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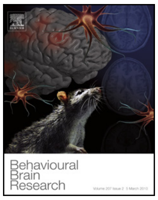

Review

# The role of alpha oscillations for illusory perception

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## HIGHLIGHTS

- We review studies showing a crucial role of alpha oscillations for illusory perception.
- Power and/or phase of alpha oscillations influence illusory perception.
- Alpha oscillations influence visual, auditory and multisensory illusions.
- Modulations of alpha oscillations are found before and/or during illusory perception.

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## ABSTRACT

Alpha oscillations are a prominent electrophysiological signal measured across a wide range of species and cortical and subcortical sites. Alpha oscillations have been viewed for a long time as an "idling" rhythm, purely reflecting inactive sites. Despite earlier evidence from neurophysiology, awareness that alpha oscillations can substantially influence perception and behavior has grown only recently in cognitive neuroscience. Evidence for an active role of alpha for perception comes mainly from several visual, near-threshold experiments. In the current review, we extend this view by summarizing studies showing how alpha-defined brain states relate to *illusory* perception, i.e. cases of perceptual reports that are not "objectively" verifiable by distinct stimuli or stimulus features. These studies demonstrate that ongoing or prestimulus alpha oscillations substantially influence the perception of auditory, visual or multisensory illusions.

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## 1. Introduction

Neuronal oscillations in the alpha band (~8–12 Hz) are a ubiquitous electrophysiological signal in the human and non-human mammalian brain [1]. Alpha oscillations have been found in several cortical areas, including sensory, motor and frontal cortices (see [2,3] for reviews), as well as in subcortical areas such as the thalamus and basal ganglia [4–6]. For sensory cortices, different labels have been assigned to the respective alpha oscillations, e.g. the mu-rhythm in somatosensory [7,8] or the tau-rhythm in auditory cortex [9]. These sublabels refer to the slightly different waveforms of alpha oscillations in different modalities. In addition, the sublabels

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suggest that the functional role of alpha oscillations in different modalities may not be completely homogenous. Since the aim of this review is to highlight similarities between the oscillations falling in the alpha frequency band in different sensory cortices, we will use the more general term alpha oscillations throughout the manuscript.

The importance of alpha oscillations for neuronal processing has been recognized long ago. For example, early studies have reported an influence of alpha power and/or phase on the perception, evoked response and reaction times (e.g. [10–14]). Only in recent years, neuroscientific research has re-gained increasing awareness that alpha oscillations substantially influence perception, behavior and neuronal processing. It has been known for a long time that alpha oscillations can be modulated intrinsically and extrinsically. For example, the power of alpha oscillations decreases after sensory stimulation, but increases if subjects are not engaged in any task. This latter effect led to the notion of alpha as an "idling" process of brain regions [15]. In contrast to this idling hypothesis, recent studies have argued for an active role of alpha in perception and cognitive processes. A common thread between different proposals on the functional role of alpha is the gating of neuronal processes, such that increased alpha power reflects inhibition of task-irrelevant areas whereas decreased power indicates processing [16–18]. Evidence for the active role of alpha comes from studies investigating working memory and attention. For example, several studies reported a modality specific increase of alpha power in visual, somatosensory, or auditory cortices in the retention period of the respective working memory tasks (e.g. [19–21]). An increase of alpha power in the retention period fits well to the notion of increased alpha power reflecting inhibition. Increased alpha power is suggested to inhibit distracting signals to interfere with the information stored in memory [17]. In addition, studies on spatial attention have demonstrated that the power of alpha oscillations can be modulated by endogenous shifts of attention in the absence of any physical stimulation. When a stimulus is anticipated or attention is directed toward the location of a stimulus, alpha power decreases in visual, auditory or somatosensory cortex, respectively, contralateral to the expected or (covertly) attended site. Conversely, alpha power increases in ipsilateral sites (e.g. [22–27]). Going beyond these well controlled and stimulus-cued alpha modulations, relatively "spontaneous" fluctuations of alpha power prior to stimulus onset can influence detection and discrimination of upcoming near-threshold stimuli [28–33]. Latter studies used stimuli at perceptual threshold and investigated one extreme side of perception where the relevant stimulus is sometimes perceived or goes completely unnoticed. On the other extreme side of perception, there are rare cases where stimuli are perceived which are physically not present. Such misperceptions can appear following stimulation (e.g. illusions) or without an external stimulus (e.g. phantom perceptions like tinnitus). Illusions can be characterized by two perceptual processes: Either subjects demonstrate a distorted perception of the stimulus (-properties) or they perceive a qualitatively and/or quantitatively additive (i.e. illusory) stimulus property which is not present in the physical stimulus.

