Human brain oscillations for perception and attention: A mosaic of perceptually relevant rhythms is concealed in the "canonical" alpha band

Insights from EEG,TMS&EEG and MEG&EEG studies

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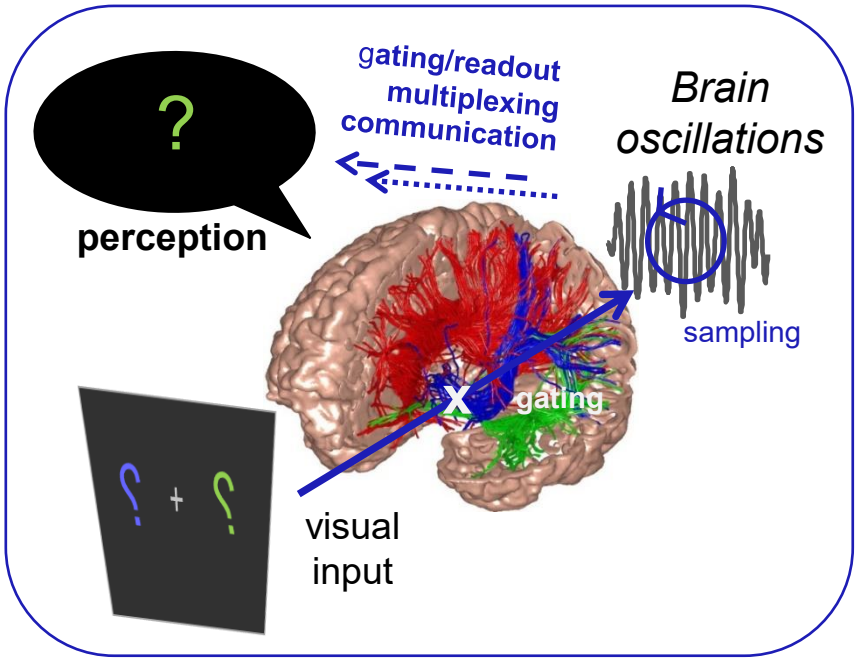
The Question/ Research Focus

how does the brain regulate input and processing of visual information (in mechanistic terms)?

From visual input to perception

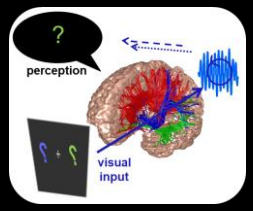
Brain oscillations as mechanistic input regulators



Approach:
Measuring (by EEG/MEG)
& Manipulating (by TMS, tACS)
of brain oscillations

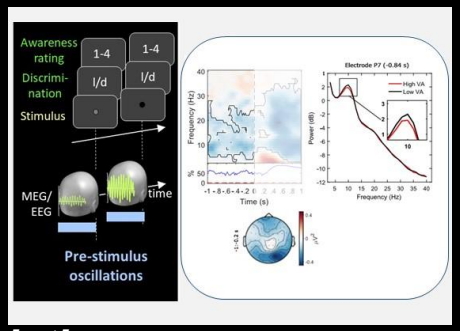
General *approach*

Mechanisms of sensory input regulation and perception



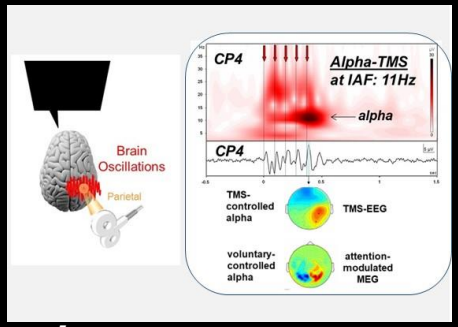
Mapping

of perceptually relevant brain oscillations



Manipulation

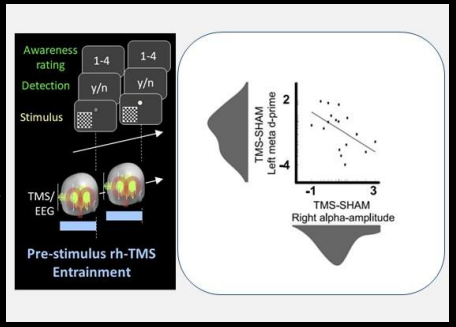
of brain oscillations to modify perception



Neuro-technologies/ therapeutics

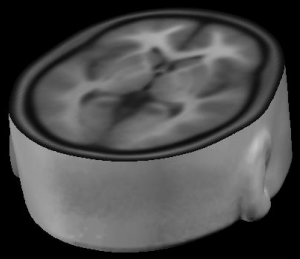
Mechanisms

manipulation of the brain-behaviour relationship to probe mechanisms of perception



Background

Focus on perceptually relevant brain oscillations prior to stimulus



External event

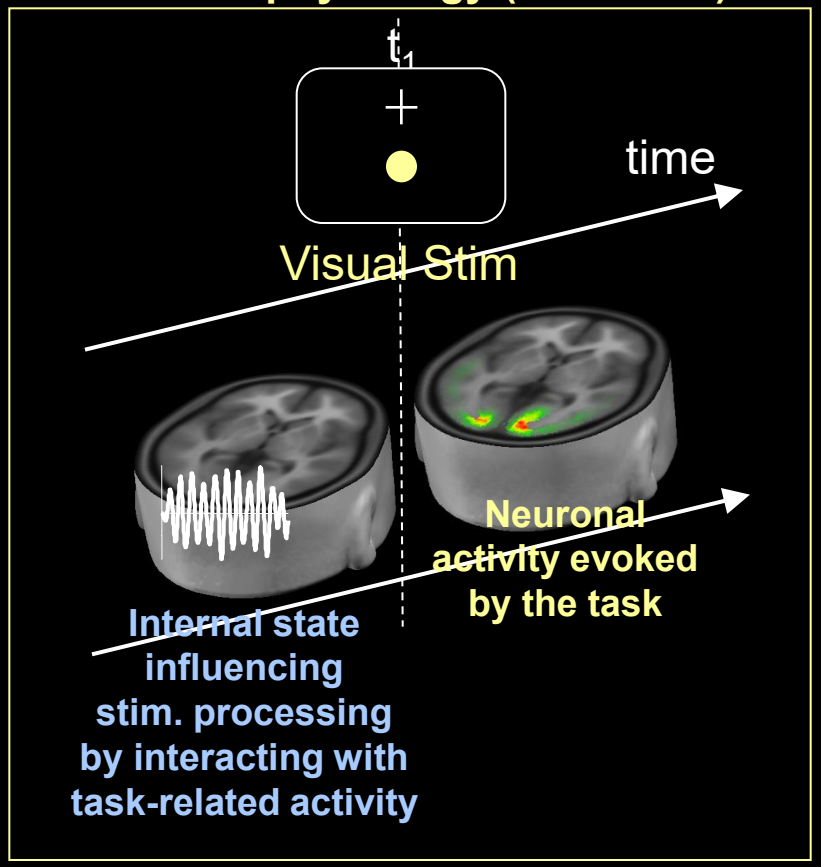
Stimulus processing

Internal State

Perceptually relevant brain activity

Pre-stimulus brain oscillations predicting visual performance

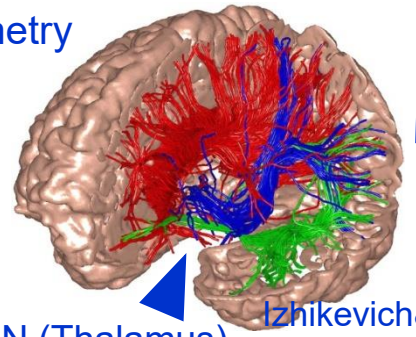
Functional Neuroimaging
Electrophysiology (MEG/EEG)

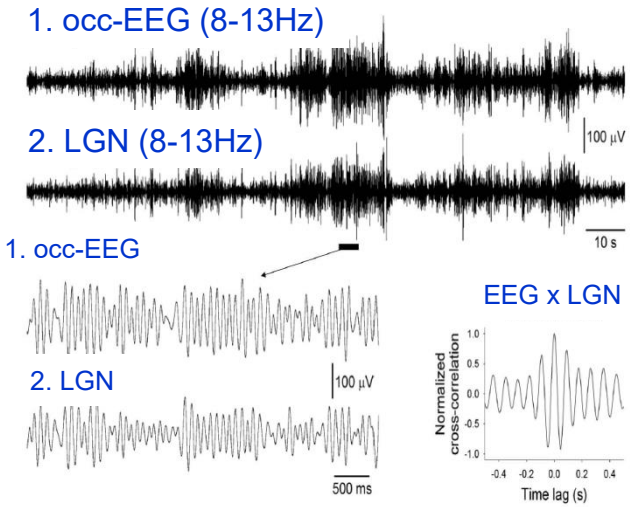


Role of oscillatory activity in this regards?

Background

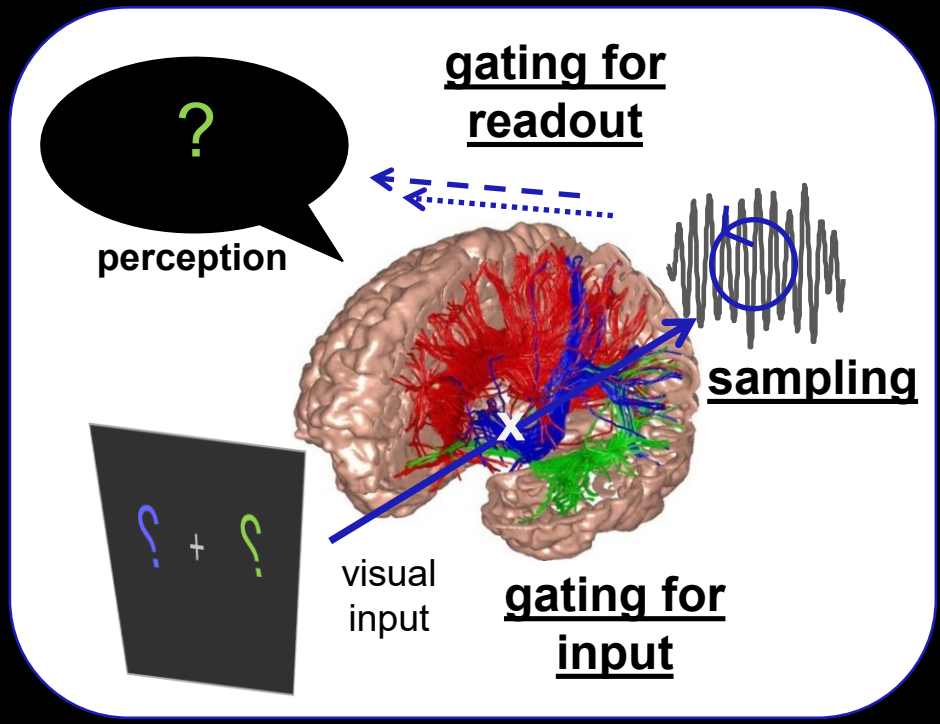
Candidate rhythms for input regulation: posterior α-rhythm (8-13Hz) of thalamo-cortical origin





Alpha oscillations (8-13Hz) in LGN and over occipital areas are in synchrony (Crunelli et al., 2011f)

Alpha activity as candidate of sensory input regulation through gating/sampling



Talk
Outline

Mechanisms of sensory input regulation and perception

Mapping - Manipulation - Mechanisms

- **Mosaic of alpha-oscillators I**

Alpha-frequency and alpha-amplitude dissociate over time on task (EEG)

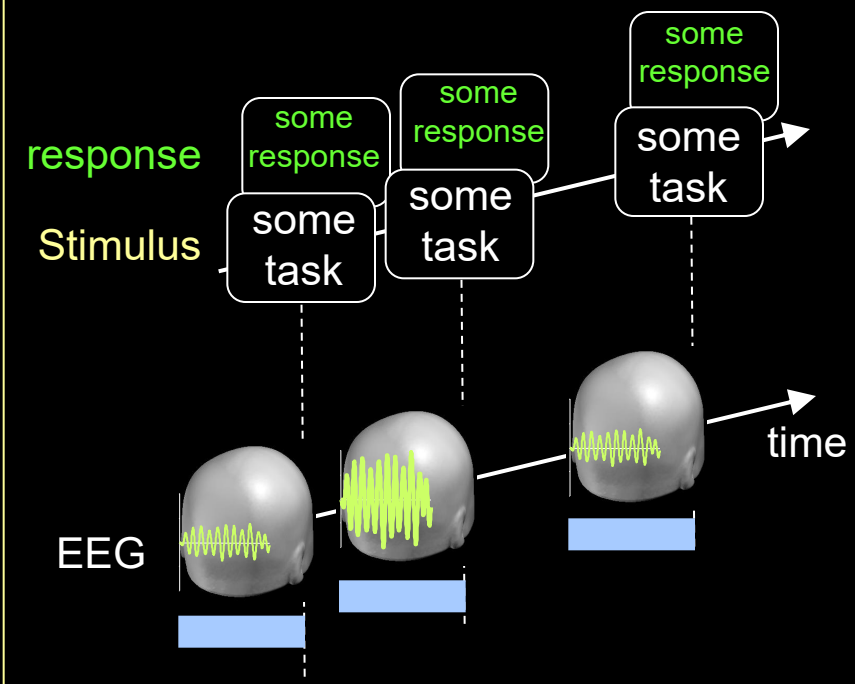
- **Mosaic of alpha-oscillators II**

Distinct regulators of visual sensitivity vs. visual awareness in occipito-parietal alpha-oscillations (EEG/TMS&EEG)

- **Mosaic of alpha-oscillators III**

Distinct occipito-parietal sources of ipsilateral alpha-increase and contralateral alpha-decrease with visuospatial attention (EEG&MEG)

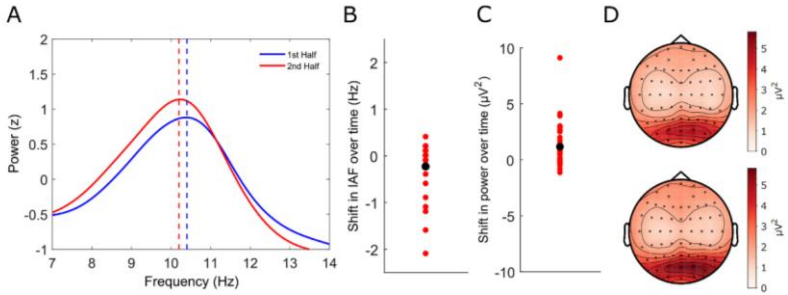
Frequency and power of human alpha oscillations drift systematically (and independently) with time-on-task.



