«Distractor inhibition by alpha oscillations is controlled by an indirect mechanism governed by goal-relevant information»

Jensen, 2024

Alpha oscillations: From resting state to inhibition

Alpha oscillations

- Frequency range of 8 to 13 Hz
- Reflect a state of rest or idling → not directly involved in neuronal mechanisms supporting cognition

BUT alpha oscillations can **remain strong during working memory retention** and **increase with working memory load**
→ Paradigm shift to alpha reflecting **inhibition of visual input** rather than a state of rest

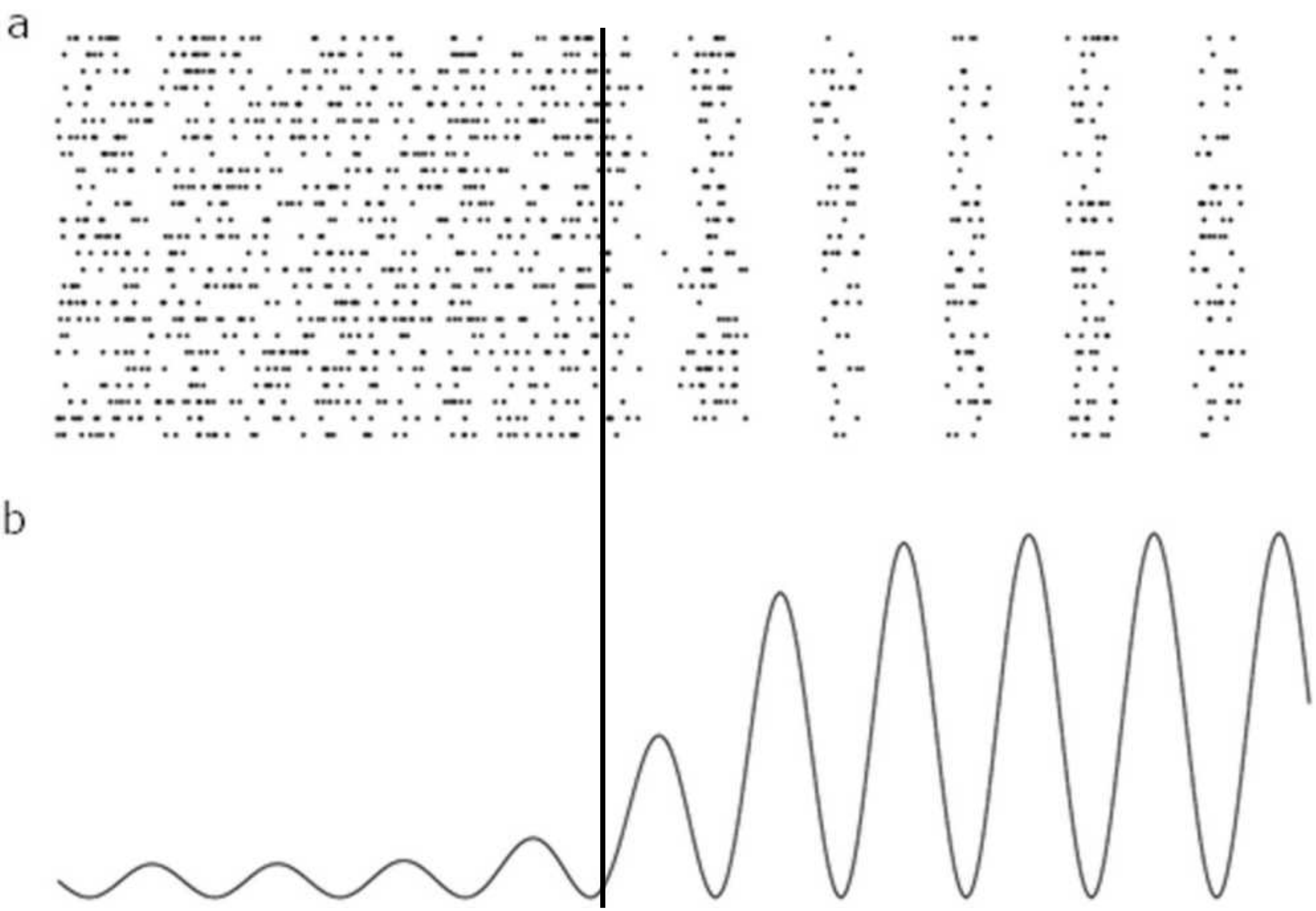
Hemispherical **lateralization** with respect to spatial attention

