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SHORT AND LONG-TERM EFFECTS OF ALPHA-BAND SENSORY ENTRAINMENT ON NEURAL OSCILLATIONS AND PERCEPTUAL PERFORMANCE

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Table of contents

Abstract

Alpha-band neural oscillations (~7-13 Hz) play a crucial role in encoding and integrating sensory information, organizing both uni- and multi-sensory perceptual experiences. Fluctuations in alpha activity have been linked to changes in sensory cortices excitability, leading to rhythmic modulations of perception, thus suggesting that the alpha rhythm may reflects a reliable electrophysiological index of sensory information processing. Interestingly, alpha activity is not a fixed neural feature but is highly plastic and dynamically shaped by neurocognitive states. A recent framework proposes modulating endogenous alpha oscillations through neural entrainment, where neural oscillations synchronize with external rhythms, inducing resonance phenomena in neural and perceptual activity. This approach allows for the direct investigation of the relationship between alpha activity and perceptual performance, as well as the functional modelling of alpha oscillations. The present thesis investigates how alpha-band sensory entrainment, administered via uni- and multi-sensory modalities, affects alpha oscillatory activity and leads to both short- and long-term changes in perceptual performance. Chapter 2 outlines the role of alpha oscillations in shaping perception, while Chapter 3 addresses their malleability following neural entrainment. Empirical studies will then be presented, demonstrating alpha-band sensory entrainment's potential to modulate oscillatory activity and induce functional changes in perceptual performance. Chapter 4 focuses on the effects of alpha-band entrainment on audiovisual temporal binding mechanisms, while Chapter 5 will explore how individual differences in cognitive-perceptual and socio-communicative styles, particularly in neurotypical individuals with varying levels of autistic and schizotypal traits, may influence the effects of alpha-band entrainment on audiovisual temporal binding processes. Finally, Chapters 6 and 7 present EEG and psychophysical studies on whether alpha-band visual stimulation can induce long-lasting changes in alpha oscillatory activity and visual detection performance. Lastly, Chapter 8 integrates these findings and suggests future applications of alpha-band entrainment for enhancing perceptual performance in both general and clinical populations.

Chapter 1

Introduction

Rhythmicity, an intrinsic feature of neural activity, is essential for the functional coordination with the sensory environment as it promotes information processing and organizes the temporal structure of human perception and cognition (Haegens & Golumbic, 2018; Gallina et al., 2023).

Among the diverse neural rhythms, oscillatory activity in the alpha band (~7–13 Hz), predominantly observable over the occipito-parietal cortices (Rosanova et al., 2009), has consistently been identified as a crucial mechanism in coordinating sensory sampling processes (VanRullen, 2016; Cuello et al., 2022; Fakche & Duguè, 2024; Wutz, 2024; Gallina et al., 2024). Historically considered an "idling" rhythm (Pfurtscheller et al., 1996), recent perspectives suggest that alpha oscillations actively contribute to sensory information processing through a periodic sampling mechanism, efficiently parsing and organizing sensory information into coherent models of the sensory environment (Klimesch et al., 2007; VanRullen, 2016; Wutz et al., 2024; Tarasi & Romei, 2024). Indeed, human perception has been shown to fluctuate rhythmically, with each oscillatory cycle of the alpha rhythm exhibiting phases that are more or less optimal for information processing (Mathewson et al., 2011; VanRullen et al., 2016; Samaha et al., 2017; Cuello et al., 2022). Within this perspective, fluctuations in alpha oscillatory activity have been closely linked to variations in visual cortex excitability, leading to rhythmic modulation of both visual and attentional performance, thus directly impacting the likelihood of processing perceptual inputs (Jensen et al., 2010; Sokoliuk & VanRullen, 2013; Spaak et al., 2014; Boncompte et al., 2016; Samaha et al., 2017; Di Gregorio et al., 2022; Benwell et al., 2022). Accordingly, alpha activity in the occipital-parietal regions has been shown to predict the excitability of the visual system in both healthy individuals (Klimesch et al., 2007; Sadaghiani & Kleinschmidt, 2016) and clinical populations (Pietrelli et al., 2019; Allaman et al., 2021; Gallina et al., 2022), suggesting that the alpha rhythm may reflects a reliable electrophysiological signature for the functionality of the visual system (Romei et al., 2008). Interestingly, the role of alpha oscillatory activity extends beyond visual information processing. Indeed, evidence suggests that alpha oscillations are involved in coordinating the encoding, filtering, and integration of information across multiple sensory modalities, playing a fundamental role in structuring and organizing both uni- and multi-sensory perceptual experiences (Cecere et al., 2015; Samaha & Postle, 2015; Samaha & Romei, 2024). Notably, a growing body of research has highlighted that alpha oscillations may represent a key neural mechanism in orchestrating unimodal and cross-modal interactions between visual and auditory inputs, which are crucial for the spatio-temporal integration of sensory information (Bastiaansen et al., 2020; Cecere et al., 2015; Keil & Senkowski, 2018; Ronconi et al., 2023). In line with this framework, it is currently hypothesized that the individual alpha frequency (IAF) may reflects the temporal unit of visual and audiovisual perception, where sensory inputs are integrated when falling within the same alpha cycle but segregated when occurring in different alpha cycles (for a recent review, see Samaha & Romei, 2024).

Interestingly, alpha oscillatory activity is not a static property of the brain, but is highly plastic and dynamically modulated during sensory information processing, shaped by task demands and neurocognitive states (Klimesh et al., 2007; Mathewson et al., 2011; Samaha et al., 2017; Lakatos et al., 2019; Alamia & VanRullen, 2024). In line with this perspective, leveraging the mechanisms of neural plasticity, a recent framework seeks to modulate endogenous alpha oscillatory activity through the entrainment mechanisms of neural oscillations, with the aim to directly investigate the relationship between alpha activity and perceptual performance, as well as to functionally model alpha neural activity (Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024). Neural entrainment involves the temporal synchronization of endogenous oscillatory activity with an external rhythmic force, resulting in phase and frequency alignment, as well as an increase in the power of endogenous oscillations (Lakatos et al., 2019; Duecker et al., 2024). Building on this mechanism, previous studies employing transcranial non-invasive brain stimulation (NIBS) and rhythmic sensory stimulation (Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024) have consistently shown that neural oscillations can be effectively entrained with external stimulation frequencies, revealing resonance phenomena in neural activity, accompanied by concurrent fluctuations in visual and audiovisual perceptual performance (Landau & Fries, 2012; Fiebelkorn et al., 2013; De Graaf et al., 2013; Spaak et al., 2014; Ronconi & Melcher, 2017; Marsicano et al., 2024). In this regard, alpha-band sensory entrainment has proven to be a highly effective tool for shaping perceptual performance by targeting alpha-band oscillatory networks and leveraging intra- and cross-modal interactions between sensory systems (e.g., Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2024). However, several key aspects of the effects induced by alpha-band sensory entrainment on neural oscillations and perceptual performance remain unexplored (for recent reviews, see Gallina et al., 2023; Duecker et al., 2024). In the current thesis, the investigation will focus on whether alpha-band sensory entrainment, administered through unisensory (i.e., visual) and multisensory (i.e., audiovisual) modalities, can shape alpha oscillatory activity, ultimately leading to both short- and long-lasting functional modulations of visual and audiovisual perceptual performance.

In particular, Chapter 2 will provide a detailed description of the pivotal role of alpha-band oscillatory activity in regulating the excitability of the occipito-parietal visual system, shaping visual performance, and orchestrating the neural processes involved in cross-modal audiovisual interactions. Chapter 3 will introduce the technique of neural entrainment, examining the empirical framework that highlights the malleability of endogenous alpha oscillatory activity through the application of alpha-band rhythmic stimulation, with a particular emphasis on the effects induced by sensory entrainment on uni-modal (i.e., visual and auditory) and cross-modal (i.e., audiovisual) information processing. Additionally, the influence of interindividual differences on the ability to functionally entrain to rhythmic sensory stimulation will be explored. In Chapter 4, the results of a study investigating the effects of alpha-band sensory entrainment on the temporal binding mechanisms of audiovisual information will be presented. Relatedly, Chapter 5 will explore how the impact of alpha-band sensory entrainment on audiovisual temporal binding processes may be influenced by interindividual differences in sensory, cognitive, and socio-communicative styles in neurotypical individuals exhibiting varying degrees of autistic and schizotypal traits. Finally, the findings from

EEG and psychophysical studies will be discussed, which aimed to investigate whether alpha-band stimulation administered through the visual modality can induce long-lasting effects on neural oscillatory activity (Chapter 6) and visual detection performance (Chapter 7), leveraging potential plastic modulations in the underlying oscillatory networks of the visual system. In conclusion, Chapter 8 will collectively discuss the findings of the present work, suggesting potential future directions for the application of alpha-band sensory entrainment within the general population and in clinical disorders to functionally enhance alpha oscillatory activity and perceptual performance.

Chapter 2

Alpha-band oscillations shape perception and cognition

2.1. Rhythmicity as an intrinsic feature of neural processing

Understanding how the human brain encodes sensory information and forms neural representations of the external environment has been a central pursuit in cognitive neuroscience for generations of research. Within this framework, neuroimaging techniques have emerged as powerful tools, providing critical insights into the nature of neural activity, characterizing its spatial origins, and revealing its temporal dynamics. For instance, among these methods, electroencephalography (EEG) and magnetoencephalography (MEG) are particularly valuable due to their high temporal resolution, providing a detailed visualization of spontaneous and evoked neural activity associated with information processing with millisecond precision (Davidson et al., 2000; Biasiucci et al., 2019). By leveraging the principles of such time-sensitive techniques, previous research has highlighted that rhythmicity represents a fundamental characteristic of neural activity, mirroring the periodic neuronal firing and regulating the physiological excitation of the cerebral system (McLelland & Paulsen, 2009; Haegens et al., 2011), reflecting a crucial aspect for the functional synchronization of the brain with the external sensory environment (Haegens & Golumbic, 2018). This intrinsic rhythmic nature of neural processes is essential for optimizing sensory processing and structuring the temporal dynamics of human perception and cognition (Lakatos et al., 2009; Haegens & Golumbic, 2018). In line with this perspective, several evidence over the past decades demonstrated that, although our subjective experience often conveys a sense of continuous temporal flow within the stream of sensory input, the brain processes information through discrete cycles of periodic sampling, reflected in the underlying neural oscillatory activity, efficiently parsing and organizing sensory information in coherent models of the perceptual environment (Hutcheon & Yarom, 2000; VanRullen, 2016; Cuello et al., 2022; Fakche & Duguè, 2024). Indeed, human perception and cognition have been shown to fluctuate rhythmically, with each oscillatory cycle of the relevant neural rhythm exhibiting phases that are more or less optimal for the specific process under consideration (VanRullen, 2016). In other words, brain rhythms orchestrate the timing of perceptual cycles, thus determining the phase of discrete optimal temporal windows for information processing (Mathewson et al., 2009; Mathewson et al., 2011; VanRullen et al., 2016; Samaha et al., 2017; Cuello et al., 2022; Di Gregorio et al., 2022).

Importantly, neural rhythms operate across multiple frequencies, and are functionally distributed across distinct brain networks, with multiple perceptual cycles coexisting within different brain circuits, each characterized by its own periodicity (VanRullen, 2016; Lakatos et al., 2019). These neural rhythms are differentially engaged depending on their relevance to the specific information being processed and the task demands (Notbohm et al., 2016; VanRullen, 2016), further highlighting the intrinsic rhythmicity of human information processing.

2.2. Shaping perception through alpha-band neural oscillations

Rhythmic neural activity, or brain oscillations, reflects periodic fluctuations in neural electrical voltage across different brain areas, generating an electrical flow of neuronal networks oscillating at various frequencies (i.e., delta, theta, alpha, beta, gamma), which can be spontaneously generated or driven by internal processes or external perturbations (Davidson et al., 2000; Biasiucci et al., 2019). Among all spontaneous neural rhythms, converging evidence suggested that the neural rhythmicity observable in the alpha frequency band (~7-13 Hz), which is prominently distributed over occipito-parietal brain areas (Berger, 1929; Rosanova et al., 2009), may orchestrate the sampling mechanisms of sensory information in discrete cycles of perceptual processing (VanRullen, 2016; Cuello et al., 2022; Fakche & Duguè, 2024; Wutz, 2024; Gallina et al., 2024).

Although this recent conceptualization, neural activity within the alpha band has historically been considered as an "idling" rhythm, predominantly observed in the awake resting brain when individuals are not engaged in demanding tasks, and thus thought to merely reflect cortical inactivity or a neural state of minimal information processing (Pfurtscheller et al., 1996). However, while the “idling” hypothesis remains a foundational perspective in the historical understanding of the alpha rhythm, this view has been increasingly challenged by recent findings, which suggest that alpha oscillations may play an active role in orchestrating the timing of neural processing by dynamically modulating neural excitability and information flow across brain networks, regulating inhibitory and excitatory phases of information processing (Klimesch et al., 2007; Samaha & Postle, 2015; VanRullen, 2016; Di Gregorio et al., 2022; Cuello et al., 2022; Fakche & Duguè, 2024; Wutz et al., 2024; Tarasi & Romei, 2024; Schoffelen et al., 2024; Samaha & Romei, 2024). Thus, rather than merely reflecting a passive, resting brain state, alpha neural activity is currently thought to orchestrate both bottom-up perceptual processes and top-down cognitive mechanisms, reflecting a crucial mechanism for gating information flow and regulating the timing of neural information processing (Mathewson et al., 2009; Busch et al., 2009; VanRullen, 2016). In line with this framework, the spectral features of alpha oscillations (i.e., phase, power, and frequency) have been consistently linked to different aspects of perceptual and cognitive processing, with observable behavioural outcomes depending on the momentary phase of ongoing oscillatory activity as a function of its power and frequency (Mathewson et al., 2009; Busch et al., 2009; Samaha et al., 2017; Ronconi & Melcher, 2017; Cuello et al., 2022; Di Gregorio et al., 2022; Benwell et al., 2022).

In the following sections, the empirical evidence supporting the central role of alpha oscillatory activity in orchestrating perceptual performance will be reviewed, with a particular emphasis on its influence in shaping visual perception and cognition, as well as its role in regulating interactions within audiovisual cross-modal mechanisms (for a graphical illustration, see Fig. 1).

