude can not only explain 35% more of the behavioral variance than power or phase, but can also predict when the cortex is most receptive to perceptual input. Scientific applications could use this information to study the flow of information throughout the cortex, while clinical applications could use the instantaneous voltage as a biomarker for neurological disease and injury, and consumer applications could make use of instantaneous voltage to determine the user's receptiveness to information input. Another possible application would be the usage of instantaneous amplitude as a feature for brain computer interfaces (BCI). Additionally, applications in the estimation of subject alertness [63] could be considered. The instantaneous amplitude might also be able to increase the success of neurorehabilitational devices. The non-invasive nature of EEG drastically increases the feasibility of all of these applications. Nevertheless, the benefits of the presented findings aren't limited to non-invasive applications. Knowledge about the state of cortical excitability could be used to increase the efficiency in deep-brain stimulators that are used in the treatment of Parkinson's Disease, Essential Tremor or for Obsessive-Compulsive Disorder.

Another important aspect is that the FBO theory opens up a completely new perspective on low frequency oscillations in the brain. Gerwin Schalk predicted in his initial paper [35], that the Function-through-Biased-Oscillation hypothesis might be able to explain, in part, phenomenons like the Bereitschaftspotential in the motor cortex which occurs before a movement execution. It might also, at least partly, explain the mechanism that generates the event related potentials. In his publication he also states that information routing in the brain is primarily dependent on the cortical excitability of the involved nodes and that the peak-to-peak amplitude of the instantaneous amplitude within a neuronal population is predictive of its involvement in a certain task. Furthermore, he hypothesis that the phase of the cortical oscillation is modulated by sensory inputs, or the expectancy of such.

## 4.1 Spatial and Temporal Fidelity

The results also show that instantaneous amplitude is most predictive of the behavioral response 62.5 ms after stimulus onset. This constitutes the time from appearance of the visual stimulus on the screen until the stimulus arrives at the visual cortex. This pathway starts when the light it strikes the retina which consists of several layers of neurons interconnected with synapses. When light strikes the photosensitive photoreceptor cells a cascade of chemical reactions and electrical events cause an excitation of the optical nerve [74]. The stimulus travels through the optic nerve to the optic chiasma. In this X-shaped structure the optic nerve fibers originating from the eyes partially cross to aid binocular vision. The stimulus then travels through the optic tract to the lateral geniculate nucleus (LGN), prectal nuclei, and superior colliculus. The lateral geniculate nucleus, which is part of the thalamus acts as the main connection between the optic nerve and the occipital lobe, specifically the primary visual cortex (V1). The LGN, is viewed as a gateway for sensory information entering the visual system [75]. The LGN therefore represents the first stage at which cortical processing could influence visual inputs and seems to be implicated in attentional response modulation caused by corticothalamic feedback [76]. After the stimulus has left the lateral geniculate nucleus, it is forwarded through the optic radiation which are the axons connecting the LGN with the primary visual cortex. The stimulus then finally arrives at the primary visual cortex. The retinotopic projections obtained in Figure 3.1 fit together with previously reported projections of the visual field on the primary visual cortex [77, 78]. Additionally, the reported time it takes the stimulus to arrive in the primary visual cortex is in line with studies that used MEG and single unit activity to investigate the arrival time of stimulus-related information in the primary visual cortex [79–85]. This result also encourages the view that perception relies on discrete processing epochs. Numerous experiments have been conducted, supporting a temporal quantization in perception [86–88]. This perceptual quantization can be observed by modulation of the interstimulus interval between two stimuli. If the stimuli are present in rapid succession they are not perceived as individual events. This perceptual window has been estimated to be around 20-50ms depending on stimulus conditions [89, 90], which could be attributed to the period of time where the instantaneous amplitude is at the trough. Another experiment discovered, that multiple distinct visual events (8 distinct flashing lights) were reported as occurring together if repeated in a cycle less than 125ms [91]. This quantization could also affect reaction times, which seem to be periodic with intervals of around 100 ms and 25 ms [92, 93]. This further supports the FBO theory by showing that variations in behavioral response could be caused by the fluctuations in cortical excitability due to the instantaneous voltage at stimulus arrival in the primary visual cortex. The results also indicate that this temporal specificity cannot be obtained with power or phase based measurements (Figure 3.4).

## 4.2 Stimulus Orientation

An analysis of the stimulus orientation showed a significant ($p \ll 0.01$, One-Way ANOVA) impact onto the behavioral response. It was therefore necessary to correlate each orientation individually with behavior. It seems that visual perception is biased towards the lower half of the visual field, and in addition primed for the right hand side. If left handed people would also be biased towards the right lower quadrant. This does not completely fall in line with other results [77], but the stimuli used in their experiment had a fine grating, which was not the case for the stimuli used in this thesis. It could be that the obtained results are different due to the nonspecific orientation within the presented quadrant.

## 4.3 Reaction Time

Simple reaction times (i.e., the response to a single stimulus) are comprised of multiple factors which include a stimulus registration time, a choice reaction time and the time to construct and execute a movement to respond (i.e., pressing a button) [94]. The analysis of the reaction times showed no significant correlation with either alpha power, alpha phase or the instantaneous amplitude, but there have been sporadic reports in the past that reaction time is correlated with alpha phase [95]. While reaction times to salient visual stimuli are around 330ms [96] our measurements show a mean reaction time of about 500ms. This is consistent with other experiments [97, 98] showing that the reaction time increases if stimulus intensity decreases.