Some illusions can be elicited reliably and constant in time (e.g. Kanisza triangle), whereas for other illusions trial-by-trial variability between veridical and illusory perception has been reported (e.g. double-flash illusion [34]). Since physical stimulation remains constant, the variability of perception has to be caused by intrinsic modulations of brain states. Therefore, such illusions offer unique insights into intrinsic brain states modulating veridical and illusory perception.

In this review paper, we will survey studies in which subjects' perception switches between illusory and veridical perception over time or on a trial-by-trial basis. We will outline that alpha oscillations play an active role for the switching between perceptual states. The modulation of alpha oscillations can be found either in the prestimulus period or in the peristimulus period, i.e. while the illusion is ongoing.

Our review will be structured in three parts. In the first and second part, we will review the role of alpha oscillations on visual and auditory illusions respectively. Finally, we will review multisensory, i.e. audio-visual and visuo-tactile illusions.

## 2. Methods to analyze alpha oscillations

Alpha oscillations can be analyzed with several approaches. While the results of these approaches are virtually identical, their applicability and practicality might differ depending on data and/or a priori hypotheses. For example, some of the reviewed studies obtained spectral estimates by Fourier transformation [35–44] others by wavelet analysis [45–47]. As a next step, the alpha-band can be chosen a priori by a defined frequency or frequency-band [35–41,46,47] and statistics are then performed on these alpha-band estimates. Alternatively, spectral estimates can be computed on broader frequency ranges and statistics reveal significant effects confined to the alpha-band [42–45,47]. Finally, some studies analyzed alpha oscillations solely on the sensor level [35–37,39,45,46]. While the topography of these analyzes often gives sufficiently good information about the distribution and sources of the observed effect, it nevertheless limits the interpretation of cortical sources. To overcome this limitation, some studies additionally computed the underlying sources of effects revealed at sensor level using e.g. beamformer techniques [42–44,47]. Other studies used a computationally more demanding approach and performed analyses directly on source level [40,41].

## 3. Visual domain

One intriguing example of a visual illusion is the phenomenon of phosphene perception. Phosphenes are flash-like illusory percepts which are typically induced by applying transcranial magnetic stimulation (TMS) over visual cortex, in the absence of retinal input and even in blind subjects [48,49].

In a series of studies, Romei et al. studied the role of alpha oscillations on phosphene perception. The authors applied single pulse TMS over visual cortex and determined individual thresholds of TMS intensity to induce phosphene perception. Simultaneously, they recorded resting state brain activity with EEG and correlated oscillatory brain activity with individual phosphene thresholds. They found that phosphenes could be induced with low TMS intensities in subjects with low resting state alpha power measured over posterior sites, presumably visual cortex. Moreover, TMS intensities required for phosphenes increased with increasing alpha power. In subjects showing the highest alpha power no phosphenes could be evoked at all [35]. In another TMS-EEG study, Romei et al. demonstrated that also individual trial-by-trial variability of phosphene perception was correlated with alpha power at the moment of the TMS pulse. If a TMS pulse coincides with low levels of spontaneously fluctuating alpha power in occipital cortex, the likelihood of perceiving phosphenes was increased. This effect was found in occipital cortex contralateral to the site of the perceived phosphenes [36].

These studies demonstrate that the likelihood of inducing phosphenes is related to the level of alpha power at the moment of application of the TMS pulse. The authors argue that alpha power reflects the state of momentary cortical excitability. If external stimulation by TMS hits visual cortex at states of high excitability (low alpha power), this may induce visual illusory percepts even in the absence of retinal stimulation.