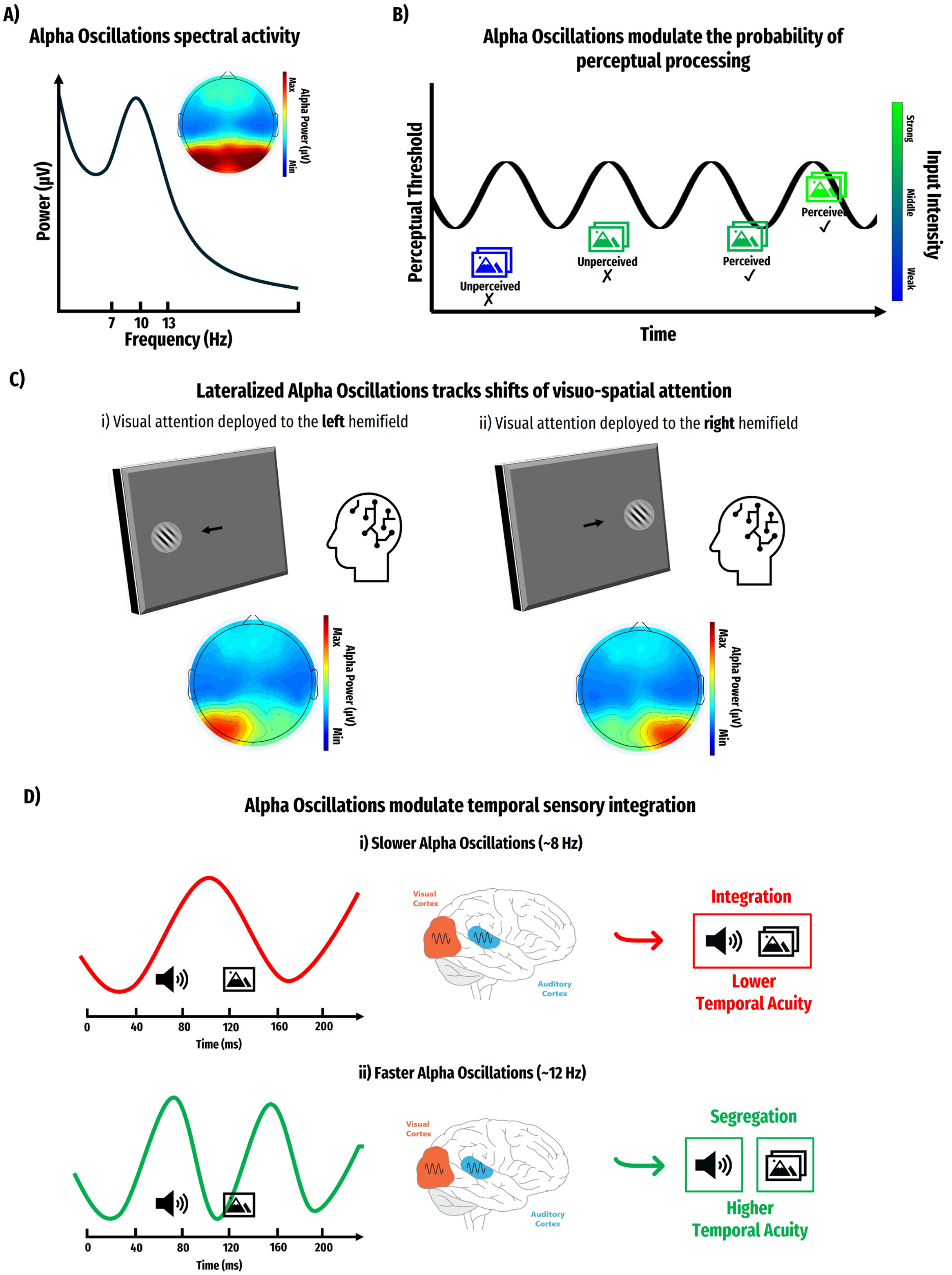

Figure 1. Graphical representation depicting the role of Alpha Oscillations in shaping perceptual performance. **A)** EEG power spectrum and alpha activity topographical distribution. An example of an EEG frequency power spectrum observed over parieto-occipital scalp electrodes during an eyes-closed resting-state condition, revealing a negative exponential decay at both lower and higher neural frequencies, except for a prominent Gaussian-shaped peak in the alpha band (7–13 Hz). The topographical scalp map illustrates the spatial distribution of alpha oscillatory activity (i.e., 7–13 Hz) across the scalp, with maximum activity commonly observed at posterior electrode regions. **B)** Alpha oscillations are hypothesized to modulate the threshold of perceptual processing. In this panel it is shown that, for two identical weak sensory inputs, the likelihood of sensory processing reaching perceptual threshold depend on the phase of the alpha oscillations at the

moment of input presentation, thus determining whether or not a sensory input is perceived. **C)** This panel describes the alpha power modulations in occipito-parietal scalp areas during visuospatial attention tasks. Cues and visual stimuli prompt individuals to shift their attention to either the left (i) or right (ii) side of the visual field. This attentional shift leads to an increase in alpha power over the posterior brain areas ipsilateral to the attended hemifield, and a decrease over contralateral regions. **D)** Alpha oscillations can serve as the temporal unit for visual and audiovisual temporal perception. The current idea is that two sensory inputs are integrated in a unique, coherent percept when they occur within the same alpha cycle (i.e., slower alpha oscillations). Conversely, when two sensory inputs are presented in different alpha cycles, they are segregated in different events (i.e., faster alpha oscillations).

2.2.1 Alpha-band neural oscillations shape visual information processing

Alpha oscillatory activity, representing the dominant rhythm of the human brain, is an intrinsic property of the visual system, with maximum power observed over the parieto-occipital regions during both resting and task-related brain states (Berger, 1929; Rosanova et al., 2009). Indeed, alpha oscillations distributed over occipital-parietal brain areas have been shown to predict the excitability of the visual system (Klimesh et al., 2007; Sadaghiani & Kleinschmidt, 2016; Pietrelli et al., 2019; Allaman et al., 2021; Gallina et al., 2022), where spontaneous decreases in alpha activity are often associated with increased visual cortex excitability, thus suggesting that the alpha rhythm may reflect a neurophysiological signature of visual system functionality (Romei et al., 2008). Importantly, fluctuations in alpha activity not only reflect the excitability of visual brain areas, but also directly influence the processing of visual information.

Over the past decades, extensive research has indicated that rhythmic fluctuations in alpha-band neural activity are closely associated with both sensory information processing and top-down attentional processes, significantly impacting visual performance (Jensen et al., 2010; Sokoliuk & VanRullen, 2013; Spaak et al., 2014; Boncompte et al., 2016; Samaha et al., 2017; Di Gregorio et al., 2022; Benwell et al., 2022). Indeed, variations in alpha spectral parameters have been strongly associated with fluctuations in visual cortex excitability, resulting in the rhythmic modulation of visual and attentional performance, ultimately influencing the likelihood of processing sensory information by regulating the timing of optimal temporal windows for information processing (Jensen et al., 2010; Sokoliuk & VanRullen, 2013; Spaak et al., 2014; Boncompte et al., 2016; Samaha et al., 2017; Di Gregorio et al., 2022; Benwell et al., 2022).

This empirical framework has shown that during phases of the alpha oscillatory cycle with high power, neuronal firing in relevant brain regions can be temporarily inhibited, reducing responsiveness to external stimuli and representing a state of minimal cortical processing (Klimesh et al., 2007; Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010; Sadaghiani & Kleinschmidt, 2016). This oscillatory mechanism helps to functionally suppress the processing of distracting or irrelevant information, influencing visuo-attentional mechanisms (Klimesh et al., 2007; Jensen & Mazaheri, 2010). On the other hand, during phases of lower alpha power, visual brain regions are more excitable and are more likely to process incoming sensory inputs (Klimesh et al., 2007; Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010; VanRullen et al., 2016). The rhythmic alternation between these oscillatory phases of alpha activity orchestrates the timing of information processing, leading to the hypothesis that alpha oscillations may play a role of "pulsed inhibition", generating alternating temporal windows of inhibition and excitation with each alpha cycle (Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010). Importantly, this evidence highlights that alpha oscillatory activity not only orchestrates the timing of bottom-up sensory processes, but also reflects the complex interaction between the visual and attentional systems in shaping visual perception (Rihs et al., 2009; Clayton et al., 2018). Indeed, alpha oscillations are retinotopically distributed in the visual cortices (Wandell and Winawer, 2011; Sokoliuk & VanRullen, 2016; Fakche & Dugué, 2024), and orchestrate visuo-spatial attentional mechanisms by regulating the cortical excitability of hemispheres depending on the spatial location of the stimulus. In line with this idea, converging evidence has shown that an increase in alpha power in the ipsilateral hemisphere relative to the visual information, gates or inhibits irrelevant sensory input from the unattended visual field, while a decrease in alpha activity in the contralateral hemisphere allows for greater cortical excitability and enhanced processing of the sensory stimulus (Clayton et al., 2018). This lateralized distribution of alpha activity generates a functional asymmetry between hemispheres, optimizing the allocation of brain's visuo-spatial attentional resources to process sensory inputs, thus orchestrating visuo-spatial attention and influencing visual performance (Sauseng & Klimesch, 2009; Clayton et al., 2018).

Within this framework, several evidence demonstrated that alpha power over the contralateral occipito-parietal brain areas is inversely related to target detection and perceptual sensitivity (Ergenoglu et al. 2004; Klimesch et al., 2007; van Dijk et al., 2008; Di Gregorio et al., 2022). For instance, Mathewson and colleagues (2009) found that transient decreases in alpha power preceding stimulus presentation enhanced participants' ability to detect visual stimuli, highlighting the role of alpha desynchronization in preparing the visual system for incoming information. Relatedly, recent evidence documented that the phase of alpha oscillations at the time of stimulus presentation can enhance or inhibit neural responses to visual stimuli, depending on whether the phase is aligned with the timing of stimulus onset (Hanslmayr et al., 2007; Samaha et al., 2016, 2017). Specifically, stimuli presented during the positive peak of alpha oscillations elicited stronger neural responses, and led to better detection and improved perceptual sensitivity (Hanslmayr et al., 2007; Spaak et al., 2014; Samaha et al., 2016, 2017), thus strengthening the idea that alpha oscillatory activity may represents a temporal marker of visual information processing.

Interestingly, alpha oscillatory activity also modulates decision-making processes underlying perceptual judgments, affecting decision criterion and subjective confidence (Samaha et al., 2016, 2017; Di Gregorio et al., 2022). For instance, it has been documented that increased alpha power was associated with a more conservative decision criterion, strengthening the idea that heightened alpha power reflects a greater degree of attentional inhibition, leading to a more stringent evaluation of sensory evidence before making a perceptual decision. Furthermore, it has been shown that alpha phase alignment can influence subjective confidence of perceptual judgements. In details, it has been reported that individuals' subjective confidence in their perceptual decisions was enhanced when participants’ responses aligned with the peak of the alpha cycle, suggesting that alpha phase may influence not only the sensory processing of visual information but also the subjective experience of confidence (Samaha et al., 2016, 2017).

In addition, while the frequency of occipito-parietal alpha oscillations (i.e., individual alpha frequency; IAF) represent a relatively stable neurophysiological marker within individuals (Grandy et al., 2013), it can exhibit significant interindividual differences (Grandy et al., 2013; Haegens et al., 2014), potentially explaining differences across individuals in processing visual information. In this realm, the current idea is that the IAF may represent the temporal unit of visual perception, shaping the temporal resolution of information processing in the visual system (Samaha & Postle, 2015; Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2022, 2024; Di Gregorio et al., 2022; Tarasi & Romei, 2024; for a recent review, see: Samaha & Romei, 2024). Multiple visual inputs are perceptually unified and integrated when presented within a limited temporal binding window (TBW; Colonius & Diederich, 2004). In this regard, several empirical studies have linked the IAF to the size of the visual TBW showing that faster IAF accounted for a higher visual temporal acuity, and indicating that visual inputs are integrated when they coincide into the same alpha oscillation, while they are segregated when presented in distinct alpha cycles (Samaha & Postle, 2015; Graziano et al., 2017; Ronconi et al., 2017, 2023). These empirical findings suggest that the IAF can reflect a fundamental temporal sampling mechanism that shapes visual performance, with higher alpha frequencies promoting enhanced sensory evidence per time frame, strengthening the idea of a close link between alpha oscillations and the natural tendency of the visual system to process sensory input within distinct temporal windows (Samaha & Postle, 2015; Tarasi & Romei, 2024; Samaha & Romei, 2024).

Overall, considering the picture emerging from these extensive findings, neural oscillations in the alpha band are closely associated with different aspects of visual information processing, further indicating that variations in its ongoing spectral features selectively affect different aspect of perceptual performance.

2.2.2 Rhythmic fluctuations in visual performance: Alpha-band behavioural oscillations

Given the intrinsic rhythmicity of visual information processing, electrophysiological techniques are not the only tools that can be employed to investigate the perceptual rhythms underlying behavioural performance. Indeed, perceptual rhythms can also be revealed with behavioural and psychophysical measurements, obtained using a methodological approach known as ‘dense-sampling’ (de Graaf et al., 2013; Drewes et al., 2015; Landau & Fries, 2012; Ronconi & Melcher, 2017; Ronconi et al., 2018). At the operative level, this approach involves using one sensory stimulus to reset neural oscillations, establishing the phase resetting stimulus as a temporal reference for assessing perceptual accuracy or reaction times in response to a second stimulus presented at varying time intervals (de Graaf et al., 2013; Drewes et al., 2015; Landau & Fries, 2012). The dense-sampling technique requires probing a large set of time intervals between the reference and target stimuli to sample perception with high temporal resolution. The resulting fluctuations in behavioural performance, (i.e., behavioural oscillations), can then be analyzed using the spectral methods (e.g., Fast Fourier Transform) classically used for electrophysiological signals, in order to uncover rhythmic patterns in perception. Employing this procedure, previous evidence has documented an intrinsic rhythmic pattern in behavioural measures which fluctuate within the alpha frequency band when individuals are required to process visual information (~10 Hz; Dugué et al., 2011; McLelland et al., 2016; VanRullen, 2016; Ronconi & Melcher, 2017; Gallina et al., 2024). Importantly, it has been reported that these behavioural rhythms correspond to the neural oscillatory activity of alpha oscillations observable over parieto-occipital brain areas (Dugué et al., 2011; McLelland et al., 2016).