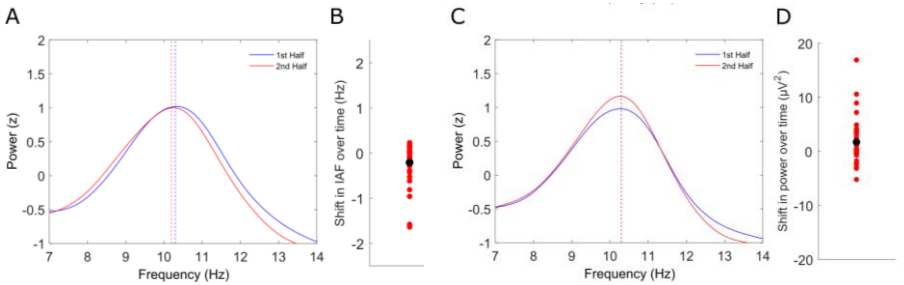
Pre-stimulus alpha: drifts over time

Benwell et al., NeuroImage 2019

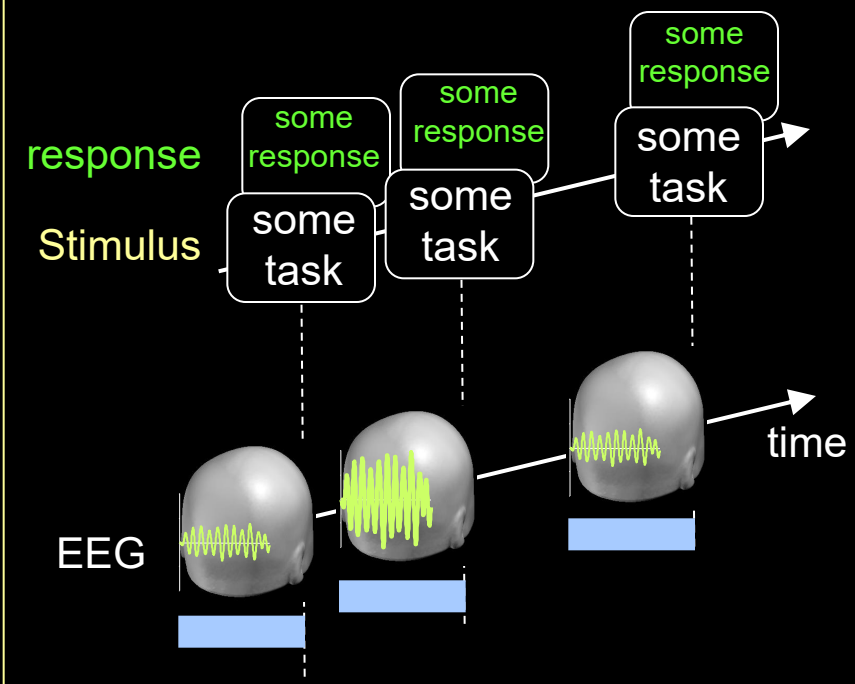
EEG in pre-stimulus window over time



EEG trial stratification indicates partial independence of power- and frequency-change over time



Frequency and power of human alpha oscillations drift systematically (and independently) with time-on-task.



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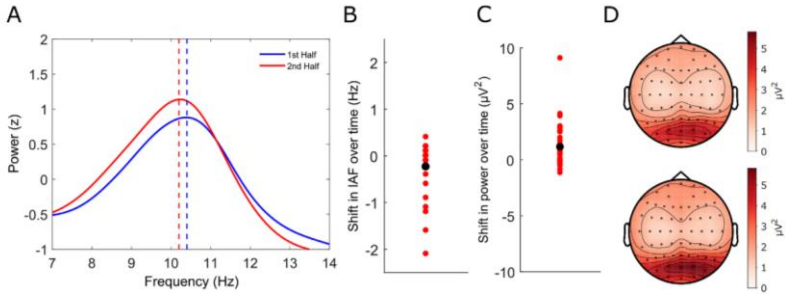
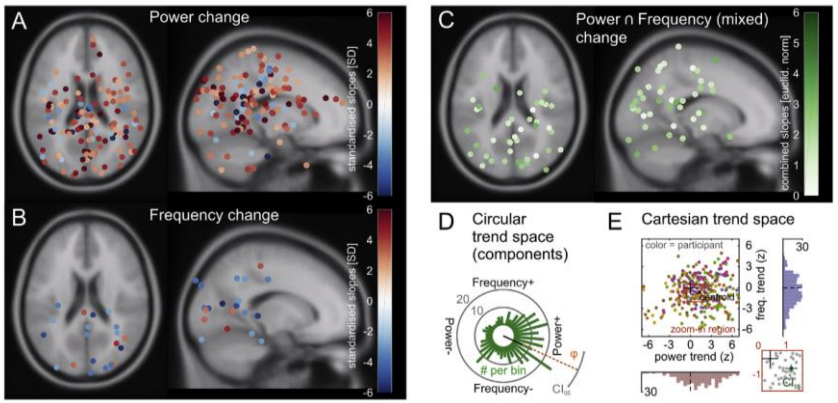


partial independence confirmed by statistical source separation



Benwell et al., NeuroImage 2019

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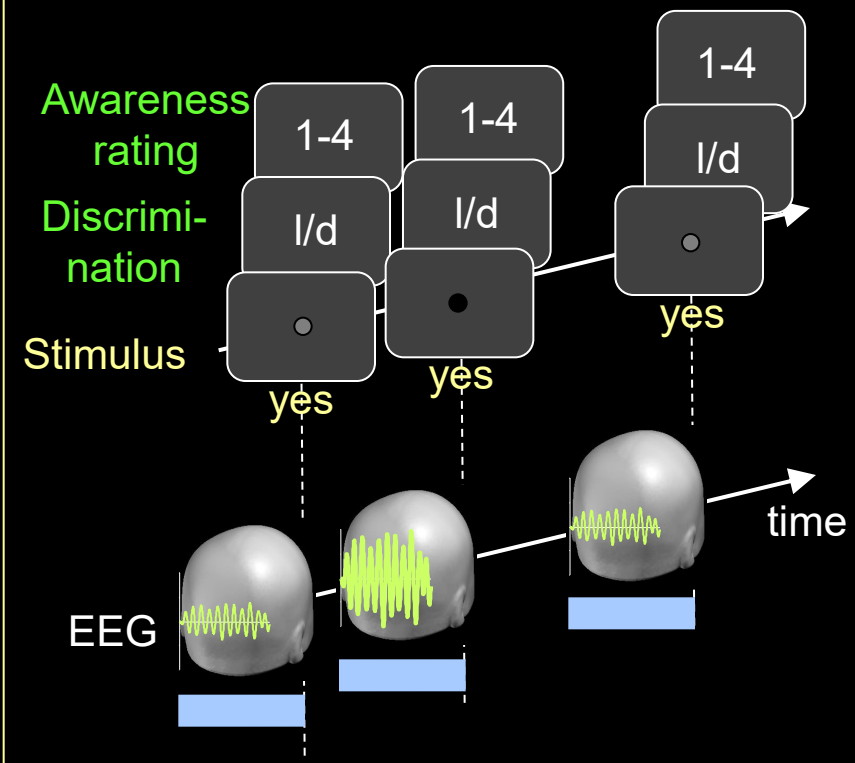
Mapping

Pre-stimulus alpha-amplitude predicts subjective awareness



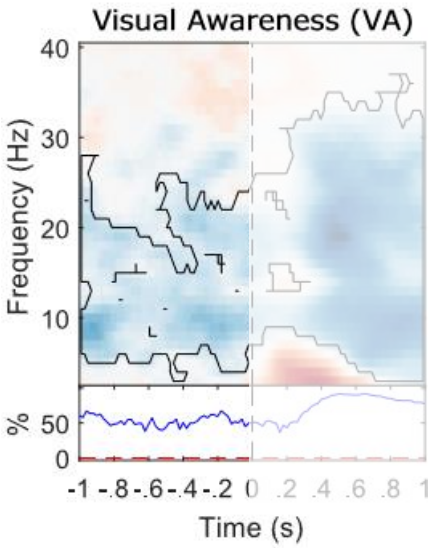
Pre-stimulus oscillations

Discrimination:
l – lighter
d – darker

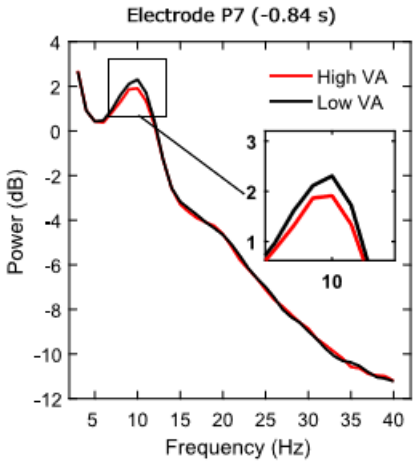
How visible was the stimulus?
1 – No experience
2 – Brief glimpse
3– Almost clear experience
4 – Clear experience