- Attention to the left: alpha decrease contralateral and increase ispilateral
- Neurofeedback studies modulating the hemispheric asymmetry provide evidence for the **causal role of alpha-band oscillations in the allocation of spatial attention**

Alpha oscillations observed in EEG recordings are due to **neuronal firing being inhibited in a phasic manner** at 8–13 Hz

Generation of alpha oscillations by pulsed inhibition

Fig. 1 | A schematic plot demonstrating how alpha oscillations can be generated by pulsed inhibition. **a** The raster represents the firing of a group of neurons. To the left, the firing rate of the neurons is high, and the firing is asynchronous. To the right, the firing is inhibited every ~100 ms, i.e. at ~10 Hz. **b** The population activity of the neurons above reflects the local field potential or scalp EEG. On the left, the neurons are firing strongly but asynchronous. As such, no modulation is observed in the population signal. The right oscillations are generated by pulsed inhibition silencing the neurons periodically. This scheme explains why an increase in alpha power is inversely correlated with the firing rate. Adapted from ref. 69.



Summary of theoretical background

(1) alpha band oscillations play a role in **orchestrating neuronal firing**
(2) alpha oscillations are associated with the **inhibition of firing rates**
(3) entrainment and neurofeedback studies speak to a **causal role** of alpha oscillations

It is, however debated whether alpha oscillations in general are under **top-down control**.

Mechanisms for the control of alpha oscillations

Alpha power increased before the onset of anticipated distractors

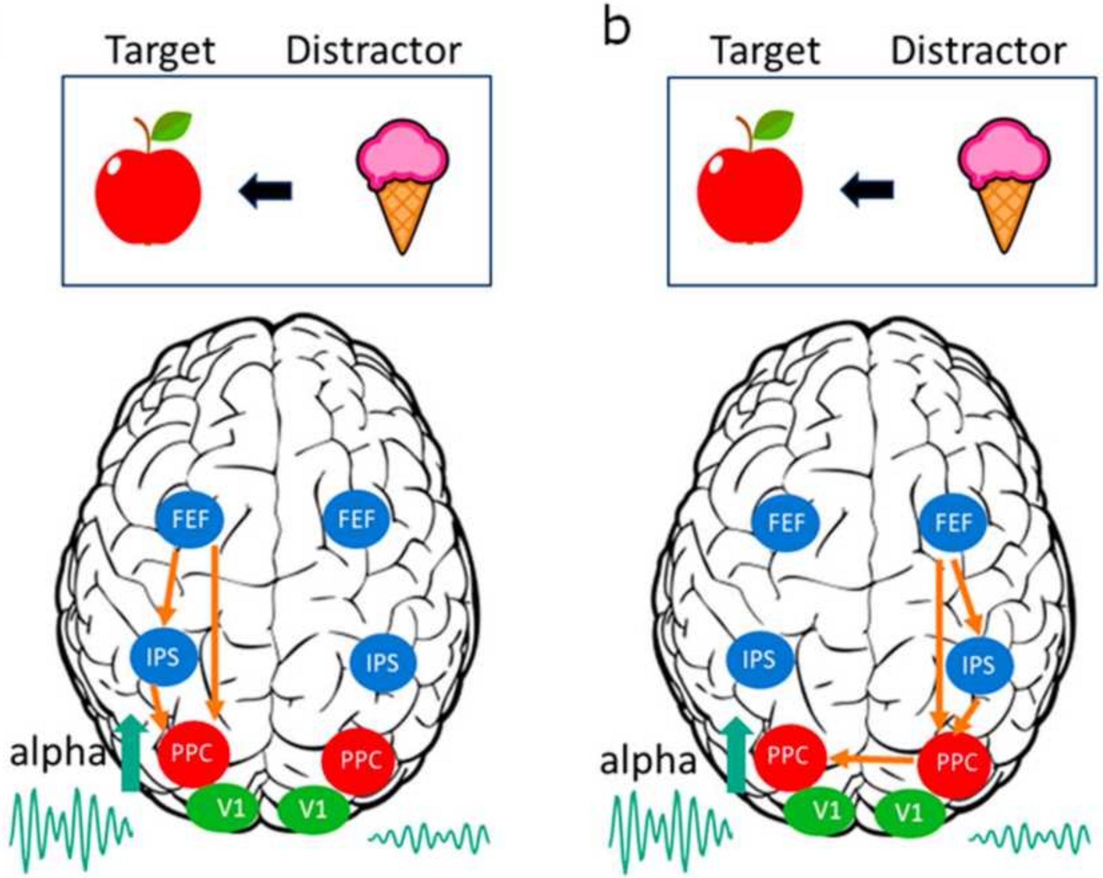
— Object-specific suppression correlated with the alpha power increasing in the hemisphere that was associated with the distractor
→ Increase in alpha power associated with the distracting stimuli
→ Alpha power associated with distractor inhibition **can be under direct control**