Importantly, the dense-sampling technique has revealed that different rhythms in visual performance coordinate specific perceptual and visuo-spatial attentional processes, varying the sampling frequency according to task demands and the spatio-temporal features of the stimuli being processed (VanRullen et al., 2007; Busch & VanRullen, 2010; Landau & Fries, 2012; Fiebelkorn et al., 2013; Holcombe & Chen, 2013; Song et al., 2014; Huang et al., 2015; Gallina et al., 2024). In this regard, in our recent study (Gallina et al., 2024) we employed two different version of a visual detection task, exploring how the manipulation of attentional demand and target presentation location could influence perceptual and attentional sampling mechanisms. In detail, visuo-spatial performance was densely sampled in two different versions of a visual detection task: in the first task, the target's presentation side was fixed, requiring participants to monitor a single hemifield, while in the second task, the target's presentation side varied across trials, requiring participants to monitor both hemifields simultaneously. The results from the first task revealed behavioural oscillatory patterns fluctuating in the alpha (~10 Hz) and theta/low-alpha (~6–9 Hz) frequency ranges for stimuli presented to the left and right hemifields, respectively, suggesting a perceptual sampling mechanism operating with differing efficiency across hemispheres, with the right hemisphere showing greater efficiency in supporting faster perceptual oscillatory rhythms. On the other hand, in the second task, when attentional resources were simultaneously deployed to both hemifields, a theta oscillatory component (~5 Hz) emerged for stimuli presented to both the left and right hemifields, reflecting an attentional sampling process that was equally supported by both hemispheres, aligning with previous evidence (Fiebelkorn et al., 2013; Huang et al., 2015; Landau & Fries, 2012; Song et al., 2014). These results suggest that distinct perceptual and attentional sampling mechanisms may operate at different oscillatory rhythms, with their prevalence and hemispheric lateralization varying according to task demands and spatio-temporal stimuli features. The data and materials from our recent study are open source and fully available at: OSF | Alpha and theta rhythm support perceptual and attentional sampling in vision..

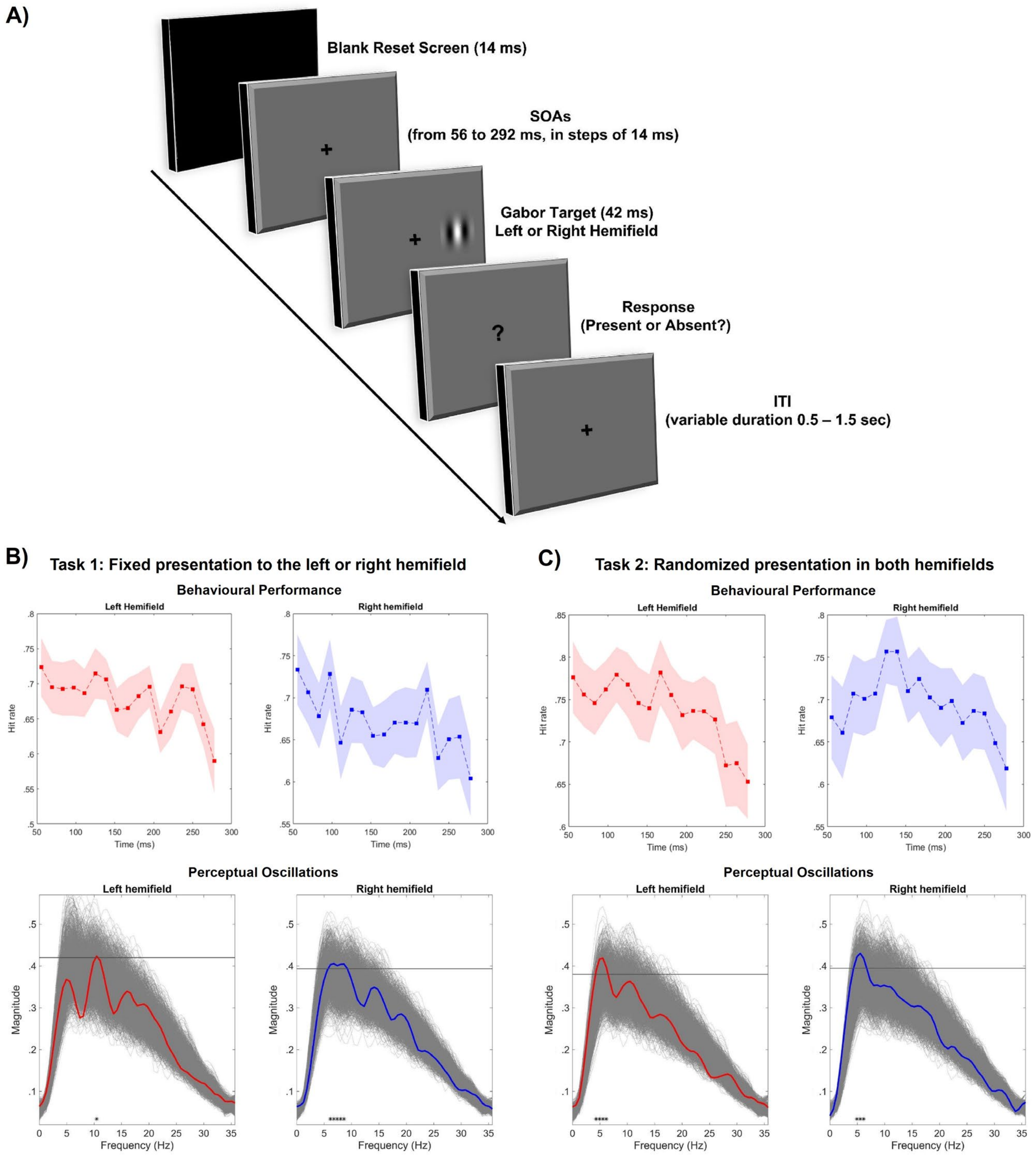

Figure 2. Graphical representation of the experimental design and results from Gallina et al. (2024). **A)** Schematic representation of the experimental design. Each trial began with a brief presentation of a blank reset screen (14 ms) to induce a phase reset of ongoing perceptual oscillations. To uncover potential oscillatory components in detection performance, perceptual performance was densely sampled over time using various stimulus onset asynchronies (SOAs; ranging from 56 to 292 ms in steps of 14 ms) preceding the appearance of lateralized Gabor target stimuli (42 ms) presented at the participants' contrast threshold. Target stimuli were delivered either to the right or left hemifield in separate experimental blocks (Task 1) or randomly presented to the left or right hemifield within the same experimental block (Task 2). At the offset of the Gabor target, participants were required to report whether the target stimulus was present or absent. Following their response, the central fixation cross reappeared for a randomly varying duration (Intertrial Interval, ITI; between 0.5 and 1.5 seconds) before the start of the subsequent trial. **B)** Results of Task 1. The upper panels display the average raw hit rates across the different SOAs for Task 1, illustrating performance relative to the left hemifield (red line) and right hemifield (blue line). In the lower panels, the power spectrum of perceptual oscillations during Task 1 is shown, where target stimuli were exclusively presented in either the left or right hemifield. The power spectrum (Magnitude) is depicted for target stimuli delivered to the left hemifield (left panel; red solid line)

and the right hemifield (right panel; blue solid line). Gray lines represent power spectra derived from permuted data, while black horizontal lines indicate the significance threshold. Asterisks denote p < .05, and black asterisks mark the frequency bins in the observed spectrum that are significantly different from those obtained through permutation testing. **C)** Results of Task 2. The upper panels display the average raw hit rates across the different SOAs for Task 2, illustrating performance relative to the left hemifield (red line) and right hemifield (blue line). In the lower panels, the power spectrum of perceptual oscillations during Task 2 is shown, where target stimuli were randomly presented in either the left or right hemifield. The power spectrum (Magnitude) is depicted for target stimuli delivered to the left hemifield (left panel; red solid line) and the right hemifield (right panel; blue solid line). Gray lines represent power spectra derived from permuted data, while black horizontal lines indicate the significance threshold. Asterisks denote p < .05, and black asterisks mark the frequency bins in the observed spectrum that are significantly different from those obtained through permutation testing. Adapted from Gallina et al., 2024.

2.2.3. Alpha-band oscillations regulate cross-modal audiovisual interactions

Although the previous sections emphasized the relevance of the unisensory visual modality in human perception, our sensory world is far more complex and intrinsically multisensory. Indeed, the brain continuously encodes, filters, and integrates information from multiple sensory modalities to structure and organize our perceptual experience. This process, known as multisensory integration, is a paramount aspect of human cognition, allowing the integration of sensory inputs from various modalities into a unified, coherent percept, while simultaneously segmenting information from different events (Spence, 2007; Stevenson & Wallace, 2013; Murray et al., 2016; Marsicano et al., 2022, 2024).

Among the different multisensory interactions, the cross-modal integration of visual and auditory information is a crucial aspect of our perceptual experiences. Indeed, several studies have demonstrated that enhanced abilities in higher-order cognitive and socio-communicative domains (e.g., speech perception and problem-solving) are fundamentally grounded in effective audiovisual (AV) multisensory mechanisms (Lovelace et al., 2003; Powers et al., 2009; Bishop & Miller, 2009; Diederich & Colonius; 2015; Zmigrod & Zmigrod, 2016). Importantly, although alpha oscillations are predominantly observed in visual brain areas (Rosanova et al., 2009), multiple findings highlighted their role in auditory information processing and, more notably, in orchestrating cross-modal AV interaction mechanisms. Studies employing AV spatial attention paradigms have documented increases in occipito-parietal alpha power during auditory attention, indicating the inhibition of visual information and the facilitation of auditory stimulus encoding (Foxe et al., 1998;

Fu et al., 2001; Banerjee et al., 2011; Keller et al., 2017), while additional research has identified an independent auditory alpha oscillatory network that is selectively modulated by auditory, but not visual, spatial attention tasks (Gomez-Ramirez et al., 2011; Frey et al., 2014). On the other hand, recent evidence highlighted that occipito-parietal alpha oscillations may represent a crucial neural mechanism for orchestrating cross-modal interactions between AV information, determining the temporal integration of different sensory information (Bastiaansen et al., 2020; Cecere et al., 2015; Keil & Senkowski, 2018; Cooke et al., 2019; Ronconi et al., 2023). In line with the temporal integration mechanisms observed for visual information, it is currently hypothesized that the individual alpha frequency (IAF) may represent the temporal unit of AV perception, where AV inputs are integrated when occurring within the same alpha cycle, but segregated when presented in different alpha oscillations (Samaha & Postle, 2015; Bastiaansen et al., 2020; Cecere et al., 2015; Migliorati et al., 2020; for a recent review, see: Samaha & Romei, 2024).

In line with this framework, employing AV temporal integration/segregation tasks, it has been revealed that interindividual differences in alpha oscillatory activity (Grandy et al., 2013; Haegens et al., 2014), may help explain the variability observed among individuals in AV information processing abilities (Bastiaansen et al., 2020; Cecere et al., 2015; Migliorati et al., 2020; Samaha & Romei, 2024). For instance, in a recent study, Bastiaansen and colleagues (2019) employed an AV Simultaneity Judgement (SJ) task, a well-established paradigm for assessing AV temporal perception where participants were requested to report the perceived simultaneity of visual and auditory stimuli presented across varying SOAs (Zampini et al., 2005; Vatakis et al., 2008; Roach et al., 2011), showing that both pre-stimulus alpha power and IAF can predict AV temporal acuity and the TBW size. In detail, they observed a decrease in pre-stimulus alpha power when participants reported inaccurate simultaneity judgments, which was interpreted as a failure of inhibitory mechanisms to filter out irrelevant sensory information, aligning with previous evidence suggesting that lower alpha power is associated with reduced inhibitory control, leading to less precise sensory processing (Foxe & Snyder, 2011; Klimesch et al., 2007; Jensen & Mazaheri, 2010; Grabot et al., 2017). More importantly, they found that participants with faster IAF exhibited a greater AV temporal acuity, supporting the idea that IAF may reflects the temporal unit of AV temporal perception (for a review, see Samaha & Romei, 2024). This evidence suggests that alpha oscillatory activity can reflect a fundamental temporal sampling mechanism shaping AV performance, with faster alpha frequencies enhancing AV temporal abilities (Samaha & Postle, 2015; Samaha & Romei, 2024).

From a neurocomputational perspective, it has been demonstrated that the functional AV interactions depend on the phase reset of alpha band neural oscillations, which can be induced both within the same sensory modality (e.g., visual stimuli resetting oscillations in visual brain areas; Landau & Fries, 2012) and across different sensory modalities (e.g., visual stimuli resetting oscillations in auditory brain areas; Fiebelkorn et al., 2013; Romei et al., 2012; Cecere et al., 2016), thus ultimately enhancing oscillatory activity in the primary sensory cortices of other modalities (Ghazanfar & Schroeder, 2006; Senkowski et al., 2008; Bauer et al., 2020). Importantly, the cross-modal phase reset dynamics that underlie the binding mechanisms of AV stimuli are significantly influenced by the "leading sense", strongly indicating that AV interactions may engage distinct neural oscillatory networks depending on which sensory modality provides the initial input (Lakatos et al., 2009; Naue et al., 2011; Thorne et al., 2011; Romei et al., 2012; Mercier et al., 2013; Cecere et al., 2016, 2017). Indeed, in the condition where auditory input precedes visual stimuli (i.e., Auditory Leading; AL), phase reset of brain oscillations is hypothesized to function as a low-level, automatic attentional mechanism that alerts the visual system to incoming sensory stimuli, thus enhancing the efficiency of AV integration/segregation processes, and resulting in a narrower AV TBW that is less prone to modulations (e.g., Powers et al., 2009, 2012; Thorne & Debener, 2014; Marsicano et al., 2024). On the other hand, visual-to-auditory interactions (i.e., Visual Leading; VL) are thought to rely on higher-order predictive mechanisms, providing greater flexibility in adapting to visual-to-auditory regularities (Besle et al., 2008; Vroomen & Stekelenburg, 2010; Arnal & Giraud, 2012; Cecere et al., 2016, 2017).