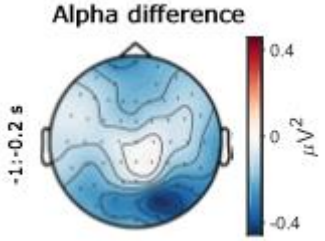
Benwell et al., eNeuro, 2017

EEG vs. Awareness correlation plot



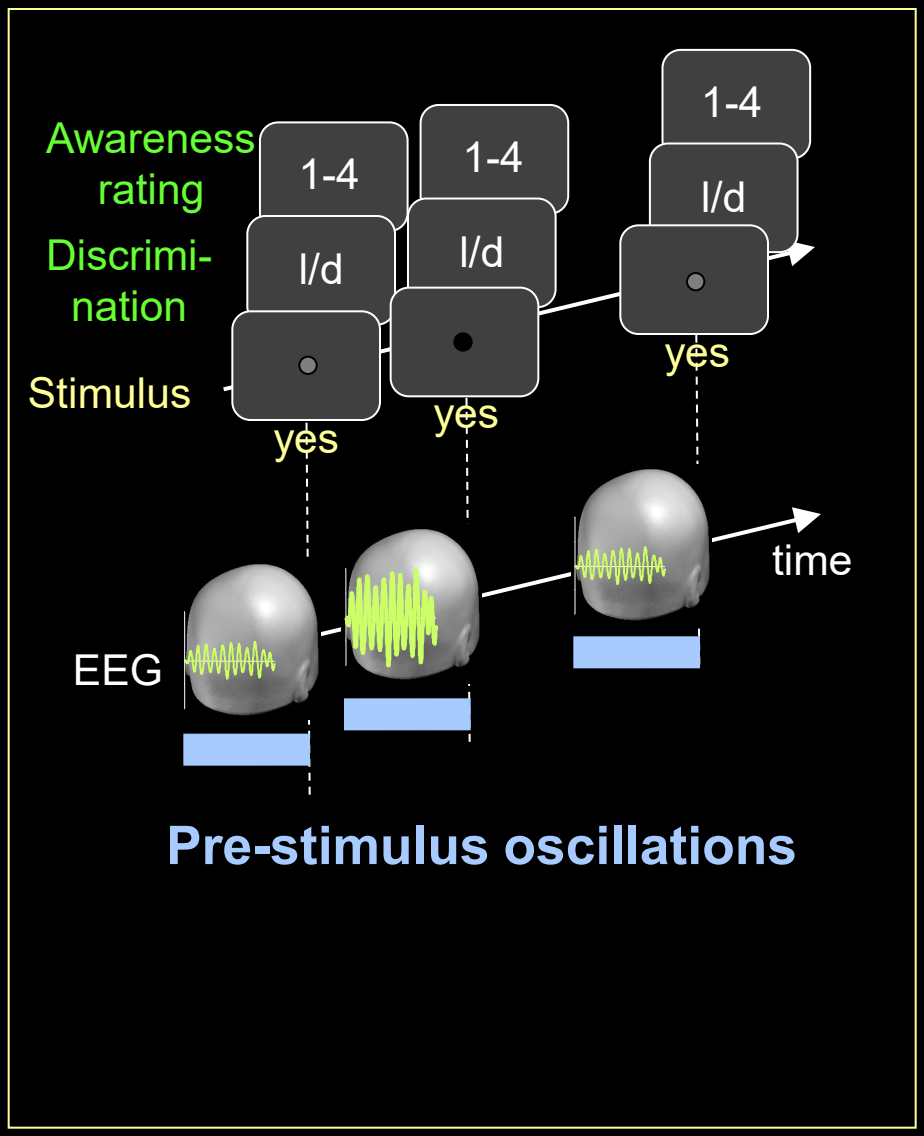
Pre-stimulus cluster

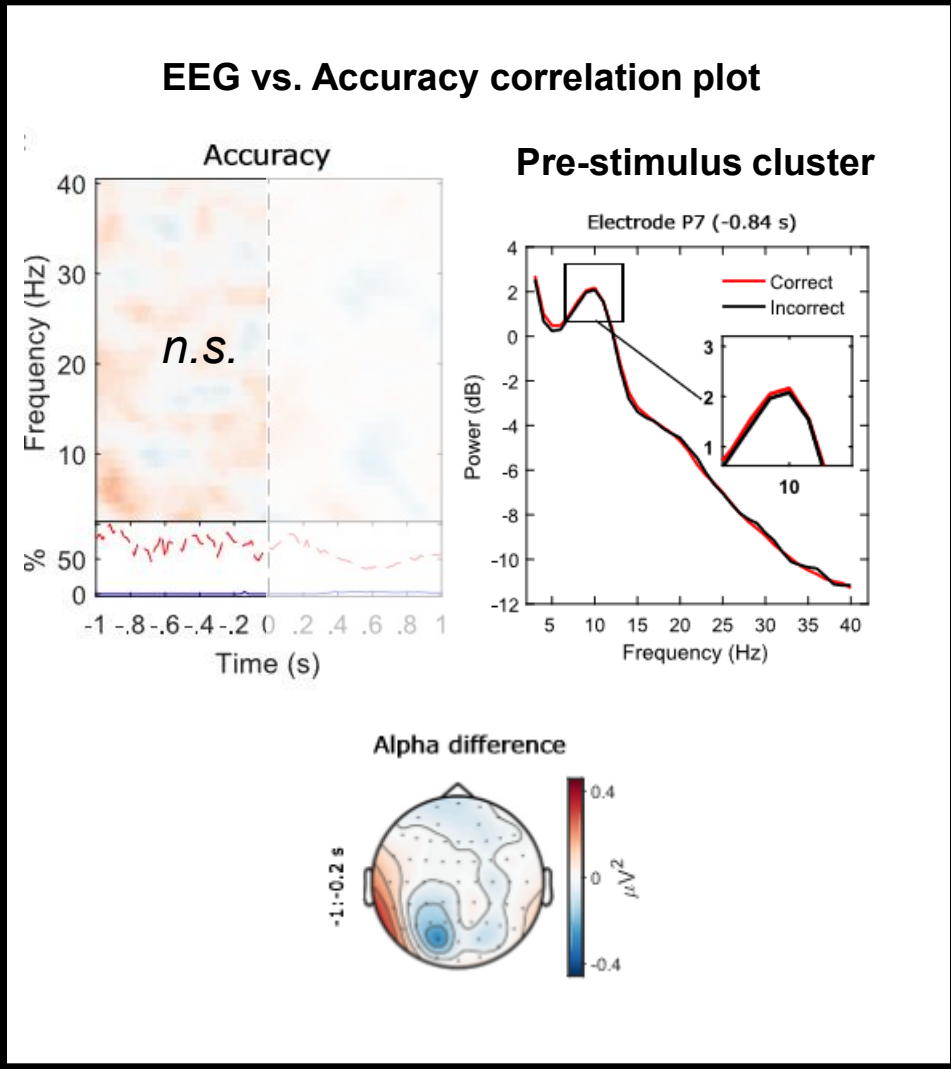




Mapping

Pre-stimulus alpha-amplitude predicts subjective awareness but not objective visual performance (accuracy, sensitivity)

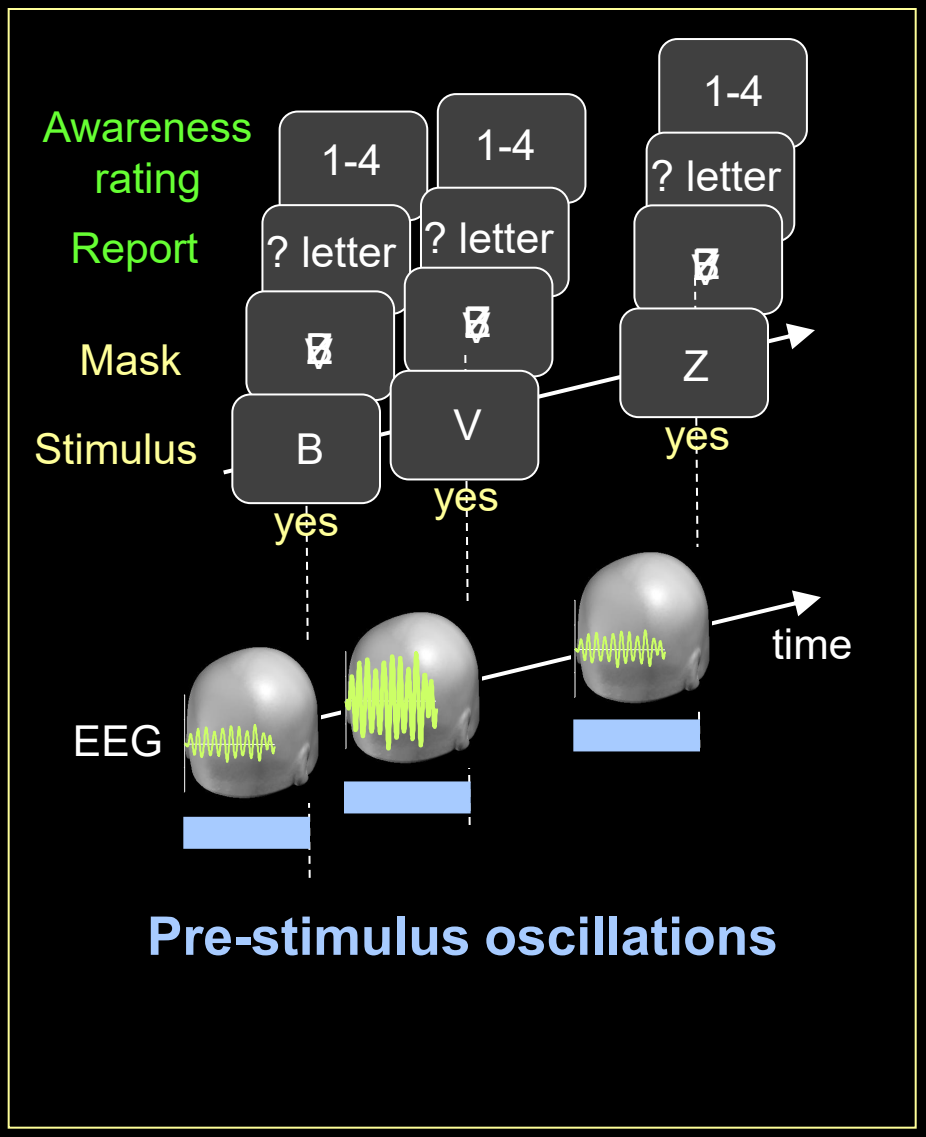


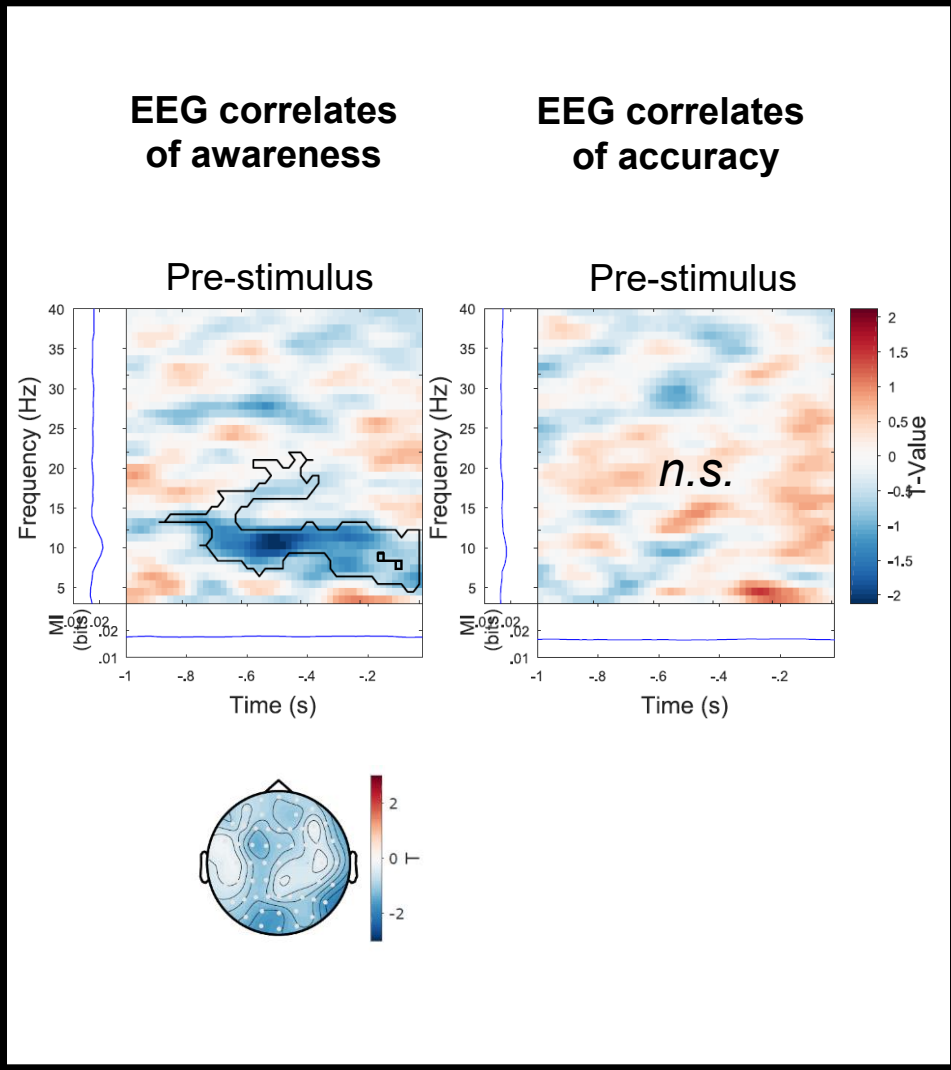


Benwell et al., eNeuro, 2017

Mapping

Replication: Pre-stimulus alpha-amplitude predicts subjective awareness, but not objective visual performance