Several studies have, however, failed to find direct evidence for a top-down driven increase in alpha power associated with distractor suppression → mixed evidence

Indirect control of the alpha oscillations is a consequence of a top-down drive engaging task-relevant regions, which then **disengages task-irrelevant regions**. While alpha oscillations are undoubtedly associated with the inhibition of neuronal activity, the mechanisms controlling the alpha oscillations need to be better understood.

Modulation of posterior alpha oscillations by direct feedback or indirect control

Fig. 2 | Two mechanisms for modulating posterior alpha oscillations: direct feedback or indirect control. a Direct top-down control of alpha oscillations driven by awareness or anticipation of, e.g. a right hemifield *Distractor* resulting in a power increase in the left posterior parietal cortex (PPC; around parieto-occipital sulcus). The alpha power increase serves to inhibit the feedforward flow of visual information associated with the *Distractor*. The control is exercised by regions in the dorsal attention network (blue regions); e.g. the frontal eye fields (FEFs) directly or via the intraparietal sulci (IPS). A subcortical route is also possible. **b** An indirect mechanism for the control of posterior alpha oscillations. The perceptual load of the left *Target* results in strong engagement of the right hemisphere dorsal attention network, thus promoting an alpha power increase in the left PPC (red regions) via lateral connections. This serves to reduce the flow of information associated with the *Distractor*. According to this revised framework, the alpha oscillations do not implement gain control by inhibiting early visual regions (green regions); rather, they serve to gate the information flow in the PPC (see also ref. 12).



Increase in distractor-related alpha power is explained by the perceptual target load