Taken together, the findings examined in this chapter have highlighted the critical role of alpha-band oscillatory activity in regulating the excitability of the occipito-parietal visual system, shaping visual performance, and orchestrating neural processes involved in cross-modal AV interactions. However, alpha oscillatory activity is not an invariant feature of the neural system, but is instead highly plastic and dynamically modulated during visual and AV information processing, shaped by the rhythmicity embedded in the sensory environment, task demands and cognitive states (Klimesh et al., 2007; Mathewson et al., 2009, 2011; Samaha et al., 2017; Lakatos et al., 2019; Gallina et al., 2023; Alamia & VanRullen, 2024). Accordingly, this empirical findings strongly suggest that endogenous alpha oscillatory activity and perceptual processing can be externally modulated and enhanced. In the next chapter, the empirical framework highlighting the malleability of endogenous alpha oscillatory activity through the application of non-invasive brain stimulation techniques will be examined, with particular emphasis on the effects induced by sensory rhythmic stimulation at alpha-band frequencies on visual and AV information processing.

Chapter 3

Entrainment of Alpha-band neural oscillations

3.1. Synchronizing neural oscillations through entrainment

As highlighted by the findings discussed in the previous chapter, alpha oscillatory activity is highly plastic and dynamically modulated during information processing, being shaped by task demands, cognitive states, and external perturbations (Klimesch et al., 2007; Mathewson et al., 2009, 2011; Samaha et al., 2017; Alamia & VanRullen, 2024).

In everyday life, endogenous oscillatory activity in the brain is influenced by the rhythmicity - and quasi-rhythmicity - embedded in environmental sensory streams through the phase synchronization of their oscillatory systems, a process commonly referred to as "entrainment" of neural oscillations (for recent reviews, see: Lakatos et al., 2019; Gallina et al., 2023). Neural entrainment is defined as the temporal synchronization of endogenous neural activity to an external driving rhythm, resulting in phase and frequency alignment and an increase in the power of endogenous oscillations (Lakatos et al., 2019). Entrainment is an adaptive feature of the human brain (Thut et al., 2011a, 2011b; Lakatos et al., 2019), as rhythmicity promotes sensory encoding by aligning endogenous and external rhythmic activity, ensuring that sensory input is processed within optimal temporal windows for information encoding (De Graaf et al., 2013; Spaak et al., 2014; Ronconi et al., 2018; Marsicano et al., 2024). Indeed, the brain's predictive models of the environment leverage neural oscillations to optimize sensory processing (for a recent review, see: Tarasi et al., 2022). When environmental sampling follows a rhythmic pattern, the brain synchronizes its neural oscillations to the frequency that most closely aligns with this external temporal structure, resulting in the entrainment process, and ultimately ensuring that inputs consistently fall within the same oscillatory phase (Lakatos et al., 2019; Gallina et al., 2023). By entraining to the timing of sensory inputs, the neural system enhances processing efficiency, facilitating the interpretation of external sensory patterns in line with the brain's predictions embedded in brain oscillations (Lakatos et al., 2019).

Interestingly, over the past decades, studies leveraging the entrainment mechanisms of neural oscillations have increasingly used non-invasive brain stimulation (NIBS) techniques, such as transcranial alternating current stimulation (tACS; Zaehle et al., 2010; Helfrich et al., 2014; Vossen et al., 2015; Minami & Amano, 2017; Borghini et al., 2018; Wolinski et al., 2018; Bender et al., 2019; Huang et al., 2021; Fig. 3A) and transcranial magnetic stimulation (TMS; Thut et al., 2011b; Coldea et al., 2022; Di Gregorio et al., 2022; Fig 3A), alongside rhythmic sensory stimulation (Mathewson et al., 2011; De Graaf et al., 2013; Spaak et al., 2014; Ronconi et al., 2016a, 2016b; Kizuk & Mathewson, 2017; Ronconi & Melcher, 2017; Ronconi et al., 2018; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Kawashima et al., 2022; Fakche & Duguè, 2024; Szaszkó et al., 2024; Fig. 3B). These studies consistently indicate an effective synchronization of alpha-band brain oscillations to external stimulation frequencies, revealing resonance phenomena in neural activity that correspond with fluctuations in perceptual and cognitive performance (Landau & Fries, 2012; Fiebelkorn et al., 2013; De Graaf et al., 2013; Spaak et al., 2014; Ronconi & Melcher, 2017; Kawashima et al., 2022; Marsicano et al., 2024; Fakche & Duguè, 2024). In this realm, rhythmic stimulation techniques have been employed both as experimental manipulations to investigate whether neural oscillations causally drive brain functions, and as rehabilitative interventions, given the association of specific neural oscillatory anomalies with different neurological, neurodevelopmental and psychiatric populations (Uhlhaas & Singer, 2010; for a recent review, see: Ippolito et al., 2022). This framework highlights that spontaneous alpha oscillations can be externally modulated, indicating that rhythmic stimulation may be employed to investigate the relationship between behavioural performance and neural oscillations via phase-locking of the endogenous and external oscillatory systems (Lakatos et al., 2019; Gallina et al., 2023). However, for the entrainment of neural oscillations to be effective, the stimulation parameters must be tuned to the targeted brain areas. Indeed, neural entrainment is highly frequency-dependent and is determined by the functional alignment between the stimulation frequency and the intrinsic oscillatory properties of the targeted brain regions (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022), requiring the stimulation frequency to fall within a specific bandwidth that aligns with the preferred neural rhythm of the targeted oscillatory system (Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022). The mechanism of neural entrainment is rooted in the Arnold Tongue phenomenon (Pikovsky et al., 2003; Huang et al., 2021), which predicts that phase synchronization between two coupled rhythmic systems occurs when the driving oscillator approaches the natural rhythm of the targeted oscillatory system. Accordingly, previous studies have demonstrated that neural entrainment tailored to the preferred frequency band of the visual system (i.e., alpha oscillations), leads to distinct modulations in alpha oscillatory activity within occipito-parietal regions, accompanied by corresponding changes in visual performance (Mathewson et al., 2011; Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019). While previous studies have employed a fixed alpha frequency for entrainment across individuals, increasing evidence suggests that the most pronounced modulations occur when the stimulation frequency is aligned with the individual's alpha frequency peak (IAF; Thut et al., 2011a; Zaehle et al., 2010; Notbohm et al., 2016).

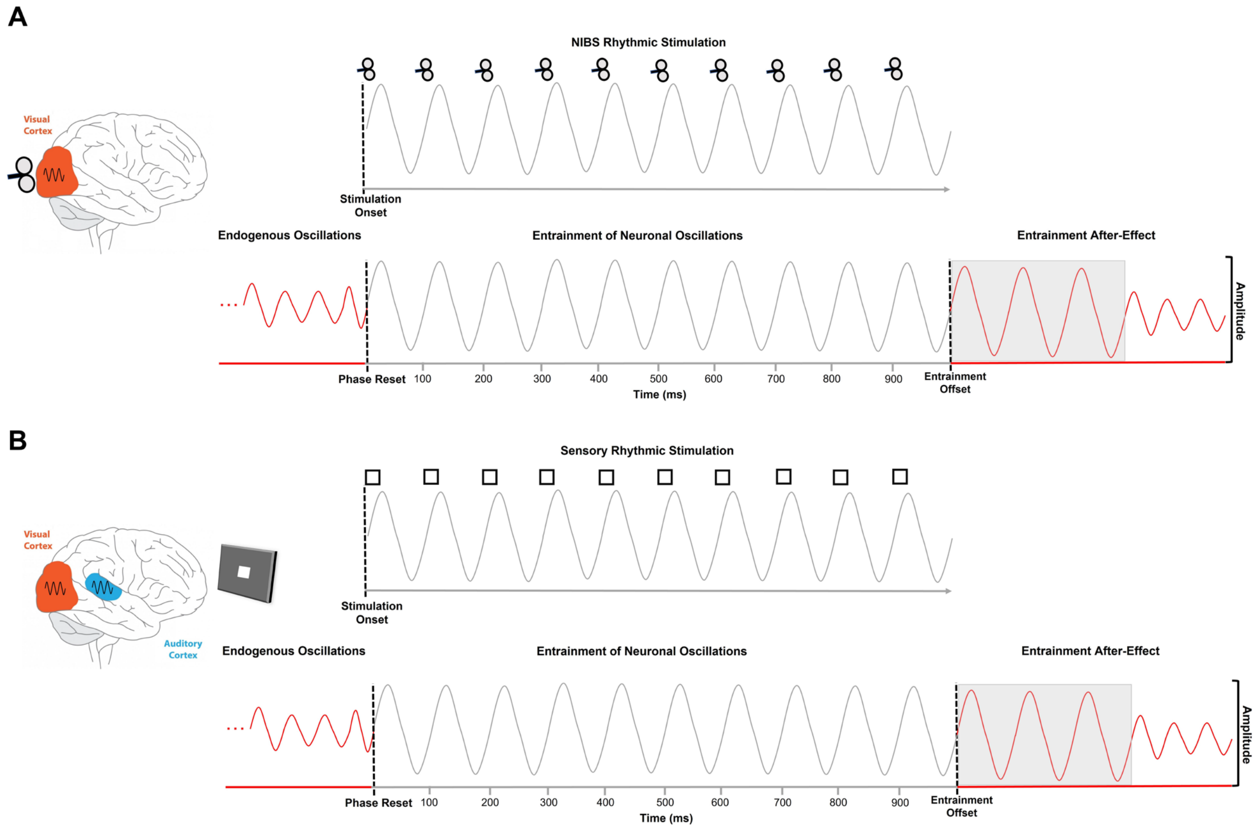

Figure 3. Graphical representation depicting the alpha-band neural entrainment mechanisms. (A) An external rhythmic force (i.e., TMS, tACS; here depicted as TMS), delivered in the frequencies of the alpha-band (here depicted as a 10 Hz entrainment), induces a phase reset of the endogenous alpha brain oscillations of the targeted visual areas, with a subsequent phase alignment, an increase in amplitude and synchronization to the external stimulation frequency. Such entrainment effects typically persist after stimulation offset for three alpha cycles (entrainment after-effect; grey shaded area). (B) A sensory stimulus (i.e., visual, auditory, audio-visual; here, a square, representing visual entrainment) streamed in the alpha-band (here depicted as a 10 Hz entrainment) induces a phase reset of the endogenous alpha brain oscillations of the sensory cortices, with a subsequent phase alignment, an increase in amplitude and synchronization to the external stimulation frequency. Such entrainment effects typically persist after the stimulation offset for three alpha cycles (entrainment after-effect; grey shaded area). Adapted from Gallina et al., 2023.

3.2. Alpha-band stimulation effects on neural and perceptual activity

From an empirical standpoint, co-registration of TMS/tACS with electrophysiological measures (i.e., EEG/MEG) has demonstrated that transcranial rhythmic stimulation can effectively synchronize the phase of alpha neural oscillations, modulating the excitability of both the visual (Helfrich et al., 2014; Battaglini et al., 2020; Di Gregorio et al., 2022; Trajkovic et al., 2023) and audiovisual systems (Helfrich et al., 2014; Ghiani et al., 2021; Bertaccini et al., 2023), aligning their alpha oscillatory systems with the stimulation frequency. For instance, it has been shown that rhythmic TMS administered at alpha frequency over occipito-parietal areas can entrain alpha oscillations, with concurrent fluctuations observable in perceptual performance (Romei et al., 2010; Thut et al., 2011a; Di Gregorio et al., 2022; Trajkovic et al., 2023). Similarly, tACS studies have demonstrated the effectiveness of this technique in synchronizing brain oscillations, with resonance effects observed in behavioral performance (Helfrich et a., 2014; Witkowski et al., 2016; Herring et al., 2019; Battaglini et al., 2020; Ghiani et al., 2021). For example, tACS administered at faster or slower frequencies of alpha oscillations has been shown to shrink or expand the AV temporal binding window, respectively, affecting audiovisual temporal acuity, and ultimately supporting the idea that the frequency of neural oscillatory activity in the alpha band can determines the sensory sampling rate (Cecere et al., 2015; Lakatos et al., 2019; Venskus et al., 2021). However, despite the demonstrated efficacy in entraining brain oscillations, electrical and magnetic artifacts deriving from the application of transcranial stimulations (e.g., TMS, tACS) can contaminate the neural oscillatory activity measurable through EEG/MEG recordings, making it challenging to disentangle the effects of stimulation on physiological oscillatory activity from potential artifacts (Noury et al., 2016; Thut et al., 2017; Liu et al., 2018; Noury & Siegel, 2017, 2018). Relatedly, somatosensory sensations experienced during transcranial rhythmic stimulation (e.g., tactile sensations or retinal phosphenes) can confound its effects on both electrophysiological and perceptual activity, potentially driving synchronization effects indirectly through sensory entrainment (Schwiedrzik, 2009; Schutter & Hortensius, 2010; Kar & Krekelberg, 2012; Asamoah et al., 2019; Lakatos et al., 2019).

In this realm, despite the potential effectiveness of methodological approaches employing rhythmic non-invasive transcranial brain stimulation (e.g., TMS, tACS), evidence from sensory entrainment techniques, such as visual, auditory, and audiovisual rhythmic stimulation, has proven to be a valuable method for directly modulating neural oscillations, providing significant insights into the mechanisms of neural entrainment. Alpha-band sensory entrainment has proven to be an exceptionally effective tool for modulating visual and audiovisual behaviour by targeting visual and auditory oscillatory networks and exploiting both intra- and cross-modal interactions between sensory systems (Spaak et al., 2014; Ronconi et al., 2016; Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2024). A fundamental aspect of sensory entrainment lies in its ability to enhance sensory inputs that align with the temporal structure of rhythmic stimulus streams, facilitating the development of temporal predictions regarding sensory patterns in the environment (Drake et al., 2000; Busch et al., 2009; Mathewson et al., 2010; Rohenkohl et al., 2011; VanRullen & Macdonald, 2012; De Graaf et al., 2013; Spaak et al., 2014; Gray & Emmanouil, 2019; Marsicano et al., 2024). As a result, when visual stimuli are presented at consistent time intervals, they evoke similar rhythmic effects, as the regular sequence of stimuli tends to enhance the processing of subsequent visual inputs that are temporally aligned with the previous rhythmic stream (Drake et al., 2000; Rohenkohl et al., 2012; De Graaf et al., 2013; Spaak et al., 2014). Additionally, another advantage of sensory entrainment relies on the possibility to be administered on a trial-by-trial basis during the pre-stimulus period, contrasting with prior tACS/TMS studies that predominantly investigated the "online" effects of alpha-band rhythmic stimulation on perceptual performance (e.g., Cecere et al., 2015; Venskus et al., 2021), thus facilitating the investigation of the "offline" effects of entrainment on neural oscillations, focusing on the induced-effects observable immediately after the stimulation offset.