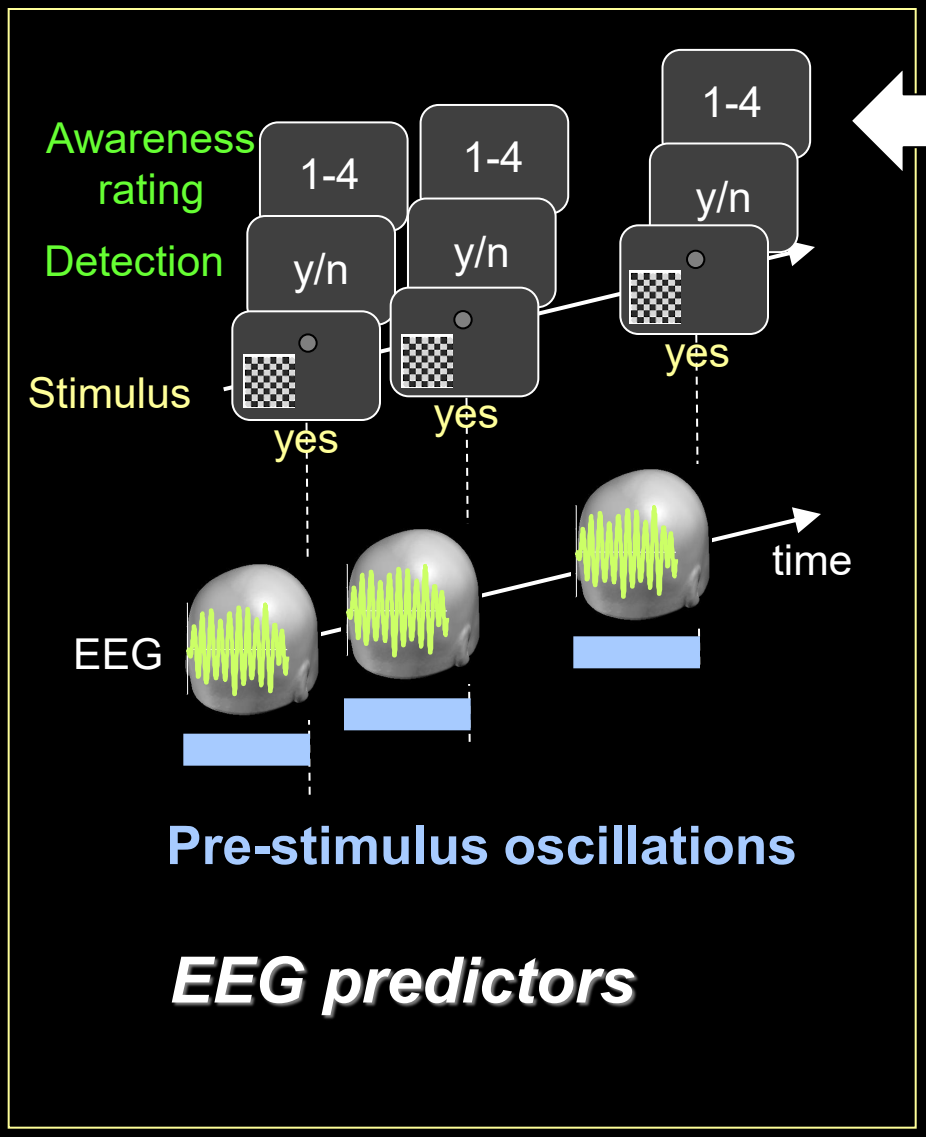




Benwell*, Coldea* at al, 2021
>>1 replications incl. in Di Gregorio et al. 2022

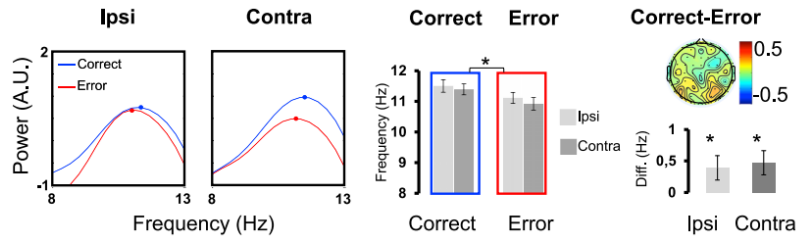
Mapping

While pre-stimulus alpha-amplitude predicts awareness, pre-stimulus alpha-frequency predicts objective accuracy



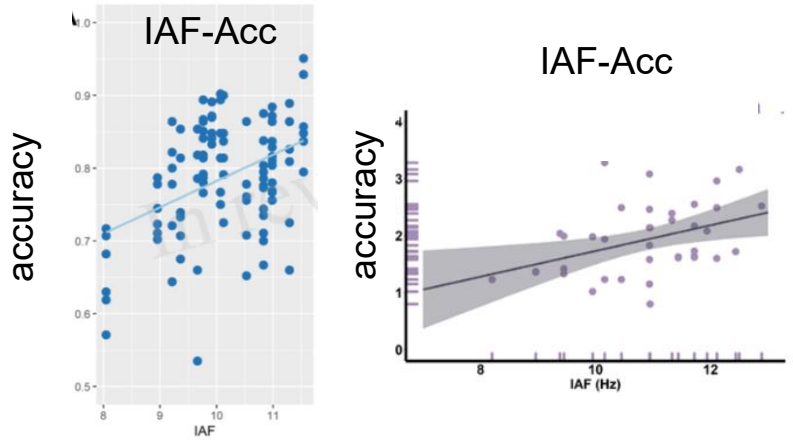
Di Gregorio et al. Curr Biol 2022

Alpha frequency predicts objective accuracy (across trials)



Coldea et al., 2022

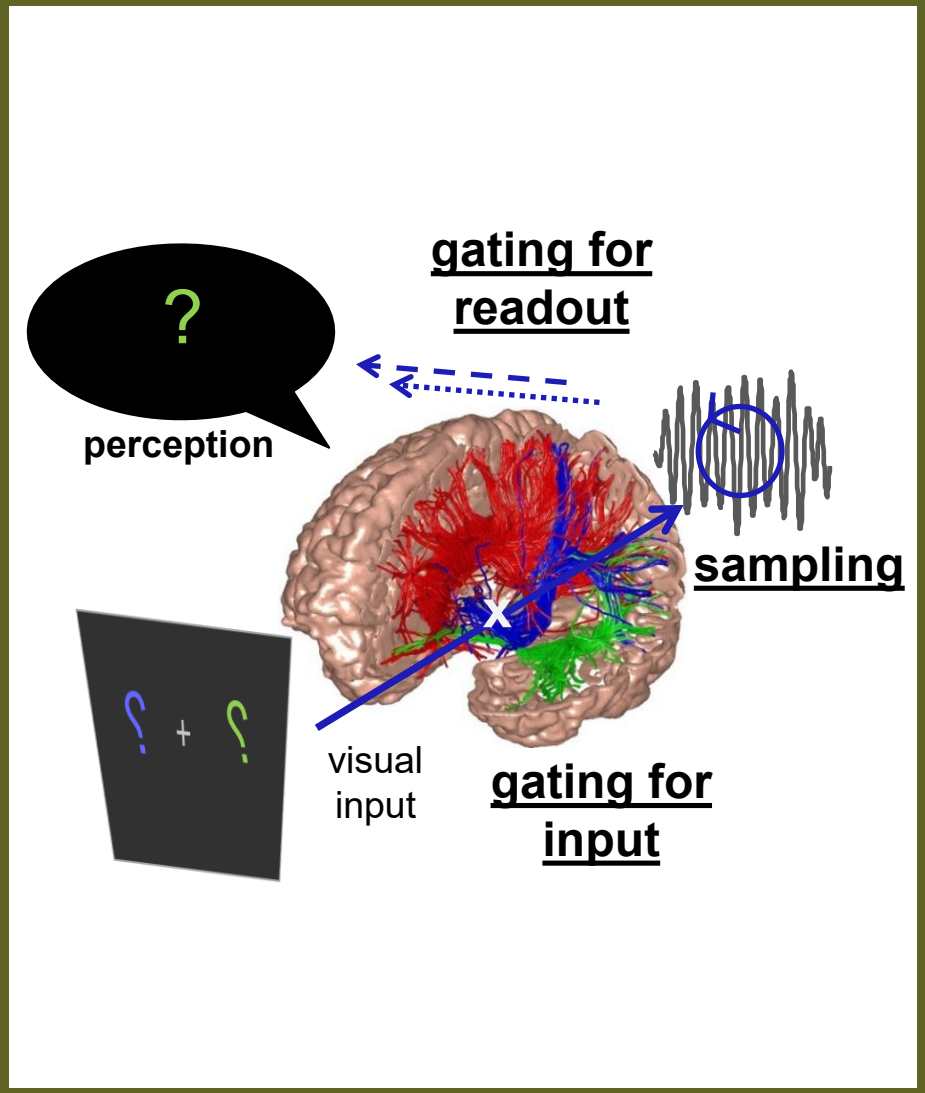
Alpha frequency predicts objective accuracy (across participants)



Trajkovic et al., 2024

Interim Conclusion Regulators of perception

- Mapping perceptually relevant brain oscillations

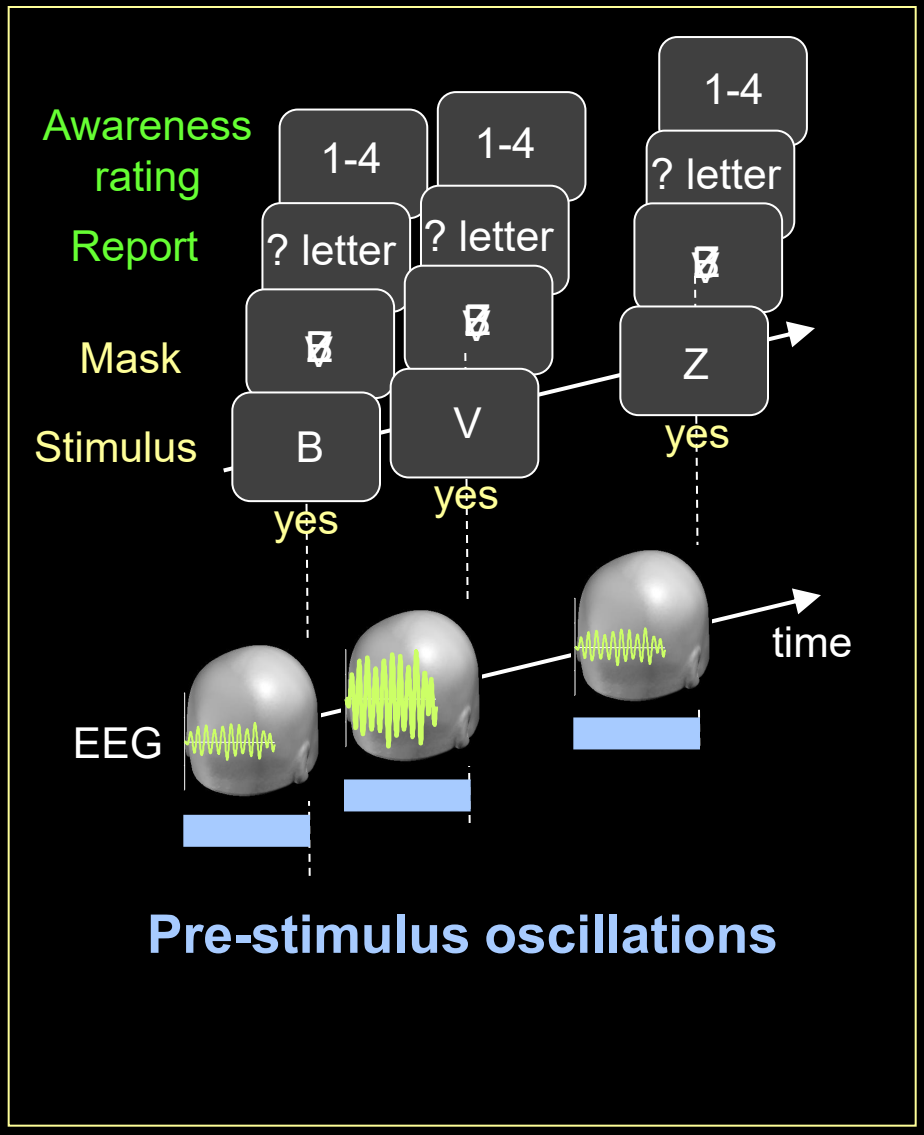


- Alpha oscillations differentially relate to awareness and objective performance through amplitude and frequency modulations

Mechanistic hypothesis?

Mapping

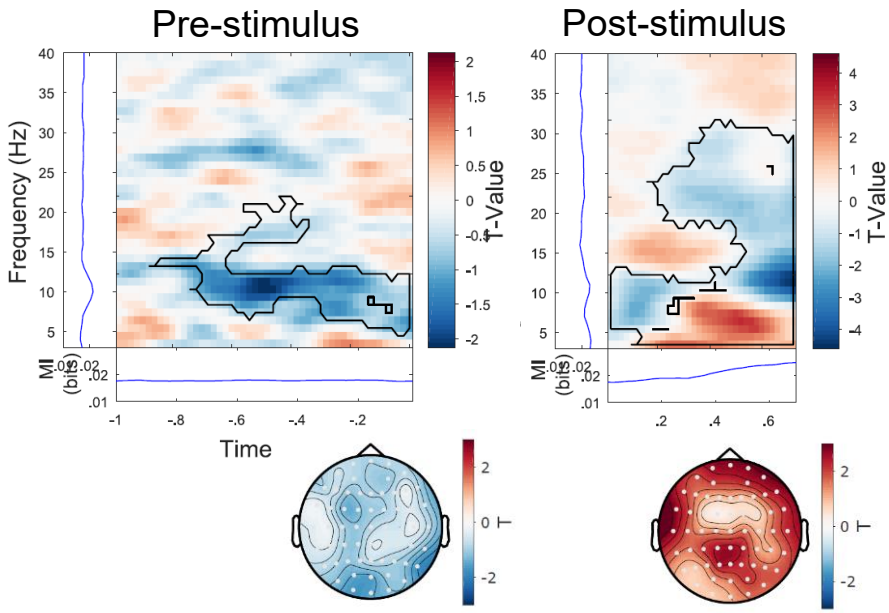
Pointer to how pre-stimulus alpha-amplitude may influence awareness: later ERP component of P300 family as mediator?