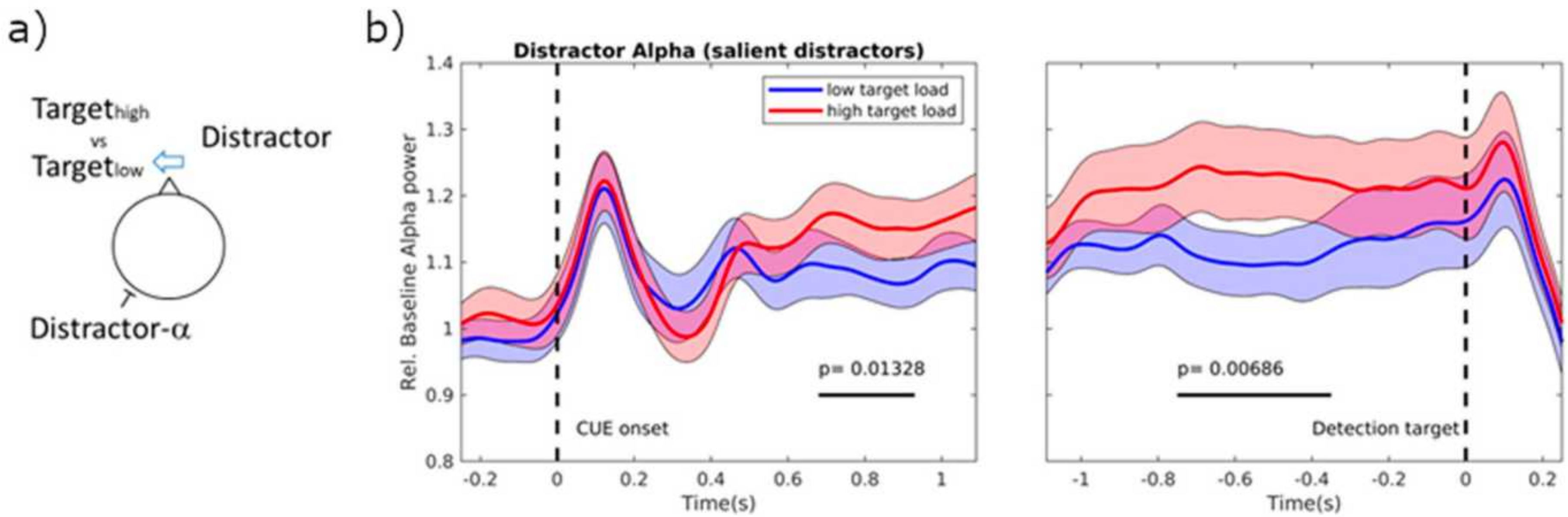


Fig. 3 | The increase in distractor-related alpha power is explained by the perceptual target load. a In this example, *Distractors* are presented to the right and *Targets* to the left. The perceptual load (visibility) of the *Targets* is manipulated. **b** The alpha power associated with the *Distractor* (i.e. the left hemisphere in this example) is stronger for high compared to low target loads. Reproduced from[82].

Increase in distractor-related alpha power is explained by the perceptual target load

Distractor inhibition is a consequence of perceptual or cognitive load

Perceptual load of the targets increased the alpha power associated with the distractors

Even though the increase in alpha power associated with distractor suppression is indirect, it is a **secondary consequence of top-down control**

«A good part» of **the modulation of the alpha power is indirect** and **controlled by the perceptual load** of the targets

— Indirect mechanism could serve the **allocation of perceptual resources**: In settings where the perceptual load is high and requires a lot of attentional resources, it is beneficial to suppress distracting stimuli. However, in settings with little perceptual load, it would make sense to also allocate resources in surplus to process stimuli of less relevance.

Alpha oscillations and the subsequent distractor suppression can be **controlled by both direct and indirect control mechanisms**

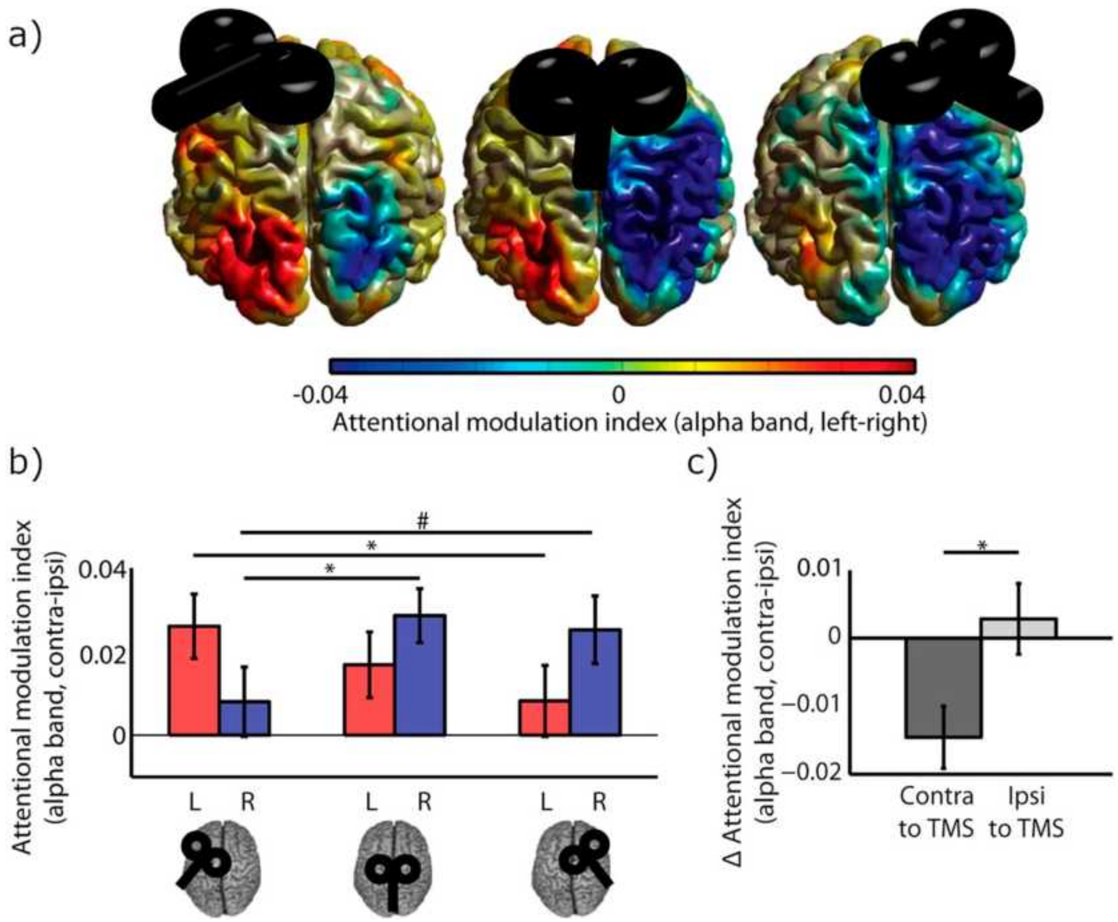
— While the indirect control mechanisms appear to be **dominant**, further work is required to uncover in which settings indirect versus direct control mechanisms are at play