The following sections will discuss evidence demonstrating the effectiveness of alpha-band sensory entrainment, in its different sensory modalities (i.e., visual, auditory, audiovisual), in synchronizing endogenous alpha oscillatory activity with concurrent modulations of perceptual performance.

3.3. Neural and perceptual effects of alpha-band sensory entrainment

Over the past decades, alpha-band unisensory (i.e., visual and auditory) and multisensory (i.e., audiovisual) entrainment have been effectively employed in various experimental studies, demonstrating their ability to induce significant changes in alpha-band spectral measures within functionally interconnected networks, both within and across the visual and auditory systems, resulting in concurrent enhancements in perceptual performance (Mathewson et al., 2011; Spaak et al., 2014; Gray & Emmanouil, 2019; Keitel et al., 2018, 2019; Wiesman & Wilson, 2019; Marsicano et al., 2024; Gallina et al., 2023; Szaszkó et al., 2024; Fakche & Duguè, 2024). Alpha-band entrainment stimulation operates on the principle that the initial stimulus in a sensory sequence induces a phase reset of ongoing alpha oscillations, aligning endogenous neural activity with the rhythm of the external stimulation, which leads to fluctuations in perceptual performance, where specific temporal phases of the synchronized rhythmic structure are associated with optimal windows of information processing (e.g., De Graaf et al., 2013; Spaak et al., 2014). In this context, the application of brief trains of alpha-band rhythmic stimulation (i.e., ~0.5 to 5 seconds) has reliably demonstrated the ability to synchronize brain oscillations with external stimuli, resulting in an enhancement of the ongoing alpha oscillations' power at occipito-parietal scalp locations (Mathewson et al., 2011; Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Szaszkó et al., 2024; Fakche & Dugué, 2024), thus strengthening the idea that neural oscillatory populations can be effectively entrained when stimulation is tuned to their resonant preferential frequency (Regan, 1982; Pikovsky et al., 2003; Thut et al., 2012). Crucially, these findings indicate that the transient effects induced by alpha-band sensory entrainment do not revert to baseline power levels immediately following the end of the stimulation. Instead, research has demonstrated that these effects can persist for ~3-5 alpha cycles (Spaak et al., 2014; Wiesman & Wilson, 2019), leading to a corresponding modulation in the temporal resolution of the sensory system, which can occur either in-phase or out-of-phase with the stimulation frequency (De Graaf et al., 2013; Spaak et al., 2014; Marsicano et al., 2024).

Collectively, these experimental findings provide consistent evidence for the causal influence of sensory rhythmic stimulation on enhancing both neural and perceptual alpha-band activity, operating within and across sensory modalities. In the following sections, the evidence regarding the effects of alpha-band sensory entrainment employing different sensory modalities of stimulation will be examined, specifically addressing findings from unisensory (i.e., visual and auditory) and cross-modal entrainment (i.e., audiovisual).

3.3.1. Alpha-band visual entrainment

Given the pivotal role of alpha oscillatory activity in sampling visual information, the majority of evidence investigating the effects of alpha-band sensory entrainment on neural activity and perceptual performance has predominantly employed rhythmic stimulation through the visual sensory modality (Mathewson et al., 2010, 2011, 2012; De Graaf et al., 2013; Spaak et al., 2014; Ronconi et al., 2016a, 2016b; Kizuk & Mathewson, 2017; Ronconi & Melcher, 2017; Ronconi et al., 2018; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Kawashima et al., 2022; Fakche & Duguè, 2024; Szaszkó et al., 2024). Collectively, these findings suggest that administering during the pre-stimulus period brief trains of alpha-band visual rhythmic stimulation (0.5–5 seconds) entrains alpha oscillatory activity, aligning its phase with the external stimulation, and leading to an increase in the power of endogenous alpha oscillations during the entrainment period (Mathewson et al., 2011; Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Szaszkó et al., 2024; Fakche & Duguè, 2024). The most pronounced entrainment-induced effects were generally observed over occipito-parietal brain regions, which correspond to the neural network most active at alpha-band (Mathewson et al., 2012; Spaak et al., 2014; Gray & Emmanouil, 2019; Keitel et al., 2018, 2019), supporting the idea that neural oscillatory populations can be functionally tuned when stimulated at their resonant frequency (Regan, 1982; Pikovsky et al., 2003; Gallina et al., 2023). Notably, the effects induced by alpha-band sensory entrainment do not immediately revert to baseline oscillatory activity after the stimulation offset, but have been observed to persist for ~3-5 alpha cycles (~500 ms; Spaak et al., 2014; Wiesman & Wilson, 2019), resulting in a corresponding rhythmic fluctuations of perceptual performance, either in-phase or anti-phase relative to the stimulation frequency (De Graaf et al., 2013; Spaak et al., 2014).

Within this framework, several studies have demonstrated that alpha-band visual entrainment can synchronize endogenous brain oscillations and improve visual detection and perceptual sensitivity, by impacting on visuo-spatial attentional mechanisms. For instance, by combining psychophysical methods with EEG techniques, it has been shown that visual stimuli presented periodically at alpha-band frequencies (i.e., ~10 Hz) for short intervals (i.e., ~1 second) during the pre-stimulus period of visual detection tasks effectively induce phase alignment and an increase in alpha-band power and inter-trial phase coherence (ITPC) in parieto-occipital scalp regions (Mathewson et al., 2010, 2012; Spaak et al., 2014; Kizuk & Mathewson, 2017; Wiesman & Wilson, 2019). These effects were observed to persist for ~3-5 cycles after the stimulation offset, along with improved detection accuracy and perceptual sensitivity for targets presented in phase with the preceding rhythmic-alpha visual streams (Mathewson et al., 2010; 2012; Spaak et al., 2014; Kizuk & Mathewson, 2017; Ronconi & Melcher, 2017; Keitel et al., 2018, 2019; Wiesman & Wilson, 2019; Gray & Emmanouil, 2019). Consistently, studies using visual cueing paradigms have shown that brief trains of alpha-band visual entrainment (i.e., 10 Hz) increased alpha power and ITPC in occipito-parietal scalp regions contralateral to the visual stimulation, with concurrent fluctuations in perceptual performance, as reflected in improved visual discrimination in the invalid condition when visual targets were presented in-phase with the rhythmic stimulation (De Graaf et al., 2013; Spaak et al., 2014). More recently, Fakche and Duguè (2024) used visual entrainment to further elucidate the role of alpha oscillations in shaping perceptual cycles. Their findings demonstrated that neural oscillatory activity aligned with both theta and alpha entrainment frequencies administered in their study, resulting in periodic modulation of visual detection performance. However, the optimal phase for target detection shifted as the target's distance from the entrainment stimuli increased, and this phase shift was observed only at alpha stimulation frequencies, not at theta frequencies, indicating that perceptual cycles can travel across the visual cortex via alpha oscillations, thus suggesting that alpha rhythms play a key role in spatially organizing visual perception (Fakche & Duguè, 2024).

Interestingly, alpha-band visual entrainment has contributed to disentangling the causal role of alpha oscillations in visuospatial attentional processes, specifically in the functional inhibition of irrelevant visual information. In a recent study, Wiesman and Wilson (2019) employed an alpha-band stimulation protocol at a frequency of 10 Hz for 1.5 seconds, revealing greater alpha power synchronization and increased ITPC compared to a control condition using non-alpha rhythmic stimulation at 30 Hz. Notably, only alpha-band entrainment led to a reduction in the congruency effect at the behavioural level, indexed by a smaller difference in discrimination rates between congruent and incongruent trials in an adapted version of the arrow-based Eriksen flanker paradigm. Similarly, Szaszkó and colleagues (2024) investigated how alpha-band 10 Hz rhythmic visual stimulation affects the suppression of attention capture by irrelevant but salient visual cues. They found evidence of cue suppression through increased spectral power and ITPC at the harmonic of the alpha stimulation frequency (i.e., 20 Hz). These findings strongly corroborate the hypothesized link between alpha oscillations and the active inhibition of irrelevant sensory information, highlighting the potential of sensory entrainment to causally disentangle the role of alpha neural oscillations in information processing. In contrast, a recent web-based study by de Graaf and Duecker (2022) investigated whether rhythmic visual stimulation at the alpha frequency (i.e., 10 Hz) could influence visuo-spatial attentional mechanisms and visual target discrimination. The aim was to entrain contralateral brain oscillations relative to the visual target, thus increasing alpha synchronization to impair visual discrimination performance by enhancing inhibitory mechanisms. However, alpha-band entrainment did not significantly affect task performance, but without M/EEG data, it is unclear whether the stimulation effectively entrained endogenous alpha oscillations.

Furthermore, alpha-band sensory entrainment has been employed to explore the relationship between alpha oscillations and the temporal resolution of the visual system. In a recent study by Gray and Emmanouil (2019), alpha-band entrainment was administered at the lower (i.e., 8.3 Hz) and upper (i.e., 12.5 Hz) boundaries of the alpha frequency range, with the aim of improving visual temporal integration or segregation, respectively, in a visual integration task where stimuli were presented at varying time lags. However, although their results demonstrated synchronization of oscillatory power and ITPC in response to both alpha stimulations, the entrainment did not induce significant behavioural modulations on visual temporal acuity. This result contrasts with previous studies employing TMS (Di Gregorio et al., 2022; Trajkovski et al., 2023) and tACS (Cecere et al., 2015; Venskus et al., 2021) techniques, which demonstrated synchronization of the alpha oscillatory activity to the external stimulation delivered at participant's IAF, accompanied by concurrent modulations in visual temporal acuity. Indeed, one potential explanation for this null finding could be that the stimulation frequencies were fixed across participants, whereas higher entrainment of alpha brain oscillations tends to occur when the stimulation is tailored to each participant's IAF (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022).

Overall, these converging results demonstrate that short trains of visual alpha-band entrainment can induce transient, functionally relevant modulations in alpha oscillatory activity, resulting in enhanced perceptual performance. However, inconsistent findings suggest that the specific stimulation protocols, task demands, and behavioural measures employed to assess perceptual performance may be crucial in revealing the full extent of entrainment-induced effects.

3.3.2. Alpha-band auditory entrainment

Although alpha oscillatory activity is predominantly observed in the occipito-parietal visual regions (Rosanova et al., 2009), multiple findings have emphasized its role in enhancing auditory information encoding, with evidence indicating the presence of a specific auditory alpha oscillatory network that is selectively influenced by auditory inputs, rather than by visual information (Gomez-Ramirez et al., 2011; Frey et al., 2014). This evidence strongly suggests that alpha oscillatory activity can be entrained through auditory alpha-band stimulation, leading to both uni- and cross-modal modulations of alpha oscillatory activity in auditory and visual brain regions. In this context, it has also been observed that auditory inputs can induce a phase reset of ongoing neuronal oscillations not only within the auditory brain regions but also across sensory modalities (i.e., from auditory to visual areas), enhancing the activity of endogenous alpha oscillations in other sensory cortices through subthreshold depolarization and by synchronizing ongoing oscillatory activity across functionally interconnected nodes of sensory brain areas (Senkowski et al., 2008; Landau & Fries, 2012; Fiebelkorn et al., 2013; Romei et al., 2012; Cecere et al., 2016, 2017; Bauer et al., 2021). For instance, several studies have demonstrated that the cross-modal phase reset mechanism of ongoing alpha oscillations in the visual system (i.e., from auditory to visual), leads to improvements in visual performance and induces rhythmic fluctuations in parieto-occipital alpha oscillations when visual stimuli are phase-locked to the auditory reset input (Lakatos et al., 2007, 2009; Kayser et al., 2008; Naue et al., 2011; Thorne et al., 2011; Romei et al., 2012; Miller et al., 2013; Mercier et al., 2013; Cecere et al., 2016, 2017). Indeed, the phase reset of visual brain oscillations induced by auditory stimuli is hypothesized to function as an adaptive low-level, attentional mechanism, capable of alerting the visual system to incoming sensory inputs, and thus enhancing its efficiency (Miller et al., 2013; Mercier et al., 2013; Cecere et al., 2016, 2017).

From an empirical standpoint, leveraging the cross-modal phase-reset mechanism induced by auditory stimuli on alpha oscillations, several studies have employed auditory alpha-band stimulation to explore its effects on perceptual performance (Ronconi et al., 2016a, 2016b; Kawashima et al., 2022; Table 1). For example, Ronconi and colleagues (2016a) investigated whether brief (~2 s) auditory or visual alpha-band entrainment (i.e., 10 Hz), administered on a trial-by-trial basis during the pre-stimulus period, could reduce the magnitude of the Attentional Blink (AB) effect (Shapiro et al., 1997; Martens and Wyble, 2010). In detail, it was expected that alpha entrainment could enhance the accuracy of detecting a second visual target (T2) presented after a first visual target (T1) in a rapid serial visual presentation (RSVP) stream. Intriguingly, their findings revealed that only alpha-band entrainment administered via the auditory modality, and not the visual modality, effectively enhanced the detection of the T2 visual target. Consistent with prior research demonstrating an auditory phase reset of endogenous alpha oscillations in the visual system (Ghazanfar & Schroeder, 2006; Senkowski et al., 2008; Lakatos et al., 2009; Cecere et al., 2016, 2017; Bauer et al., 2021), the authors hypothesized that the auditory rhythmic stimulation enhanced target detection by synchronizing ongoing alpha oscillations in the visual brain areas (Ronconi et al., 2016a). These findings suggest that, given the auditory system's higher temporal resolution compared to the visual system and its greater sensitivity to rhythmic patterns (Lakatos et al., 2009; van Wassenhove, 2013), auditory entrainment may induce stronger neural modulations through cross-modal auditory-to-visual phase reset mechanisms. In line with this hypothesis, additional evidence has demonstrated that auditory rhythmic temporal sequences can modulate the perception of flickering visual stimuli (Shipley, 1964; Escoffier et al., 2015), likely relying on cross-modal auditory-to-visual phase reset phenomena (Ghazanfar & Schroeder, 2006; Senkowski et al., 2008; Lakatos et al., 2009; Bauer et al., 2020). In a subsequent study, Ronconi and colleagues (2016b) provided EEG evidence supporting this hypothesis by replicating their behavioural findings on the effectiveness of alpha-band auditory entrainment in reducing the Attentional Blink (AB) effect, while also revealing a correlation between increased posterior and frontal alpha activity during the rhythmic auditory stimulation and improved detection of the T2 visual target.