Pre-stimulus oscillations

Benwell*, Coldea* at al, Eur J Neurosci 2021

EEG correlates of awareness

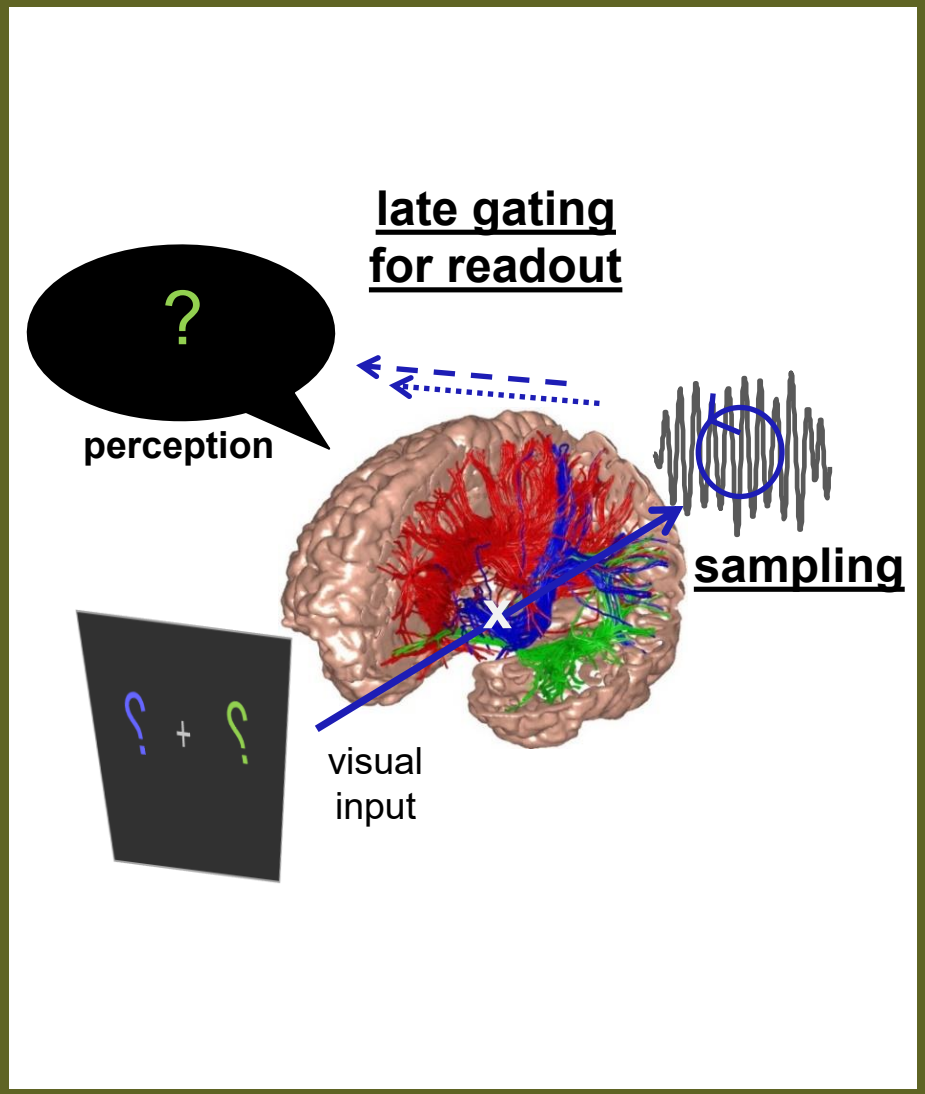


Of note:

Late post-stimulus ERP (peaking at theta) has been identified as EEG signature of
i) sensory evidence accumulation (see Central Posterior Positivity, CPP) **and/or**
ii) conscious access (see Late Potential)

Interim Conclusion Regulators of perception

- Mapping perceptually relevant brain oscillations



- Alpha oscillations differentially relate to awareness and objective performance through amplitude and frequency modulations

Mechanistic hypothesis

- Alpha amplitude affects awareness through a late gating process, interacting with (post-stimulus) readout for evidence accumulation/ conscious access
- Alpha frequency affects accuracy through modulating speed of sensory sampling, interacting with an early visual input process

Talk
Outline

Mechanisms of sensory input regulation and perception

Mapping - **Manipulation** - Mechanisms

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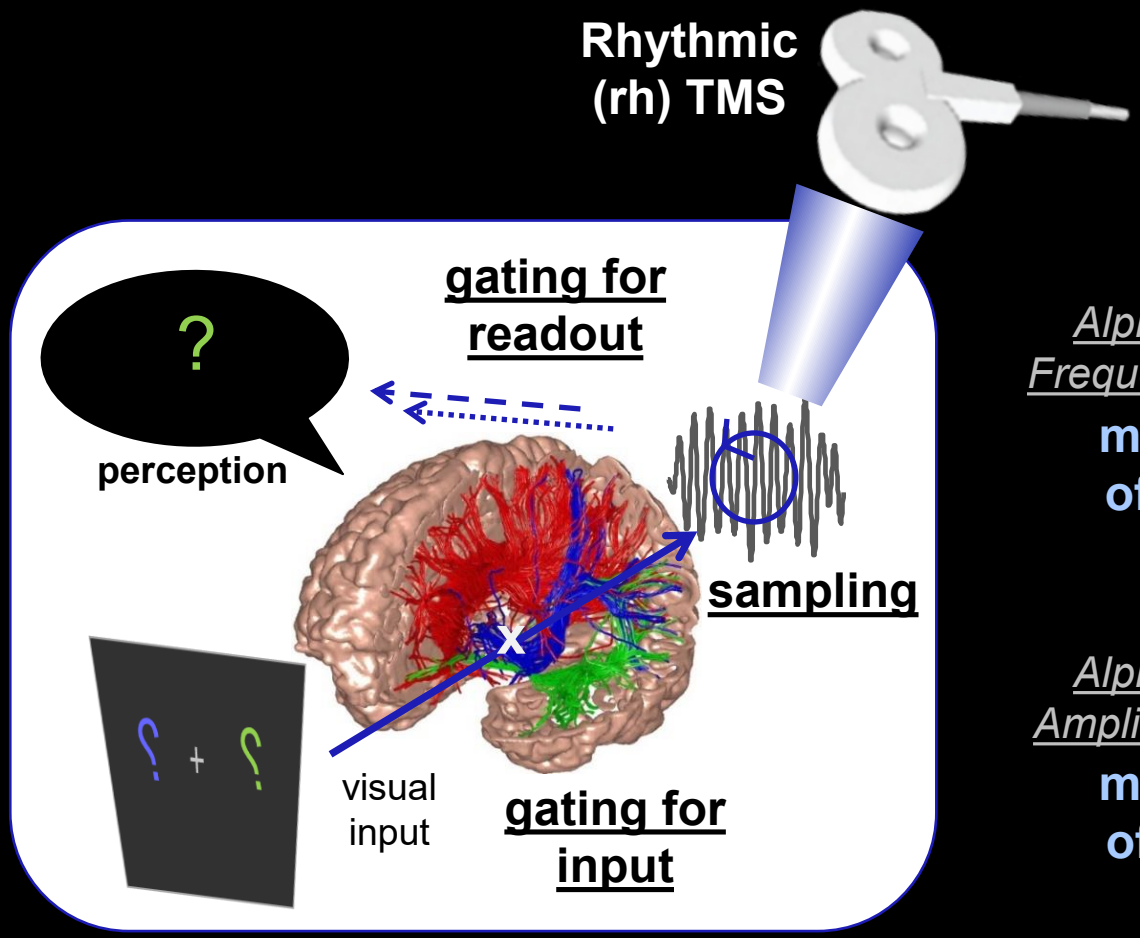
Manipulation

Can we shape awareness versus accuracy by entraining alpha-oscillations through rhythmic TMS

Mapping - Manipulation - Mechanisms



Alpha Frequency → Objective Accuracy (sensitivity)

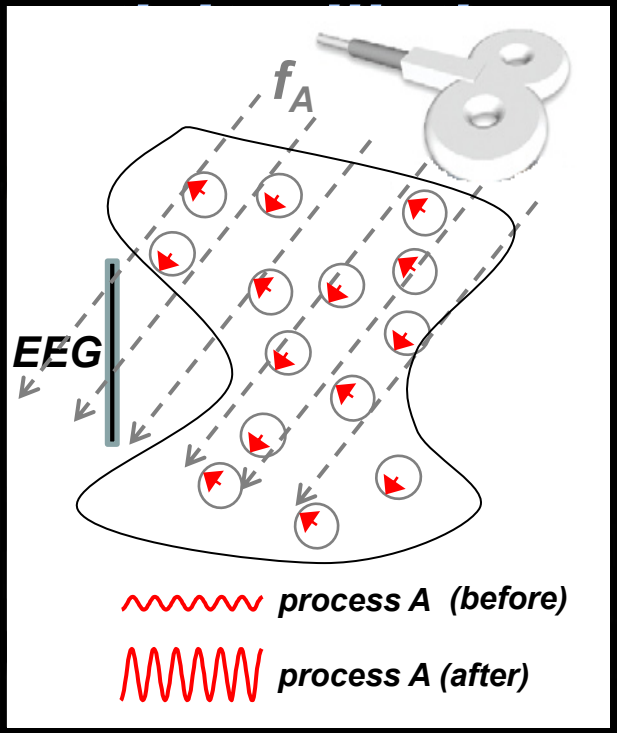
manipulation of frequency

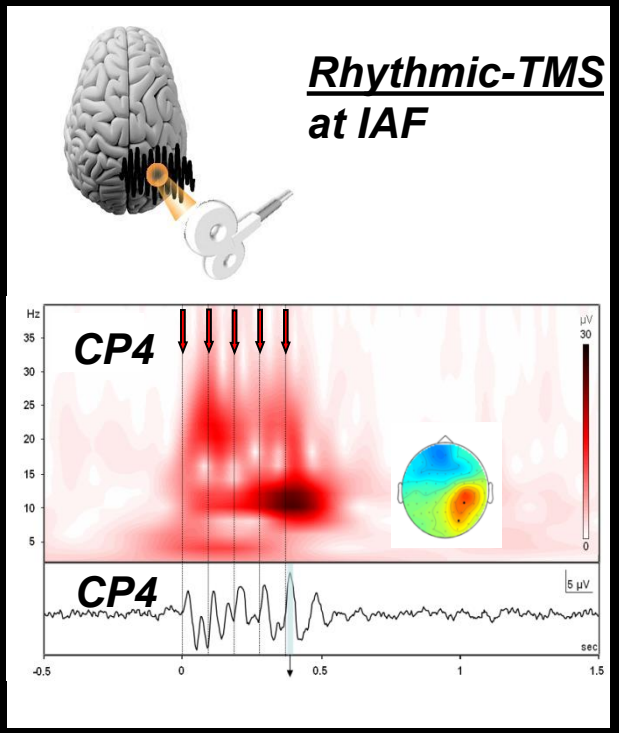
Alpha Amplitude → Subjective Awareness (confidence)

manipulation of amplitude

Method of manipulation:
interacting with brain oscillations

By entrainment of oscillatory activity



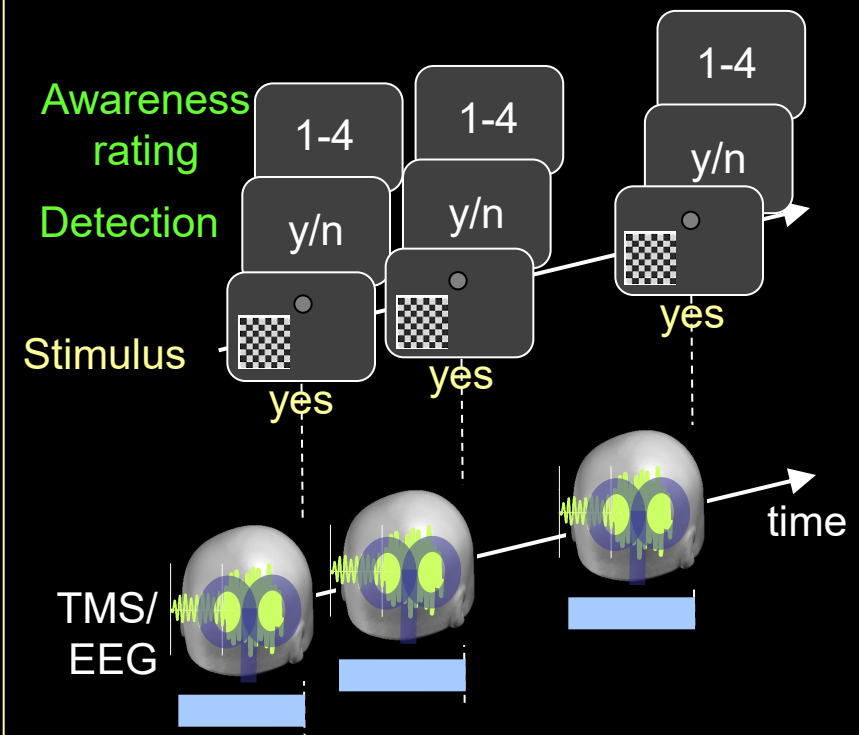


Thut et al., 2011

Rhythmic TMS: Thut et al., 2011; Hanslmayr, 2014; Romei et al., 2015 ; Albouy et al., 2017
tACS: Ozen et al., 2010; Fröhlich & McCormick, 2010; Neuling et al., 2012; Ali et al., 2013; Reato et al., 2013; Helfrich et al., 2014; Helfrich et al., 2014; Helfrich et al., 2014; Voss et al., 2014; Zoefel et al., 2020