## 4.4 Potential Confounds

In this thesis, I controlled all confounding factors that could potentially have affected the behavioral response or the EEG signals. One potential confounding factor was the subject's ability to predict the time and location of the stimulus. To prevent this, the pre-stimulus period and stimulus location was randomized. Another potential confounding factor was the variability in performance throughout the experiment. To counter this variability, a bright masking stimulus at the beginning of each trial was used to prevent retinal adaptation, practice runs to familiarize the subjects with the task, and breaks in-between blocks to prevent fatigue. The success of this approach was supported by the subjects' high compliance to the catch trials.

Further, stimuli were only presented after the subjects fixated gaze and did not blink for the duration of the entire pre-stimulus period. This measure ensured that the subjects perceived the stimulus within foveal vision and at the time of presentation. It also prevented the confounding effects of eye-blinks and ocular artifacts on the EEG. This precaution, together with rejecting all trials affected by EMG- or movement-related artifacts, ensured that only EEG signals that relate to neural activity, caused by the perception-threshold, task were analyzed. However, to account for the unlikely possibility that I might have failed to reject trials affected by artifacts, the outlier-resistant Spearman's rank-order correlation was used whenever possible.

To avoid electrical artifacts on the EEG signal, an additional ground cable connected the subject with the amplifier case to reduce the overall influence of 60 Hz noise. Together with the Laplace filter, which also reduced noise from common sources, all necessary measures were taken to ensure signal quality. This included a strain relief for the EEG cables from the subject to the amplifier, measurement of the elecrode impedance and it was also ensured that the reference electrode, positioned on the earlobe, did not move.

Another concern was that the subjects could have potentially responded to the presence of the stimulus instead of its onset. I considered this to be an unlikely possibility, because the stimuli were embedded in a dimmed white noise background, making them virtually impossible to detect if their onset was missed. Nevertheless, I performed a control analysis to determine whether subjects responded to the presence or to the onset of the stimulus. For this, the distribution of reaction times to the perception-threshold stimuli was compared to that of a salient stimulus [99]. This analysis unequivocally rejects the possibility that subjects responded to the presence and not to the onset of the perception-threshold stimuli.

To account for other confounding factors regarding the stimulus itself, the stimulus intensity and background intensity was considered. It is known [100] that the background intensity on which the stimulus is presented influences the ability to perceive the stimulus itself. Due to the limited granularity of the presenting screen (255 steps maximum), the background intensity was kept low to increase the perceived difference for the subject. Since the subjects were in a dark room, in front of a dark screen for a long time, it is probable that their eyes would adapt to the darkness over time. To avoid this retinal adaption, which would influence their perception, every trial ended with a long bright masking stimulus. This masking stimulus resets the visual system to provide consistent experimental conditions during the whole length of the experiment. I also considered the use of backward masking as done by others. In this type of experiment, the likelihood that a presented stimulus (the target) is detected is reduced by another stimulus (the mask) [101]. In this interesting concept, a mask which is presented after the stimulus influences the perception of the target. This is thought to be achieved by the masks ability to erase visual information or interrupt its further processing. This concept was not used because of the concern that the measured reaction times would be due to the mask instead of the stimulus.

Although single trial correlations between power and behavioral outcome are small, the control analysis (Figure 2.1) confirmed that the results are in line with previously published results [42, 46, 49, 50, 102]. The analysis also revealed that the detection of stimuli presented in the quadrants was significantly different. This may have been due to the retinotopic representation of the visual field, and its mapping onto different functional areas of the visual cortex. Consequently, the electrode Oz may have been affected differently by each visual field. To ensure that this did not influence the results, all analyses were performed for each quadrant individually. The results confirmed that the retinotopic representation of the visual field did not affect the outcome of this study. Specifically, the average across all quadrants, as well as each quadrant itself, yielded the same conclusion, i.e., that instantaneous voltage explains variability in visual perception better, and at a higher temporal fidelity, than alpha power or alpha phase.

To avoid any influence due to the signal processing, I used identical filter parameters for all features. An additional analysis was performed to check the influence of the filter parameters on the results, but the results did not markedly change favor a certain feature. The alpha frequency was chosen in a way to ensure reproducibility and consistency over all subjects. I also tried different spatial filter configurations, as well as other methods like current source density estimation, neither showed significant changes in the result. Only if no filter, or a common average filter was used the results changed, most likely due to the loss in spatial selectivity. The results were reported with the Laplacian filter because it is a well established but simple technique to increase spatial selectivity.

## 4.5 Conclusions

In conclusion, I propose the usage of instantaneous voltage as an informative neural correlate, and advocate for a different perspective on neural oscillations. The results support the important realization that the asymmetric and non-sinusoidal nature of oscillations are informative of brain function [9, 28–33]. This valuable information should lead to more studies using measures that take into account the physiological nature of oscillatory activity (e.g., amplitude fluctuation asymmetry [AFA; 32], lagged coherence [103], and physiologically-inspired base functions [104]). The instantaneous amplitude provides a simple but powerful interpretation of the physiological mechanisms that control cortical excitability and perceptual phenomenons. These measures could also be the basis for uncovering new biomarkers of neurological function, injury or diseases. The presented findings show that the FBO hypothesis provides new insight about gating mechanisms in the brain, and might prove as a valuable tool in the investigation of phenomena that involve multiple cortical areas.

## 4.6 Acknowledgments

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