Overall, this empirical framework suggests that alpha-band auditory entrainment can serve as an effective tool for entraining alpha brain oscillations not only within auditory regions but also across sensory brain areas (e.g., visual brain areas), potentially through cross-modal phase-reset phenomena of alpha neuronal oscillatory activity, further indicating that endogenous oscillatory activity can be influenced by sensory events to functionally modulate perceptual performance.

3.3.3. Alpha-band audiovisual entrainment

As highlighted in the previous sections, considering the cross-modal phase-reset mechanisms of alpha oscillations within the functionally interconnected nodes of the auditory and visual sensory systems (Ghazanfar & Schroeder, 2006; Senkowski et al., 2008; Lakatos et al., 2009; Cecere et al., 2016, 2017; Bauer et al., 2021), it is conceivable to postulate that alpha-band multisensory entrainment administered through audiovisual (AV) modality may enhance the entrainment effects of alpha neural oscillations compared to unisensory stimulation, leading to more pronounced functional modulations of perceptual performance.

At the neural level, compelling empirical evidence in this context was provided by the pioneering findings of Teplan and colleagues across several studies (Teplan et al., 2003, 2006a, 2006b, 2011), which demonstrated the ability of AV alpha-band stimulation to synchronize endogenous oscillatory activity. Their research revealed an increase in alpha power and ITPC that was not only short-lived and observable in parieto-occipital areas (Teplan et al., 2006a), but also persisted after the offset of stimulation (i.e., lasting up to 20 minutes post-stimulation), with effects extending to both ipsilateral and contralateral posterior, central and frontal brain regions (Teplan et al., 2006b). Similarly, it has been shown that AV entrainment delivered at participants' IAF can lead to increases in both alpha power and ITPC, with significant effects lasting for up to 30 minutes following the offset of the entrainment stimulation (Timmermann et al., 1999; Frederick et al., 2005), while higher baseline resting-state alpha power has been associated with prolonged entrainment effects on alpha oscillations (Rosenfeld et al., 1997).

However, despite these studies demonstrated the effectiveness of AV entrainment on neural oscillatory activity, it is only in the last decade that alpha-band AV entrainment has been systematically employed as an experimental tool to uncover the effects of alpha-band stimulation on perceptual and cognitive performance. In this regard, Ronconi and Melcher (2017) investigated whether an AV entrainment administered in the pre-stimulus interval at the alpha (i.e., upper alpha: 11.5 Hz; lower alpha: ~8.5 Hz), theta (~6.5 Hz) and beta (~15 Hz) frequencies could shape visual temporal perception, affecting the temporal resolution of the visual system in a visual temporal integration/segregation task. The rationale behind this study relied on the idea that the speed of parieto-occipital alpha oscillations can reflects the temporal sampling capacity of the visual system (Cecere et al., 2015; Cooke et al., 2019; Venskus & Hughes, 2021; Marsicano et al., 2024; Ronconi et al., 2023; Samaha & Romei, 2024), and it aimed to investigate whether stimulation at the lower (i.e., ~8.5 Hz) or upper (11.5 Hz) boundaries of the alpha band could enhance integration or segregation performance, respectively. Overall, their findings revealed that while AV alpha-band entrainment as compared to entrainment at other frequencies (i.e. theta, beta) improved temporal segregation, enhancing the temporal resolution of the visual system, the comparison between slower and faster alpha stimulations showed no significant difference in the temporal segregation/integration performance. This result contrasts with prior findings indicating that faster alpha frequency is generally associated with an enhanced sensory sampling of visual information (Cecere et al., 2015; Cooke et al., 2019; Venskus & Hughes, 2021; Marsicano et al., 2024; Ronconi et al., 2023; Samaha & Romei, 2024). A potential explanation for this null result could be that the researchers did not tailor the stimulation frequencies to the individual participants' IAF. Accordingly, the slower and faster alpha stimulation frequencies may have fallen outside the participants' IAF range, resulting in the inability of AV rhythmic stimulation to effectively align ongoing alpha oscillations through neural entrainment mechanisms (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022). To address this potential methodological concern, Ronconi and colleagues (2018) conducted a subsequent study in which they administered audiovisual entrainment tailored at IAF -2 Hz and IAF +2 Hz during the pre-stimulus interval of a visual temporal integration/segregation task. Consistent with prior evidence, their findings revealed that faster and slower alpha AV entrainment induced opposing effects on perceptual performance observable at the stimulation offset: AV entrainment delivered at IAF +2 Hz enhanced segregation performance, while IAF -2 Hz stimulation improved integration mechanisms. Additionally, the accuracy of participants' performance in segregation and integration tasks was densely sampled over time to examine whether the stimulation frequency could induce a shift in the alpha peak of behavioural oscillations. Their findings indicated a shift in the averaged alpha peak toward the stimulation frequency, accompanied by a concurrent increase in phase concentration, highlighting faster fluctuations following IAF +2 Hz stimulation compared to IAF -2 Hz (Ronconi et al., 2018).

Although this evidence has demonstrated the efficacy of AV entrainment in modulating unisensory (visual) temporal perception, it is still unclear whether alpha-band sensory stimulation can shape the temporal resolution of the AV temporal binding system. In a recent study that will be discussed in detail in the following sections (Marsicano et al., 2024; see Chapter 4), we employed an AV entrainment experimental paradigm in which participants were asked to report their perceived synchrony of visual and auditory stimuli presented at different time intervals. Importantly, during the pre-stimulus interval of the AV simultaneity judgment (SJ) task, AV entrainment was applied for a brief period (~2 seconds) at the lower (~8.5 Hz) and upper boundaries (~12 Hz) of alpha oscillations. Collectively, our findings indicated that upper alpha sensory stimulation enhanced AV temporal perception by reducing perceived simultaneity compared to the lower alpha conditions, thus aligning with previous findings linking the speed of alpha activity to the temporal resolution of the AV system (Cecere et al., 2015; Cooke et al., 2019; Venskus & Hughes, 2021; Ronconi et al., 2023), and strongly supporting the efficacy of AV alpha-band entrainment in shaping AV perceptual performance.

Overall, despite empirical evidence supporting the efficacy of alpha-band AV entrainment in functionally modulating perceptual performance being still scarce, these findings seem to support the existence of functional modulations following AV alpha-band entrainment (e.g., Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2024).

3.4. A World Out of Sync: Interindividual differences in neural entrainment

Imagine of walking into a lively party where music is playing, people are dancing, and conversations are buzzing. Now, imagine that the music is suddenly stripped of its beat, and the dancers are all moving in random, uncoordinated motions. The conversation around you is similarly fragmented, people’s voices lack cadence, words collide without flow, and responses lag unpredictably. This is a dystopian scenario where rhythmicity is absent from human experience, making synchronization between individuals and their environment impossible. Without neural entrainment, this is what life would feel like. In such a scenario, the clarity of language would fade, understanding others’ intentions would take longer, and the interpersonal synchronization would be shattered into unrelated gestures. Just as dancers need music’s steady beat to synchronize their steps, our brains rely on external rhythmic sensory patterns to align neural oscillatory activity with the sensory world around us (Lakatos et al., 2019; Gallina et al., 2023). The natural alignment between our brain oscillatory activity and the rhythms of speech, music, or even simple sensory patterns enhances our ability to anticipate and interact efficiently with the environment, ensuring that sensory input falls within optimal neural phases of information processing (De Graaf et al., 2013; Spaak et al., 2014; Ronconi et al., 2018; Lakatos et al., 2019; Marsicano et al., 2024).

However, while neural entrainment is an adaptive feature of the human brain, high interindividual variability in the ability to functionally synchronize with the sensory environment is often observed both in neurodevelopmental and psychiatric disorders, and even in the general population (Lakatos et al., 2019). This is evident, for example, in Autism Spectrum Disorder (ASD) and Schizophrenia Spectrum Disorder (SSD), and in neurotypical individuals showing higher ASD- and SSD-like traits (Lakatos et al., 2019; Gallina et al., 2023; Ampollini et al., 2024), where individuals often exhibit an impaired ability to entrain to rhythmic sensory sequences, displaying reduced neural and behavioural synchronization to sensory rhythmic streams (Riečanský et al., 2010; Ghuman et al., 2017; Northoff, 2018; Noel & Stevenson, 2018; Bharathi et al., 2019; Beker et al., 2021; Black et al., 2024). Although such difficulty in encoding rhythmic sensory patterns can often present with similar phenotypes, these atypicalities may stem from different neural oscillatory profiles (Noel & Stevenson, 2018; Tarasi et al., 2022).

For example, in individuals with higher ASD features, the difficulty in synchronizing neural activity to rhythmic sequences may be associated with deficits in generating functional predictions from the rhythmic structure of the sensory environment (Pellicano & Burr, 2012; Coll et al., 2020; Vishne et al., 2021; Cannon et al., 2021). Individuals with higher ASD features might place excessive emphasis on prediction errors, leading to a perception of top-down predictions as incorrect (Chan & Naumer 2014; Van de Cruys et al. 2014; Karvelis et al., 2018; Coll et al., 2020). This atypicality in ASD may arise from anomalous top-down alpha-band connectivity, hypothesized to be responsible for transmitting predictive information (Seymour et al., 2019; Tarasi et al., 2022). Thus, every sensory experience is perceived as novel, which ultimately lead to difficulty in generating reliable sensory representations from rhythmic streams of sensory stimuli (Van Boxtel & Lu 2013; Van de Cruys et al. 2014; Lawson et al., 2017; Karvelis et al., 2018; Tarasi et al., 2022). This impaired synchronization of oscillatory neural dynamics typically results in atypical uni- and multisensory processing, particularly in the temporal integration of sensory stimuli, representing one of the primary sensory deficits in ASD and hypothesized to underlie its key socio-communicative atypicalities (Van de Cruys et al. 2014; Lawson et al., 2017; Karvelis et al., 2018).

Anomalous perceptual experiences and clinical symptoms in individuals with higher SSD characteristics have been linked to a failure in exhibiting oscillatory entrainment to attended rhythmic sensory streams (Jonsson & Sjöstedt, 1973; Lakatos et al., 2013; Silverstein et al., 2015; Northoff, 2018). However, in SSD, such sensory encoding atypicalities may arise from anomalies in bottom-up oscillatory dynamics (Tarasi et al., 2022), where greater weight is given to prior representations and less to incoming sensory inputs, resulting in a dysfunctional integration of sensory information into prior models (Sterzer et al., 2019; Liddle & Liddle, 2022; Tarasi et al., 2022). Contrary to ASD, sensory atypicalities in individuals exhibiting higher SSD features may stem from increased top-down alpha connectivity (Schmack et al., 2013) and anomalous alpha speed (Uhlhaas & Singer, 2015; Ramsay et al., 2021), which can result in a greater reliance on predictive information and prior knowledge, thus leading to an atypical sampling of sensory information that biases sensory cortex activity (Tarasi et al., 2022).

Hence, based on the findings outlined above, which highlighted interindividual differences in neural entrainment, when neural oscillations are not aligned to the temporal structure of relevant sensory streams, this often results in impaired sensory processing and chaotic perceptual experiences (Lakatos et al., 2019). Thus, neural entrainment represents an essential mechanism for processing sensory and internal information, and a failure in this mechanism can lead to widespread perceptual, cognitive and socio-communicative impairments.

3.5. Scope of the present work

Overall, the findings from the alpha-band entrainment studies discussed in the previous sections strongly support the idea that alpha oscillatory activity can be externally modulated, with concurrent functional enhancements in perceptual performance achieved through sensory rhythmic stimulations delivered via unisensory (i.e., visual or auditory entrainment) and multisensory (i.e., audiovisual entrainment) modalities. However, despite its promising potential, some key aspects of the induced-effects of alpha-band sensory entrainment on neural oscillations and perceptual performance are still unexplored.

First, although the efficacy of AV entrainment in shaping visual temporal integration and segregation processes has been demonstrated, it remains unclear whether alpha-band sensory stimulation can similarly influence the temporal resolution of the AV temporal binding system, as distinct neurocomputational mechanisms regulate uni- and multisensory perception (Senkowski et al., 2008; Lakatos et al., 2009; Cecere et al., 2016, 2017; Bauer et al., 2020). In Chapter 4, the results of a study aimed at investigating the effects of AV sensory entrainment on AV temporal binding mechanisms will be discussed. Furthermore, Chapter 5 will explore how the effects of alpha-band sensory entrainment on AV temporal binding processes may be driven by interindividual differences in sensory, cognitive, and socio-communicative features of the personological profile in neurotypical individuals exhibiting varying degrees of ASD- and SSD-like traits. Indeed, as previously discussed, interindividual differences are often overlooked in neural entrainment studies, despite the presence of high variability in the ability to functionally entrain to rhythmic sensory sequences, which ultimately can lead to differential behavioral and neural outcomes (Ghuman et al., 2017; Northoff, 2018; Noel & Stevenson, 2018; Lakatos et al., 2019; Beker et al., 2021; Black et al., 2024).

Furthermore, whether alpha-band stimulation administered via the visual modality can induce long-lasting effects on neural and perceptual performance remains unexplored. Indeed, previous research has predominantly employed short-lasting trains of rhythmic sensory stimulation (~0.5–5 seconds) on a trial-by-trial basis, resulting in transient neural and perceptual effects that typically persist only for a brief period following the end of the entrainment (~100–550 milliseconds; Mathewson et al., 2012; Spaak et al., 2014; Kizuk & Mathewson, 2017; Wiesman & Wilson, 2019; Gray & Emmanouil, 2019), leaving unresolved the question of whether persistent modulations of neural oscillations and perceptual performance can be obtained via more prolonged alpha-band sensory stimulation.