Manipulation

Tuning alpha-amplitude shapes subjective awareness



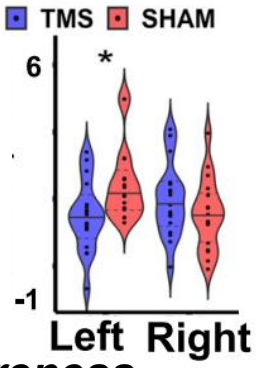
Pre-awareness rating

- short TMS bursts (n=5 pulses)
- TMS over right posterior alpha sites
- IAF-TMS to influence alpha-amplitude

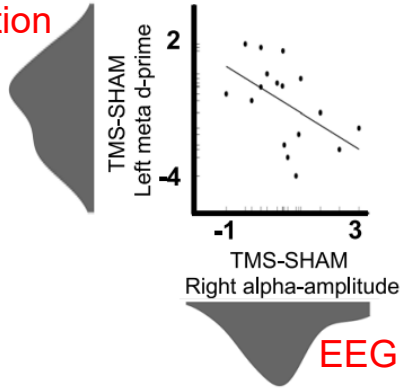
Di Gregorio et al. Curr Biol 2022

rhTMS at individual alpha
(increasing alpha-amplitude)
influences subjective awareness

Subjective awareness measure

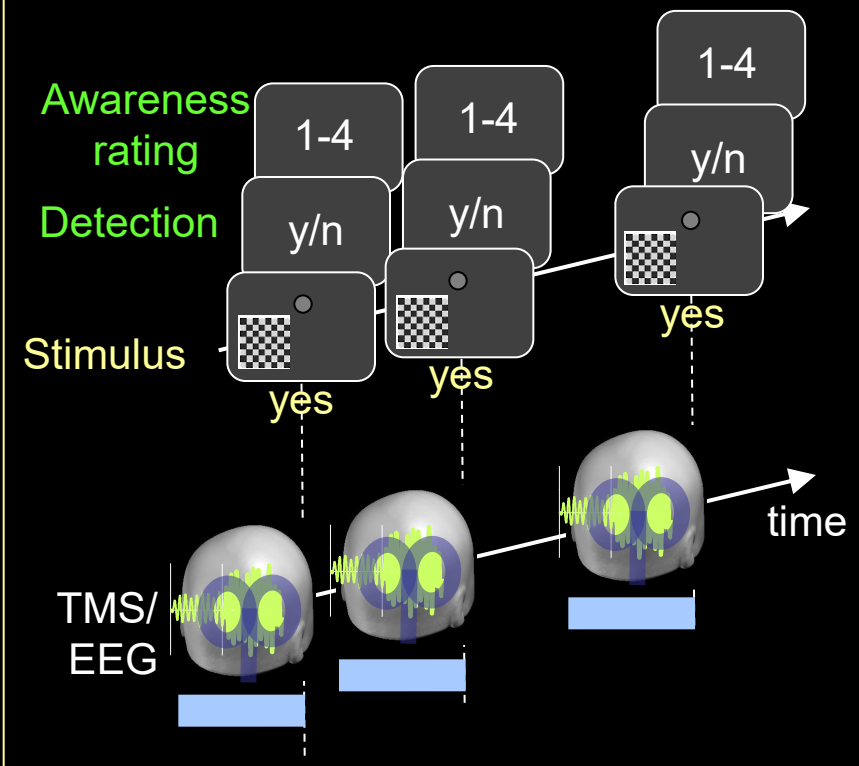


Subjective awareness and TMS-induced Alpha-amplitude



Manipulation

Tuning alpha frequency shapes objective accuracy



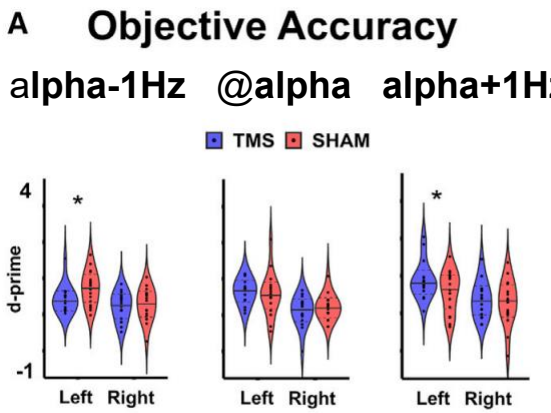
Pre-stimulus

- short TMS bursts (n=5 pulses)
- TMS over right posterior alpha sites
- IAF-/+1Hz to influence alpha-frequency

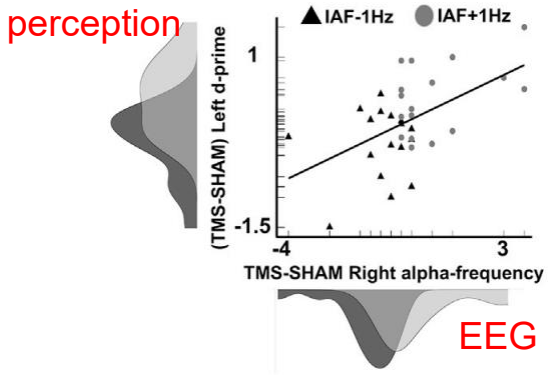
Di Gregorio et al. Curr Biol 2022

rhTMS at distinct alpha-paces (alpha-1Hz, @alpha, alpha+1Hz) influences objective accuracy

A Objective Accuracy

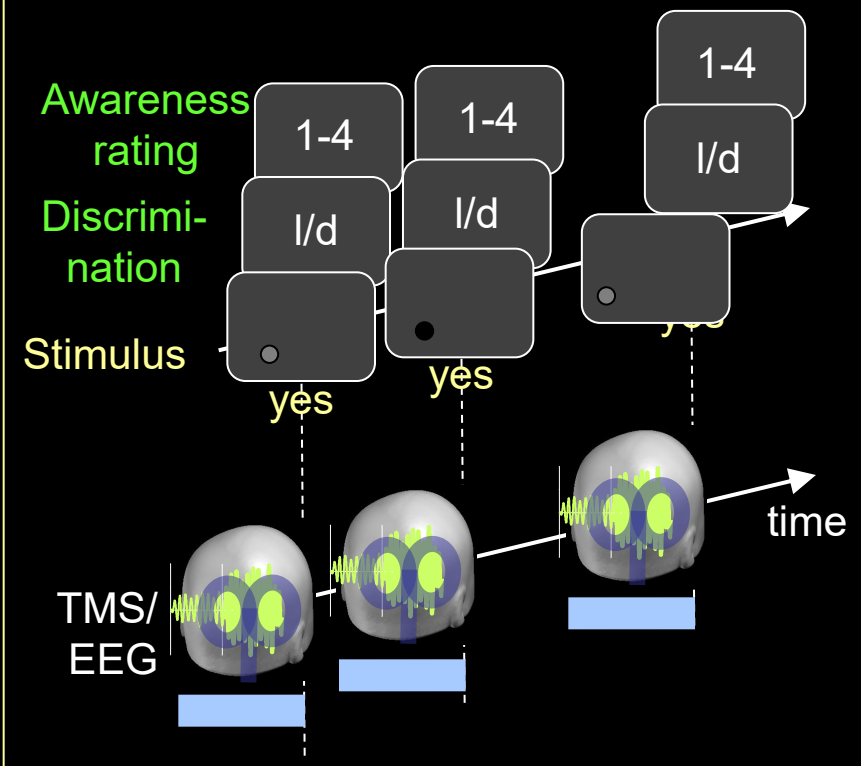


B Objective Accuracy and Alpha-frequency



Manipulation

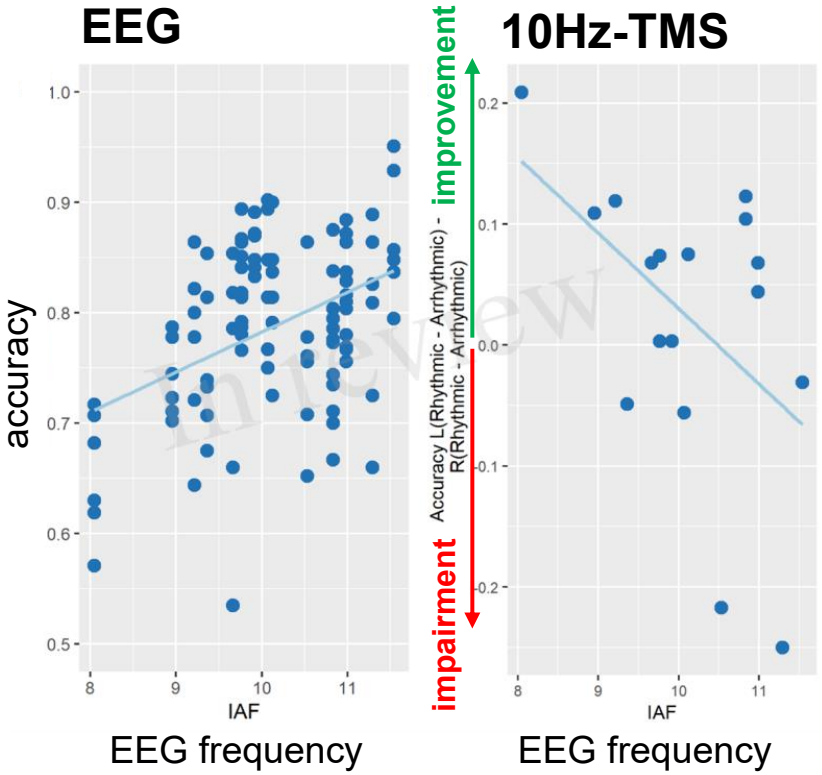
Tuning alpha rhythms to shape perception: Replication of TMS alpha-pace accuracy link



- short TMS bursts (n=5 pulses)
- 10Hz-TMS over posterior alpha sites

Coldea et al., Frontiers. 2022

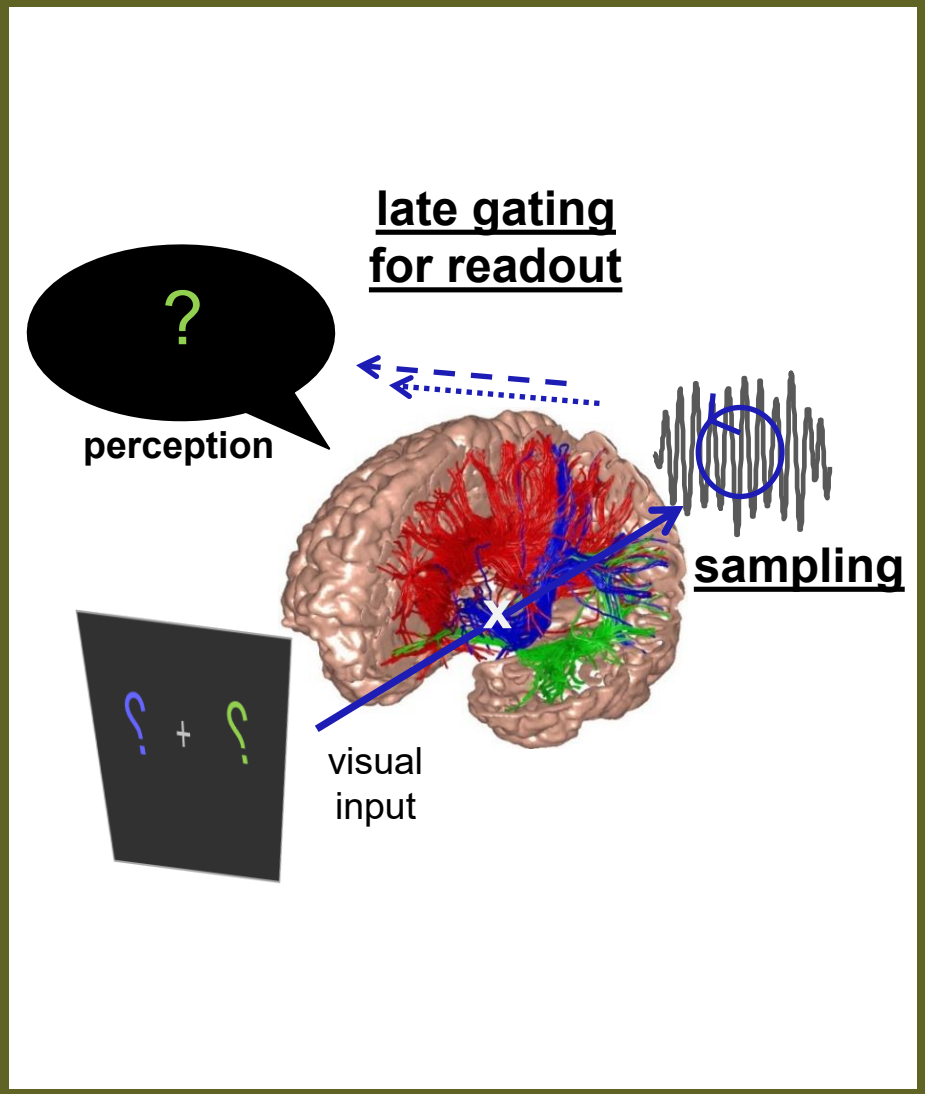
TMS alpha-pace (10Hz) relative to IAF shapes objective accuracy