TMS at FEF diminishes the ability to modulate alpha power in the contra-lateral hemisphere

When rTMS was applied to the right FEF, the participants had **a reduced ability to modulate the left parieto-occipital alpha oscillations** when spatial attention was allocated.

This finding is **consistent with indirect control of the alpha oscillations**: when one side of the dorsal attention network is impaired by rTMS, this reduces the ability to modulate the contralateral alpha oscilla-tions

The rTMS findings are **not consistent with direct top-down control of alpha oscillations**. In that case, impairing one side of the dorsal control network should impact the ability to modulate alpha power in the same hemisphere.



How general is the role of alpha oscillations for resource allocation?

Question: Is the functional role of the alpha oscillations generalized beyond parieto-occipital areas and other sensory modalities?

Sensorimotor
Alpha is depressed both during motor and somatosensory tasks

Eye movements
Alpha is modulated by the **planning of eye movements** as they decrease in the hemisphere contralateral to the direction of the saccade
Micro-saccades and alpha oscillations are co-modulated in spatial attention tasks
→ Ample evidence for the **generation and task-specific modulation of alpha-band oscillations in the motor system**.
→ Visual domain: Alpha decrease in sensorimotor as well as parietal regions associated with engagement while they increase in areas not required for the task

Language
Same findings also for language areas by presentation of words and for executive control ("distributed neuronal activity in the alpha band supports the **de-selection of rules** to be applied in a visual task")

Audition
Hemispheric lateralization with alpha increase in non-relevant areas

Network interactions revealed by alpha band activity

Frontal eye field (FEF) seems to exercise control of posterior alpha oscillations in attention tasks

— TMS studies demonstrate that the ability to modulate alpha oscillations is impaired when the FEF is perturbed
→ Top-down control emerging from the FEF

«It remains to be further uncovered whether the FEF exercises a direct or indirect modulation of the alpha oscillations. Subcortical regions are likely to play an important role.»

Conclusions and directions

While there is no doubt that **alpha oscillations are inhibitory** and correlated with a reduction in neuronal excitability, they **might not be under direct top-down control in general**. Alpha oscillations are modulated by an **indirect control mechanism**, in which the **load of goal-oriented processing** results in the control of the alpha power increases in task-irrelevant regions.

Is there a lateral competitive mechanism between the two hemispheres (Fig. 2B)?

— The framework in which alpha power increases in task-irrelevant regions when task-relevant regions are engaged points to **competitive interactions**.

Might alpha oscillations be involved in implementing inhibition between competing modalities?

— When competing auditory and visual stimuli are presented, the alpha power has been found to **increase in the extra-sensory regions associated with the distracting modality**

— Parieto-occipital alpha oscillations increase in tasks requiring attention allocated to the somatosensory modality

— Competition between the dorsal and ventral stream might also be reflected in the alpha band. In a working memory study in which participants had to maintain either the identity or orientation of a face (engaging, respectively, the ventral or dorsal stream), alpha oscillations increased in the dorsal stream when face identity was maintained