Relatedly, the optimal properties of rhythmic stimulation for effectively modulating alpha oscillatory activity remain debated. While earlier studies often applied fixed alpha frequencies, prior research suggests participants' IAF stimulation may enhance entrainment modulations (Thut et al., 2011a; Notbohm et al., 2016), but remains unclear whether deviations from may IAF lead to differential outcomes. Furthermore, previous studies employing short-term entrainment have demonstrated that these effects are primarily observed in posterior brain areas contralateral to the stimulation (Thut et al., 2011a; Spaak et al., 2014), but it is still unclear whether prolonged alpha-band entrainment, unlike short-term stimulation, may induce more widespread effects strengthening alpha communications over the scalp (Zhang et al., 2018; Alamia & VanRullen, 2019, 2024). In the following sections, to address these questions, the results of two different studies will be presented, in which the effects of alpha-band visual entrainment on neural oscillatory activity (Chapter 6) and visual detection performance (Chapter 7) were investigated, utilizing both EEG and psychophysical measurements.

Chapter 4

Alpha-band audiovisual entrainment improves audiovisual temporal acuity[1]

4.1. Introduction

An essential feature of human cognition is the accurate perception of the multiple sensory inputs coming from the environment, requiring our brain to encode stimuli from different sensory modalities on the basis of their spatio-temporal features (Spence, 2007; Stein & Stanford, 2008). The temporal features of sensory stimuli drive multisensory integration processes, determining the functional integration of sensory inputs having the same origin, and the adaptive segregation of information coming from separate events/objects (Stevenson et al., 2013; Murray et al., 2016; Pasqualotto et al., 2016).

In the case of audiovisual (AV) temporal perception, visual and auditory sensory inputs are transmitted from the external environment to sensory cortical areas at different propagation speeds, requiring different sensory and neural processing times (for example, see: Recanzone, 2009; Vroomen & Keetels, 2010; Noel et al., 2016). A certain degree of temporal tolerance of AV asynchrony has a functional value for constructing coherent sensory percepts (Wallace & Stevenson, 2014), reflecting a key aspect for functional multisensory integration. Indeed, even when AV stimuli are not physically synchronous, they are perceptually bound when presented asynchronously within a limited temporal range, a process that is better described in the construct of the "temporal binding window" (TBW; Colonius & Diederich 2004; Noel et al., 2016; Stevenson et al., 2017a). The TBW is a probabilistic measure, indexing the likelihood that two sensory stimuli are perceived as a unique percept across a range of stimulus onset asynchronies (SOAs). The current hypothesis is that a narrow TBW represents higher perceptual temporal acuity, with high AV temporal acuity being linked to greater detection abilities of sensory stimuli (Lovelace et al., 2003; Diederich & Colonius, 2015), higher-order

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[1] The data, figures and tables presented in this study were previously published in: Marsicano, G., Bertini, C., & Ronconi, L. (2024). Alpha-band sensory entrainment improves audiovisual temporal acuity. *Psychonomic Bulletin & Review, 31*(2), 874-885.

cognitive processes (e.g., speech perception; Grant et al., 2000; Bishop & Miller, 2009), and complex verbal and non-verbal problem solving (Zmigrod & Zmigrod, 2016).

Interestingly, recent evidence revealed that occipital brain oscillations in the alpha band (8–12 Hz) can represent a key neural mechanism to orchestrate temporal integration/segregation of sensory stimuli, as it would reflect the temporal unit of AV temporal perception (Bastiaansen et al., 2020; Cecere et al., 2015; Keil & Senkowski, 2018; Cooke et al., 2019; Ronconi et al., 2023). The current idea is that two sensory inputs are integrated when they fall into the same alpha cycle. On the contrary, two sensory inputs are segregated when presented in different alpha cycles, leading to higher temporal acuity (Samaha & Postle, 2015; Bastiaansen et al., 2020; Cecere et al., 2015; Migliorati et al., 2020). In line with this framework, recent evidence has shown that individual alpha frequency (IAF) negatively correlates with the width of visual (Samaha & Postle, 2015) and AV TBWs (Cecere et al., 2015; Venskus & Hughes, 2021; Ronconi et al., 2022). To disclose the causal link between alpha oscillations and TBWs, non-invasive brain stimulation (NIBS) techniques have been used in few studies in order to demonstrate that stimulations at faster or slower frequencies of alpha oscillations can shrink or expand, respectively, the width of the TBW, modulating AV temporal perception (Cecere et al., 2015; Venskus et al., 2021). Interestingly, similarly to what happens for transcranial Alternating Current Stimulation (tACS), it has been shown that the application of a rhythmical sensory force can act as "sensory entrainment", inducing a phase alignment to the external rhythmical stimulation of the endogenous brain rhythms, that start to oscillate at the same stimulation frequency, thus resulting in resonance phenomena in neural and perceptual activity (De Graaf et al., 2013; Lakatos et al., 2019; Ronconi et al., 2016a, 2016b; Spaak et al., 2014; for a review, see: Haegens & Golumbic, 2018). Regarding the implementation of sensory entrainment with the aim to shape temporal perception, the results are currently mixed. In a first study of Ronconi and Melcher (2017) in the unisensory (visual) domain, results showed that although alpha sensory entrainment as compared with entrainment at other frequencies (i.e., theta, beta) improved temporal segregation, the comparison between slower vs. faster alpha showed an opposite (but non-significant) trend compared with findings of previous tACS evidence (Cecere et al., 2015; Venskus et al., 2021). In a subsequent study, it has been shown that AV stimulation at the upper boundary of the alpha band improves segregation of visual stimuli, but only for a short period after the stimulation offset (Ronconi et al., 2018). Although this evidence suggests a relative efficacy of audiovisual entrainment in modulating the temporal perception in unisensory (visual) domain, whether alpha-band sensory stimulation can shape the width of AV TBW remains unknown. Given the different neurocomputational mechanisms that orchestrate uni- and multi-sensory perception (Lakatos et al., 2007, 2009; Kayser et al., 2008; Naue et al., 2011; Thorne et al., 2011; Mercier et al., 2013; Cecere et al., 2016, 2017) alpha-band sensory entrainment on AV binding mechanisms of sensory inputs could have different effects with respect to unisensory visual temporal perception. Visual and auditory signals require different neural processing timings (Noel et al., 2016; Vroomen & Keetels, 2010), and these temporal differences characterize the complex dynamic of how AV stimuli interact in order to be temporally integrated/segregated (Recanzone, 2009). Visual and auditory stimuli induce a "phase reset" of neural oscillations within (i.e., from visual stimuli to visual areas; Landau & Fries, 2012) and also across sensory modalities (i.e., from auditory stimuli to the visual areas; Fiebelkorn et al., 2013; Romei et al., 2012), enhancing the oscillatory activity in the primary sensory cortices of other sensory modalities (Ghazanfar & Schroeder, 2006; Senkowski et al., 2008; Bauer et al., 2020). Moreover, the cross-modal phase reset dynamics underlying the binding mechanisms of AV stimuli is strongly influenced by the leading sense (Thorne & Debener, 2014; Cecere et al., 2016). In the condition in which auditory stimuli precede visual ones (Auditory Leading; AL), the auditory stimulus resets the phase of the brain oscillations in the visual cortex to anticipate the imminent presentation of the visual input, ultimately increasing the efficiency in AV integration/segregation processes (i.e., narrow and less malleable TBW). On the contrary, the visual leading (VL) condition might be driven by higher-level prediction mechanisms, resulting in an increased perception of synchrony of the AV stimulus pairs (i.e., a large and more plastic TBW; Thorne & Debener, 2014; Cecere et al., 2016, 2017). From another perspective, the differing temporal resolutions of the visual and auditory systems can explain the difference between AL and VL. As proposed by van Wassenhove (2013), in the AL condition, auditory stimuli, with their higher temporal resolution, can drive the AV interaction, resulting in a narrower TBW. Conversely, when the visual stimulus leads the AV interaction, the lower temporal resolution of the visual system results in a broader TBW.

Another critical point to consider is that, differently from previous tACS evidence that investigated the “online” effects of alpha-band stimulation on AV temporal acuity (Cecere et al., 2015; Venskus et al., 2021), sensory entrainment can be administered trial-by-trials for a short pre-stimulus period prior to onset of the AV target pairs, allowing to investigate the “offline” effects on the AV TBW for a short period after the stimulation offset.

Hence, in the current study we have employed a web-based version of a Simultaneity Judgment (SJ) task, a consolidated experimental paradigm to measure TBWs (Zampini et al., 2005; Roach et al., 2011; Vatakis et al., 2008), to investigate the potential modulations of the AV TBW induced by slower and faster alpha frequencies. Using a SJ task combined with EEG technique, recent evidence highlighted that faster individual alpha frequency (IAF) accounted for narrower AV (Bastiaansen et al., 2020) and tactile-visual (Migliorati et al., 2020) TBWs. In our study, the SJ task was preceded, trial by trial, by AV sensory entrainment at different frequencies in the alpha band: (i) ~8.50 Hz (lower alpha condition); (ii) ∼12 Hz (upper alpha condition). Furthermore, to control for a potential increment in temporal expectation induced by pre-stimulus rhythmic sequences, we implemented a nonrhythmic condition where only the first and the last entrainers were employed. Since AV temporal perception is driven by the occipital alpha rhythm (e.g., Bastiaansen et al., 2020; Cooke et al., 2019), we expect a lower simultaneity rate and a narrower AV TBW in the trials of the SJ task following the upper alpha (∼12 Hz) condition of sensory stimulation. On the contrary, we expect an enlargement of the TBW in trials following AV rhythmic stimulation delivered at the lower alpha frequency (~8.5 Hz). Furthermore, we might expect that sensory entrainment modulates simultaneity judgments differently as a function of the leading sense (e.g., Powers et al., 2009; Zerr et al., 2019).

Finally, a peculiar aspect of our study concerns the implementation of this paradigm in an online, web-based modality. In our recent study (Marsicano et al., 2022), we demonstrated the possibility of implementing an accurate SJ task through a web-based platform. Adapting lab-based experiments to online context allows to collect data from a heterogeneous sample, optimizing the timing of testing (Bridges et al., 2020; Sauter et al., 2020). Recently, online sensory alpha-band entrainment has been successfully implemented (De Graaf & Duecker, 2022; Kawashima et al., 2022), opening new and broader applications for rhythmic sensory stimulation protocols. Following such evidence, in the current web-based study, we aim to investigate whether AV alpha-band entrainment may shape the AV temporal acuity.

4.2 Methods

4.2.1 Participants

A total of 61 volunteer participants were recruited from among university students through advertisements and word of mouth. No compensation or course credits were provided. All participants had normal or corrected-to-normal vision and hearing. Exclusion criteria included self-reported neurological or attention disorders, as well as epilepsy/photosensitivity. One participant was excluded from the analysis due to difficulty in performing the SJ task, reporting to the experimenters a lack of understanding of the task instructions. During data collection, the refresh rate of the monitor/display was recorded for each participant. A 60 Hz refresh rate, which ensures accurate timing of auditory and visual stimuli, was confirmed for 59 participants based on log files generated at the end of the experiment. Two additional participants were excluded for having used a monitor with an invalid refresh rate that did not match the optimized 60 Hz required for accurate stimulus presentation. Consequently, the final sample for analysis consisted of 58 participants (32 females, mean age = 24.6 years, SD = 3.26). All participants were provided with detailed instructions on how to complete the web-based experimental paradigm properly. We emphasize the importance of sitting in a dimly lit and quiet room, using headphones or earbuds at a comfortable volume, maintaining a viewing distance of approximately 50 cm, and performing the task exclusively from a PC rather than mobile devices. The determination of the sample size was informed by previous entrainment studies on temporal perception (Cecere et al., 2016; Ronconi et al., 2018; Venskus et al., 2021). The research project was approved by the Ethical Committee of the University of Bologna (Prot. n. 0159726), and all participants gave their informed consent.

4.2.2 Apparatus and Stimuli

The task was developed using PsychoPy3 (Peirce, 2007) and translated to PsychoJS to facilitate remote administration via Pavlovia (https://pavlovia.org/), a web-based platform for presenting psychophysics experiments through standard web browsers. This setup enabled the remote collection of experimental task data. Both the audio and visual stimuli were initially created using *Psychtoolbox* in MATLAB 2019a (The MathWorks, Inc) and subsequently edited with *Wondershare Filmora 9* (Wondershare) to produce videos of audiovisual (AV) stimuli with varying stimulus onset asynchronies (SOAs). The AV stimuli for the AV entrainment were similarly generated. All stimuli in the experimental paradigm were optimized for a 60 Hz monitor refresh rate. We gathered data directly from PsychoPy/Pavlovia regarding participants' operating systems (Windows: 37 participants, MacOS: 23 participants). Participants were instructed to run the experiment using Mozilla Firefox, Google Chrome, or Microsoft Edge, as pilot testing revealed these browsers were the most reliable for presenting stimuli across different operating systems. Assuming participants maintained the recommended viewing distance of approximately 50 cm from the screen, the visual stimulus used for entrainment was a white square with a diameter of 6° of visual angle, presented at the screen’s center. The auditory stimuli for entrainment were 500 Hz sinusoidal tones presented binaurally via headphones or earbuds at a comfortable volume. For the AV target stimuli in the SJ task, a white circle (6° of visual angle) was presented at the center of a black background on the screen, while a 750 Hz sinusoidal tone was presented binaurally, also through headphones or earbuds at a comfortable volume. All visual stimuli were presented centrally on a black background.

4.2.3 Experimental Design

We employed an AV SJ task, preceded trial-by-trial by rhythmic sensory stimulation (entrainment) at two different frequencies within the lower (~8.50 Hz) or upper (~12 Hz) alpha range, as well as a non-rhythmic control stimulation condition, to explore potential modulations in AV temporal acuity (i.e., temporal binding window, TBW) following sensory entrainment (see Fig. 4). To maximize the effect of neural entrainment, AV rhythmic stimuli were used (Ronconi et al., 2018; Ronconi & Melcher, 2017). In the experimental paradigm, each trial began with the onset of either one of the two rhythmic entrainment conditions (i.e., lower or upper alpha entrainment) or the non-rhythmic control condition. These stimulation conditions lasted ~2 seconds, with the duration of each AV stimulus set to three refresh cycles (49.98 ms). In the lower alpha condition (~8.5 Hz), the AV stimuli were presented for three refresh cycles, followed by four cycles of a blank screen, resulting in a SOA of 116.62 ms. In the upper alpha condition (~12 Hz), the AV stimuli were also presented for three refresh cycles, but were separated by two cycles of a blank screen, resulting in an SOA of 83.3 ms. For the control condition, the AV stimulus was presented only during the first and last three refresh cycles of the ~2 seconds pre-stimulus time window before the AV target of the SJ task appeared. This non-rhythmic pre-stimulus condition controlled for any potential increase in temporal expectation induced by rhythmic pre-stimulus sequences, while simultaneously evaluating each participant's natural AV temporal sampling. The presentation of these experimental pre-stimulus conditions was randomized and counterbalanced across trials.