Interim Conclusion

Biasing perception

- Interacting with brain oscillations and functions



Overall Conclusion:

- *i) Alpha oscillations:*
  are not only epiphenomena but are causally involved in shaping perception, and this along 2 "axes" of alpha, likely associated with 2 distinct generators
- *ii) alpha pace (frequency) shapes objective perceptual performance*
- *iii) alpha amplitude shapes subjective awareness*

- *Mechanisms) Alpha oscillations*
  drive different aspects of perception through different mechanisms
  -> frequency-modulated input sampling at early stages rhTMS->P1
  -> amplitude-modulated gating during readout at a later stage for conscious access rhTMS->P300

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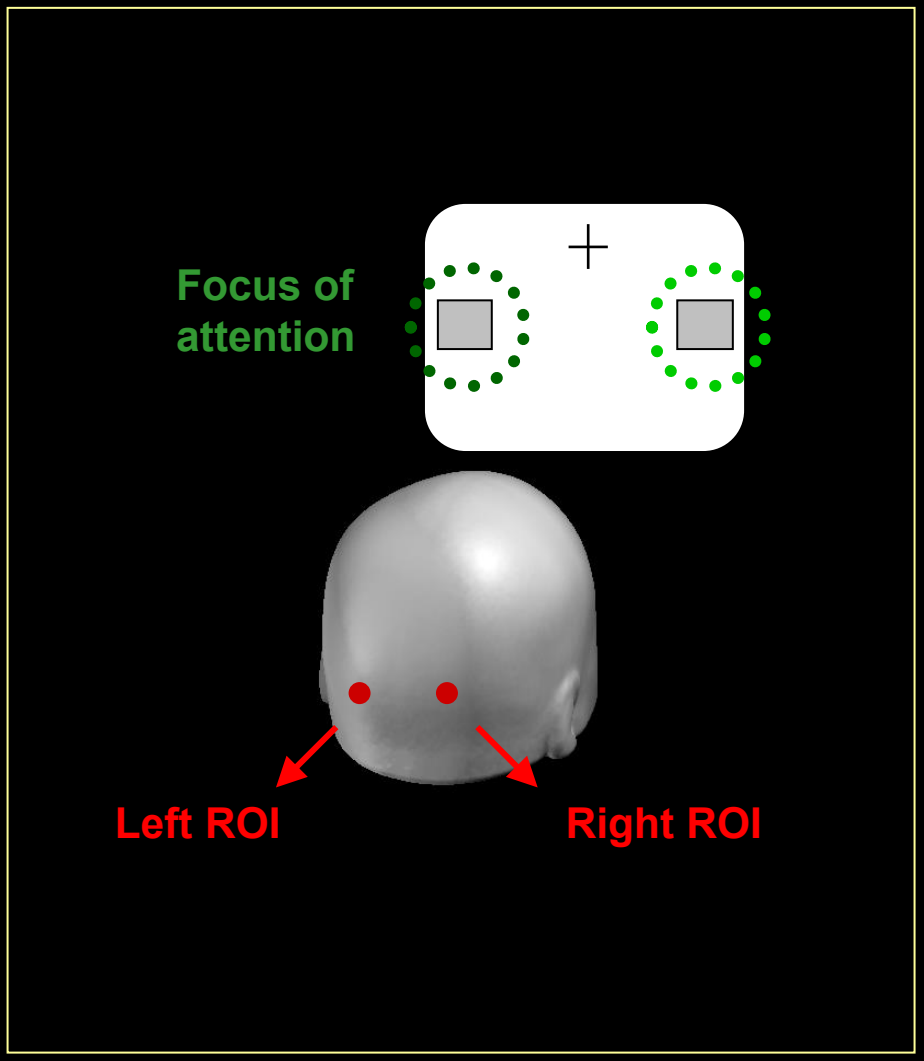
Distinct occipito-parietal sources of ipsilateral alpha-increase and contralateral alpha-decrease with visuospatial attention (EEG&MEG)

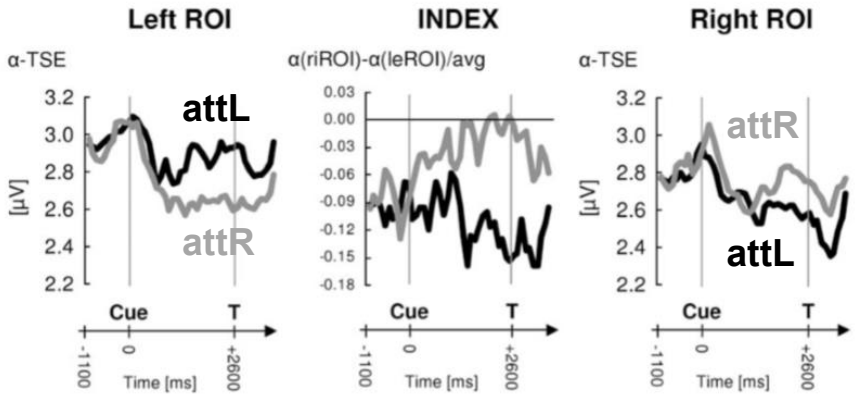
Visuospatial attention lateralises alpha-oscillations

Interpreted to reflect up- or down-regulations of excitability in sensory areas facilitating target engagement or suppressing distractor information



Thut et al. J Neurosci 2006

aLI: $\frac{RH-LH}{(RH+LH)/2}$



AMI:

LH (attL-attR) RH (attL-attR)

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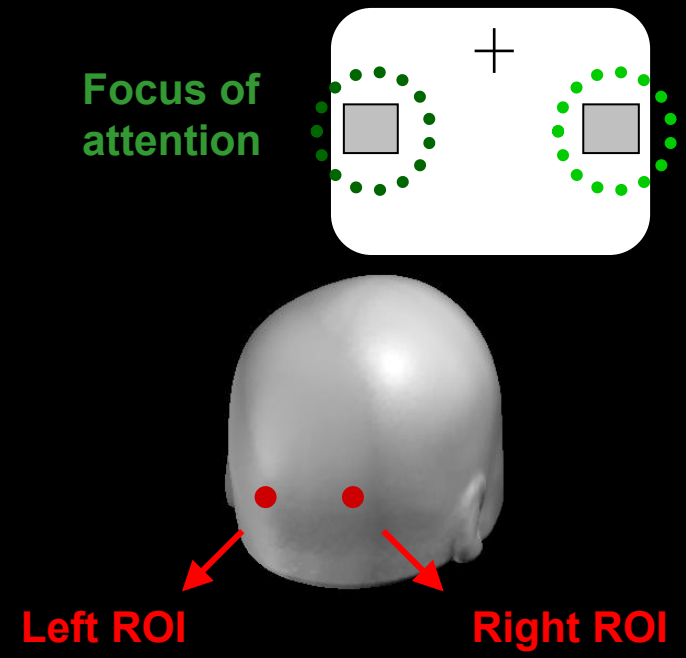
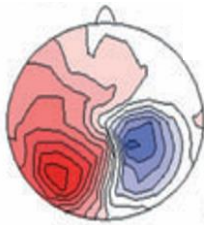
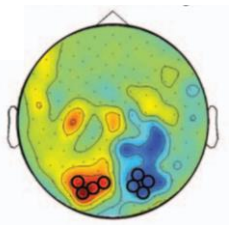
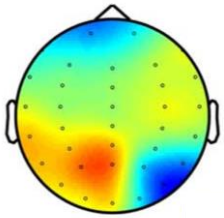
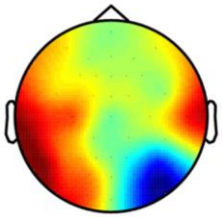


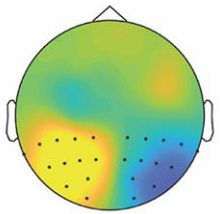
Alpha-pattern highly replicable

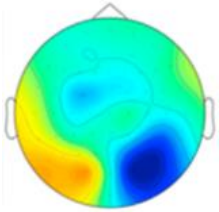

Rihs et al. 2007


Haendel et al. 2011

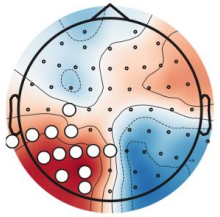

Myers et al. 2015


Van Ede et al. 2017


Woestmann et al. 2019


Gallotto et al. 2020

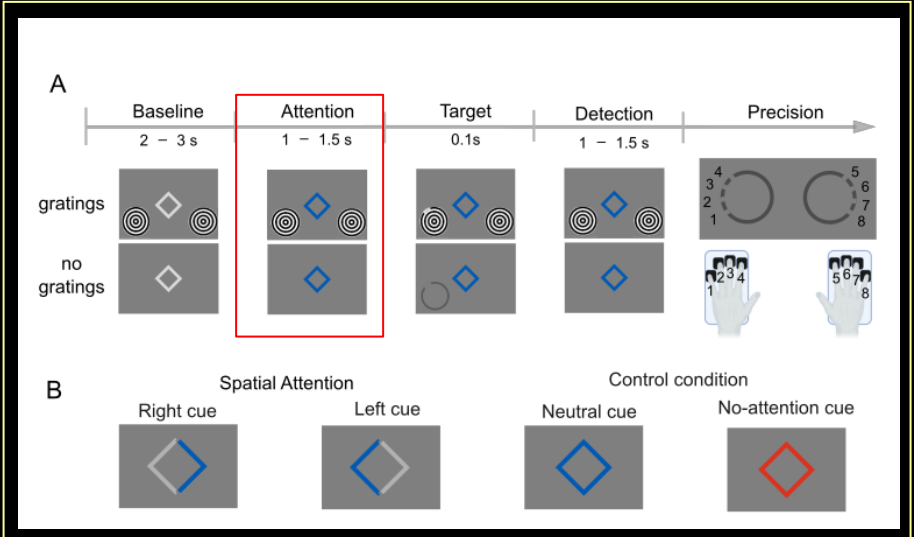

Liu et al. 2022


Pylo et al. 2023

Etc..

Visuospatial attention lateralises alpha-oscillations

Revisting alpha-lateralization with simultaneous MEG&EEG&eye tracking study



In 32 participants:

Simultaneous measurements of:

- **MEG**
- **Multichannel EEG**
- **Fixational micro-saccades**

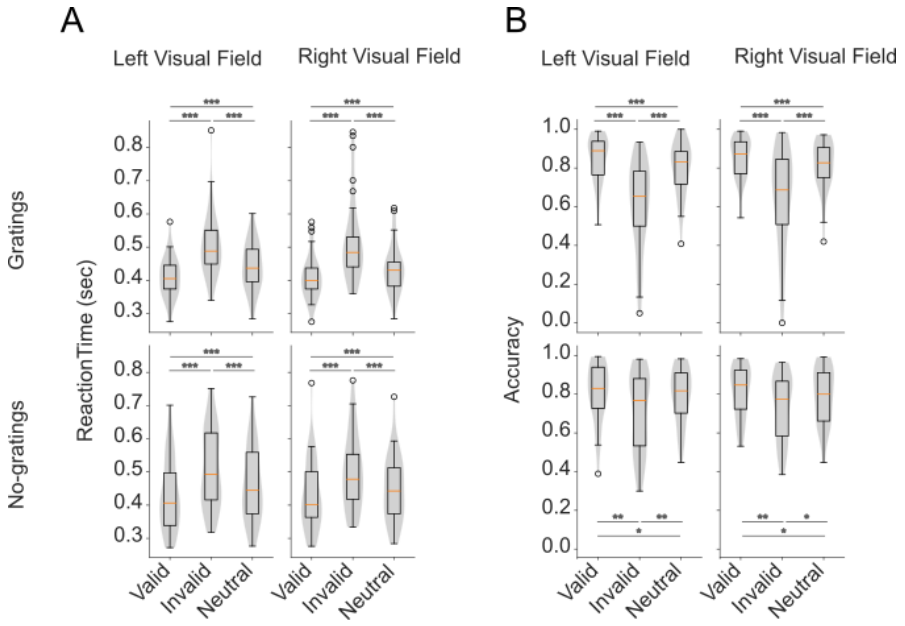
while “covertly” shifting attention

Analyses in attention window

Cruz et al. J Neurosci 2025

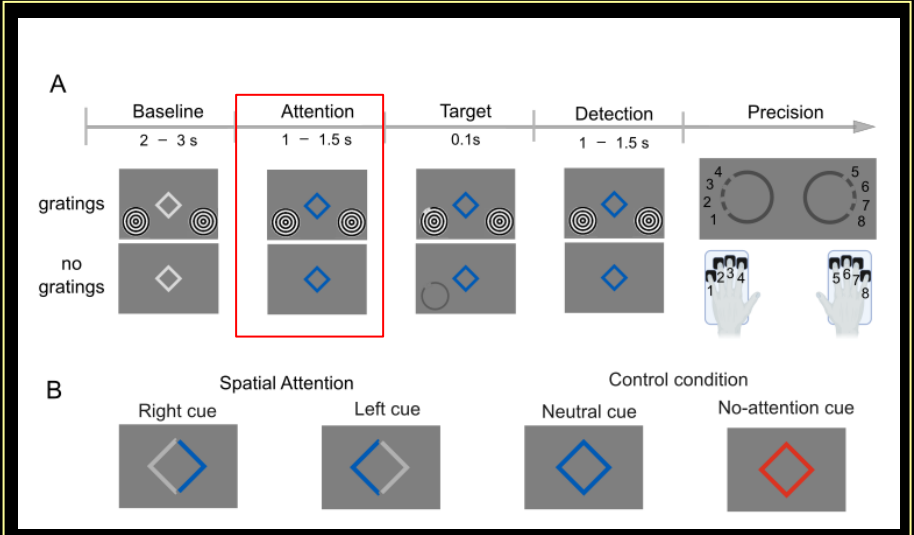
Behavioural results:

Participants deployed spatial attention



Visuospatial attention lateralises alpha-oscillations

Revisting alpha-lateralization with simultaneous MEG&EEG&eye tracking study



In 32 participants:

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- **MEG**
- **Multichannel EEG**
- **Fixational micro-saccades**

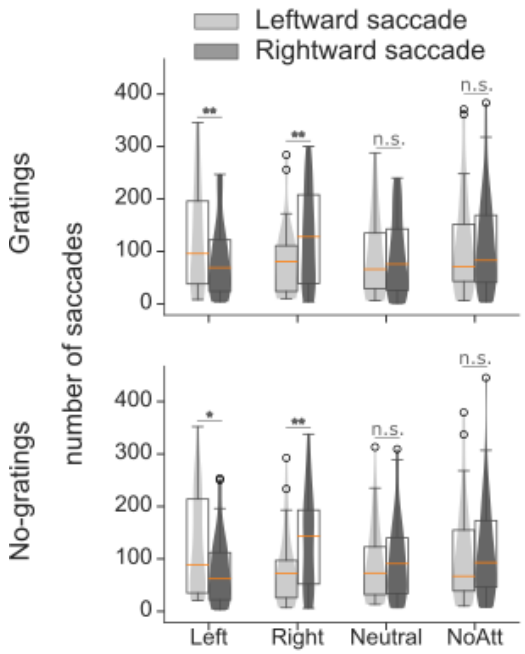
while “covertly” shifting attention

Analyses in attention window

Cruz et al. J Neurosci 2025

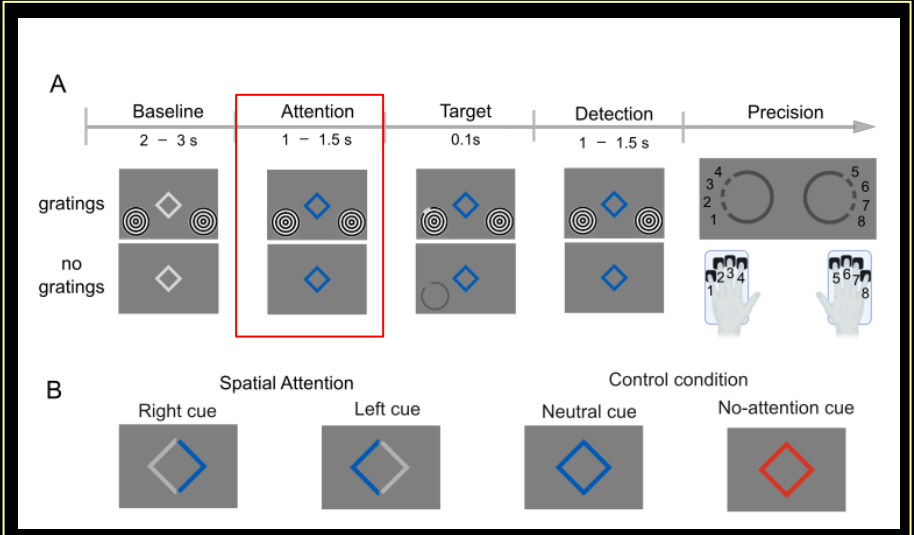
Behavioural results:

“Covert” spatial attention biases directional microsaccades



Visuospatial attention lateralises alpha-oscillations

RESULTS: Alpha-oscillations not a unitary phenomenon as more than one oscillator accounts for typical alpha lateralisation pattern



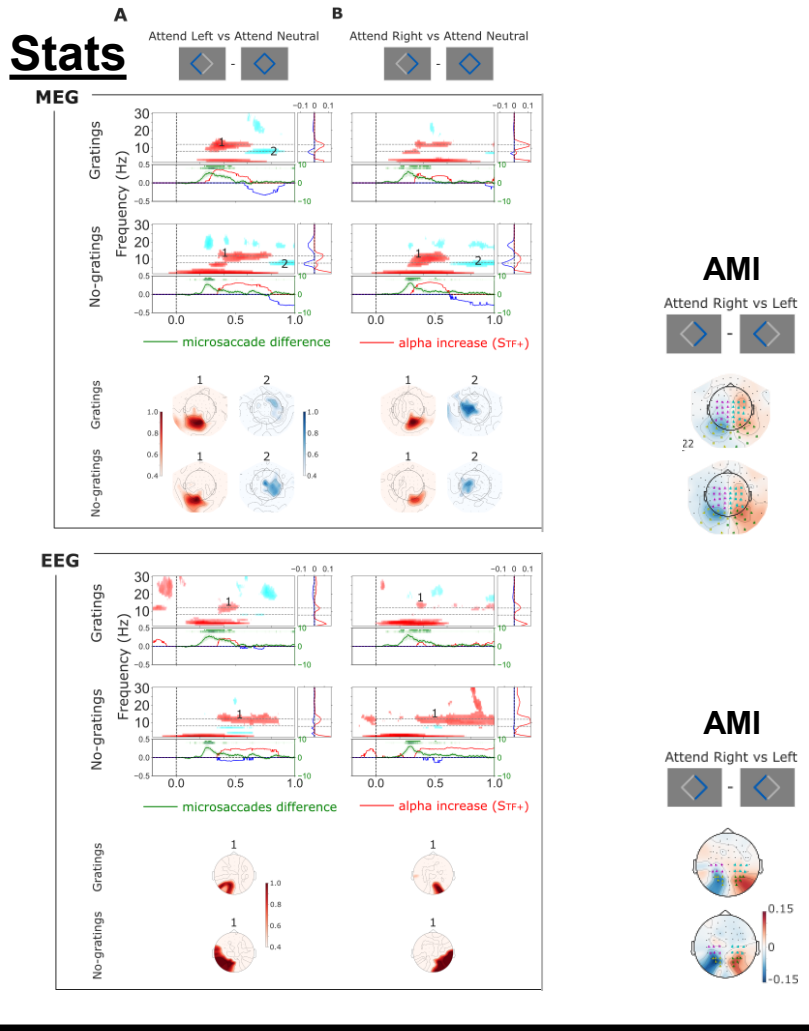
RESULTS: Attention-driven ipsilateral alpha-increases and contralateral alpha-decreases are four-fold dissociated in terms of:

1) localization (occipital vs parietal),
2) timing (early vs late),
3) frequency (low vs high alpha), and
4) association with micro-saccades

MEG<>EEG results

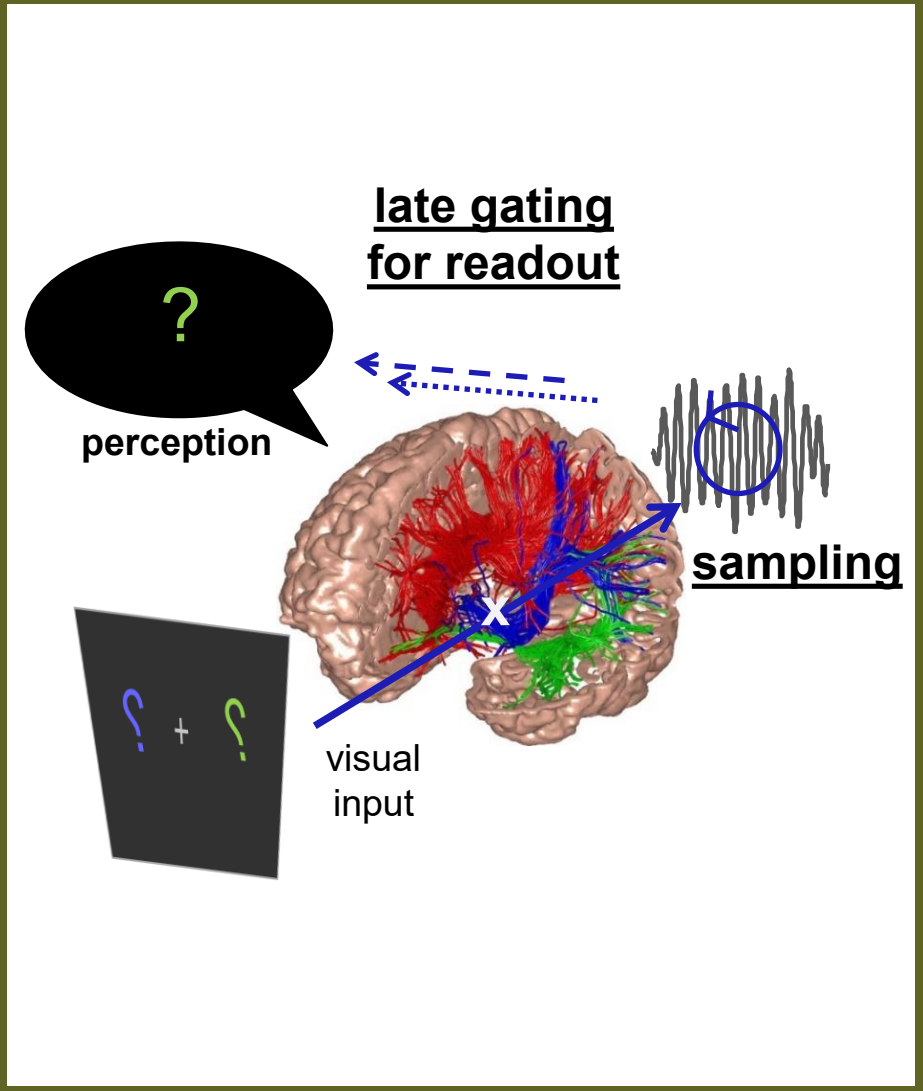
Cruz et al. J Neurosci 2025

MEG/EEG results: Source-level



Summary and Outlook

- mechanisms of input regulation



Overall Conclusion:

- *Brain oscillations at baseline (pre-stimulus) are perceptually relevant*
- *Perceptual performance is shaped by alpha-rhythms.*
- *Alpha oscillations regulate input through interacting with post-stimulus processes through distinct mechanisms (early sampling, late gating).*
- *There is more than one perceptually relevant posterior alpha-rhythm, which need to be dissociated for a detailed account of the role of alpha-oscillations in perception and attention.*

Together with:

Lab members

(past and present)

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Matias Palva
Joachim Gross
Stephanie Morand
Monika Harvey

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wellcome trust

MRC Medical Research Council

BBSRC bioscience for the future

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