The inter-stimulus intervals (ISIs) between the end of the entrainment stimulation and the presentation of the AV target were randomly manipulated, with values ranging from 83.3 ms to 233.24 ms in steps of one refresh cycle (16.67 ms). To assess AV temporal acuity, the AV target could be presented at the following stimulus onset asynchronies (SOAs): ±400, ±300, ±200, ±100, and 0 ms. Negative SOAs corresponded to auditory-leading trials (AL), while positive SOAs represented visual-leading trials (VL), consistent with prior research (e.g., Conrey & Pisoni, 2006; Hillock-Dunn & Wallace, 2012). All AV target stimuli in the SJ task were displayed for three frames (49.98 ms). Following each trial, participants were instructed to report the simultaneity of the auditory and visual stimuli using a three-point scale, with a rating of 1 indicating perceived simultaneity (synchronous), a rating of 2 indicating perceived asynchrony (asynchronous), and a rating of 3 signifying uncertainty or failure to perceive the stimuli. This approach aimed to ensure that participants provided simultaneity judgments only when confident, thereby minimizing potential contamination of the data analysis from random responses. Indeed, such uncertain responses were subsequently excluded from the analyses as non-informative. Participants responded without time constraints, and the overall duration for completing the experiment was approximately ~25 minutes. Specifically, the task duration was ~20 minutes, preceded by ~5 minutes allocated for reading instructions and conducting practice trials. Given the limited control and oversight achievable in online testing, participants were urged to concentrate their attentional resources on the stimulation period and to make selective judgments regarding the temporal synchrony of the AV stimuli presented during the SJ task. Additionally, participants were advised to blink and rest their eyes only when responding to the SJ task, if necessary. To further mitigate potential issues in sustained attention during task execution, participants were informed that short breaks could be taken during the response screen presentation, as responses were not time constrained. Each participant completed a total of 276 trials, which included six practice trials and 270 experimental trials. The 270 experimental trials were conducted in a single block, incorporating 10 repetitions for each combination of SOAs and entrainment conditions, randomly distributed across participants.

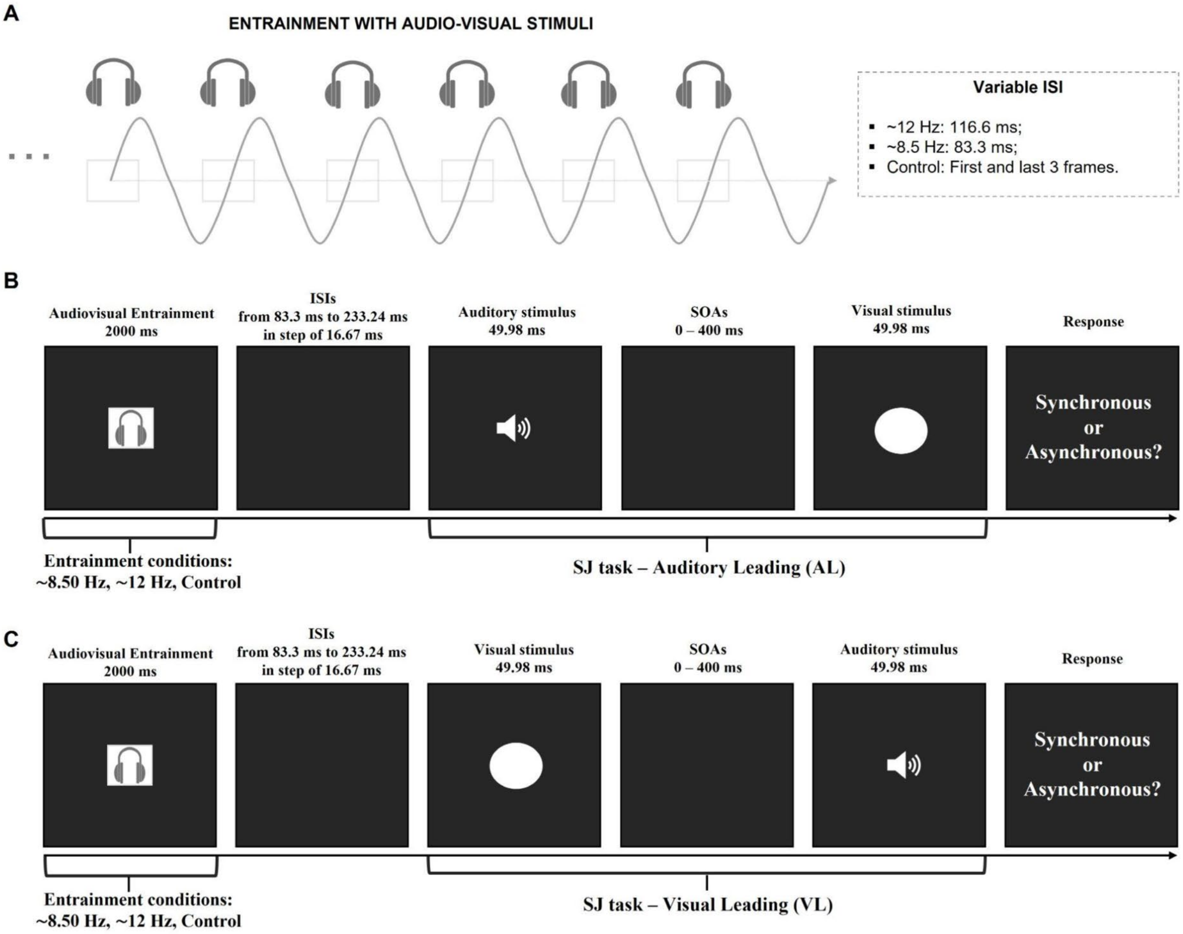

Figure 4. Schematic representation depicting the experimental paradigm. **A)** Each trial started with the AV entrainment condition (i.e., lower alpha or upper alpha entrainment) or the control condition (no stimulation). After a variable interstimulus interval (ISI) ranging between 83.3 ms and 233.23 ms (in steps of 16.67 ms), the AV target of the SJ task appeared at the center of the screen. For all trials, a fixed array of stimulus onset asynchronies (SOAs) was used between the first and second stimulus: ±400 ms, ±300 ms, ±200 ms, ±100 ms, and 0 ms. **B)** Auditory Leading (AL) Trials: In this condition, the auditory stimulus was presented first, followed by the visual stimulus after the predefined SOA. **C)** Visual Leading (VL) Trials: Here, the visual stimulus was presented first, followed by the auditory stimulus. (Adapted from: Marsicano et al., 2024).

4.2.4 Data Analysis

AV Alpha-band Entrainment effects: Simultaneity rate and Gaussian fitting analysis

This analysis aims to investigate whether AV temporal acuity is modulated by the different conditions of sensory entrainment. To this end, we investigated the modulations deriving from the entrainment on the overall simultaneity rate and on the TBW indexed by the Gaussian fitting (see procedure below) of the responses to the SJ task. After obtaining the psychometric values of each participant, we excluded from the statistical analysis the subjects whose results fitted poorly to the Gaussian fitting (adjusted $R^2 < 0.3$), following the previous literature (for example, see Bedard & Barnett-Cowan, 2016; Hillock-Dunn et al., 2016). Following this criterion, we excluded 4 subjects from the data analysis whose data fitted poorly, obtaining a final sample of 54 participants on which all the analyses were performed. In the final sample, the mean adjusted R^2 across subjects were the following for each experimental condition: lower alpha: adjusted $R^2 = 0.844$; upper alpha: adjusted $R^2 = 0.843$; control: adjusted $R^2 = 0.845$. We first performed a repeated-measures analysis of variance (ANOVA) on the rate of synchronous responses with the aim of testing whether performance was influenced by the stimulation condition (three levels: lower alpha, upper alpha, control condition) and SOAs (nine levels: −400 ms, −300 ms, −200 ms, −100 ms, 0 ms, +100 ms, +200 ms, +300 ms, +400 ms), which were used as within-subjects factors. The Greenhouse–Geisser correction was applied when the sphericity assumption was violated. In a second step the observed distribution of responses to the SJ task for each stimulation condition was fitted to a Gaussian function using the Curve Fitting Toolbox in MATLAB 2019a (The MathWorks, Inc). In details, the Gaussian fitting was performed using the following formula through the nonlinear least squares method: *a1*exp(-((x-b1)/c1)^2).* In this formula, *x* represents the SOA, a is the height of the curve's peak (the higher bound was set at 1 and the lower bound was set at 0), *b* is the position of the center of the peak, and *c* is the standard deviation indicating the width of the curve. In such analysis, the parameter *b* indicates the point of subjective simultaneity (PSS), and the parameter *c* indexes the TBW. We chose to use the Gaussian fitting according to these criteria as this method is a gold-standard in this type of analyses (McGovern et al., 2022; Noel et al., 2017; Simon et al., 2017; Stecker, 2018; Van der Burg et al., 2013; Venskus et al., 2021; Wallace & Stevenson, 2014). We performed two separate repeated-measures ANOVAs, one on TBW and one on PSS, to evaluate differences between the stimulation conditions (within-subjects factor, three levels: lower alpha, upper alpha, control). The Greenhouse–Geisser correction was applied in cases where the sphericity assumption was violated. All post-hoc comparisons were two-tailed paired-sample t tests on the measures of interest (i.e., Simultaneity rate and TBW), performed separately for each SOA, and corrected for multiple comparisons using the Bonferroni–Holm method.

AV Entrainment leading sense modulations: Logistic fitting analysis

This analysis aims to investigate potential asymmetries in the modulation of AV temporal acuity induced by the entrainment sequences, which may exhibit distinct effects for auditory-leading (AL) and visual-leading (VL) trials. Participants whose results did not fit the logistic model adequately (adjusted $R^2 < 0.3$; see procedure below) were excluded from the statistical analysis, ultimately resulting in a sample of 45 participants. The mean adjusted R^2 values across all subjects for each experimental condition and leading sense were as follows: AL lower alpha adjusted $R^2 = 0.914$; AL upper alpha adjusted $R^2 = 0.925$; AL control adjusted $R^2 = 0.930$; VL lower alpha adjusted $R^2 = 0.869$; VL upper alpha adjusted $R^2 = 0.885$; VL control adjusted $R^2 = 0.888$. The fitting of the psychometric logistic curve was performed for each subject separately, considering both the AL and VL conditions across the stimulation conditions (i.e., lower alpha, upper alpha, and control). This procedure allowed for the derivation of individual 50% threshold values from the fitted logistic curves. The individual 50% threshold values were chosen as they provide a more sensitive representation of the simultaneity rate distribution obtained in our experiment. Specifically, for each participant, we employed a logistic equation combined with a nonlinear least squares method to fit the proportion of simultaneity responses reported in the SJ task as a function of the SOA. The formula utilized was as follows: $y = 1/(1 + \exp(b \times (t - x)))$. In this equation, x represents the SOA between audio and visual stimuli, while y reflects the proportion of simultaneity responses to the SJ task. The lower bound for y was set at 0, and the upper bound was set at 1, where 0 indicates that AV stimuli were never perceived as synchronous, and 1 indicates that they were always perceived as synchronous. The free parameters of this function included b (the slope of the function) and t (the 50% threshold), both of which were constrained to positive values above zero. Both the AL and VL curves were fitted using the data point corresponding to SOA = 0 ms. For AL trials, the absolute value of the threshold, which is typically negative (i.e., extracted from the left side of the psychometric curve), was determined. In contrast, the VL threshold generally yields a positive value, as indexing from the right side of the psychometric curve. The optimal fitting parameters were derived for each participant individually. Subsequently, two separate repeated measures ANOVAs were conducted on the 50% threshold values to assess whether performance was influenced by the stimulation condition (with three levels: lower alpha, upper alpha, control) and the leading sense factor (with two levels: AL and VL), both included as within-subject factors. The Greenhouse–Geisser correction was applied where the assumption of sphericity was violated, and all post-hoc comparisons were conducted using the Bonferroni–Holm correction method.

4.3 Results

4.3.1 Simultaneity Rate

As expected, the time interval (i.e. SOAs) between auditory and visual stimuli significantly influences performance, and the different stimulation conditions modulate the performance on the SJ task (see Fig. 5). The repeated measures ANOVA conducted on the simultaneity rate, examining the effects of stimulation condition and SOAs, revealed a significant main effect of stimulation condition ($F(1.87, 99.30) = 7.681$, $p < .001$, $\eta p^2 = 0.127$), as well as a significant main effect of SOA ($F(2.49, 132.20) = 130.713$, $p < .001$, $\eta p^2 = 0.712$). Furthermore, this analysis indicated a significant interaction between stimulation conditions and SOA ($F(10.76, 570.51) = 2.152$, $p = .016$, $\eta p^2 = 0.039$). The main effect of stimulation condition suggests that entrainment modulates the average simultaneity rate reported by participants on the SJ task (see Fig. 4). Consistent with our hypotheses, participants exhibited a lower simultaneity rate in the upper alpha entrainment condition ($M = 0.505$, $SD = 0.113$) compared to both the lower alpha entrainment condition ($M = 0.551$, $SD = 0.133$; $t(53) = -3.481$, $p = .006$, and the control condition ($M = 0.549$, $SD = 0.122$; $t(53) = -3.301$, $p = .008$). Conversely, no significant difference was found between the lower alpha entrainment and the control condition ($t(53) = 0.180$, $p = 0.865$). Regarding the interaction between stimulation condition and SOA, post hoc paired-sample t-tests (Bonferroni–Holm corrected) indicated a significantly lower simultaneity rate in the upper alpha entrainment condition compared to the control condition at SOAs of −300, −200, and −100 ms, as well as compared to the lower alpha condition at SOAs of −300 and −200 ms in AL trials (see Table 1). For VL SOAs, although statistically significant effects were absent, post hoc paired-sample t-tests revealed a trend towards significance in the upper alpha stimulation condition, where participants demonstrated a lower simultaneity rate compared to the control and lower alpha conditions only at a +200 ms SOA (see Table 1). No additional significant effects were observed when comparing the simultaneity rate among the various entrainment conditions at the different SOAs (all p-values > .078).

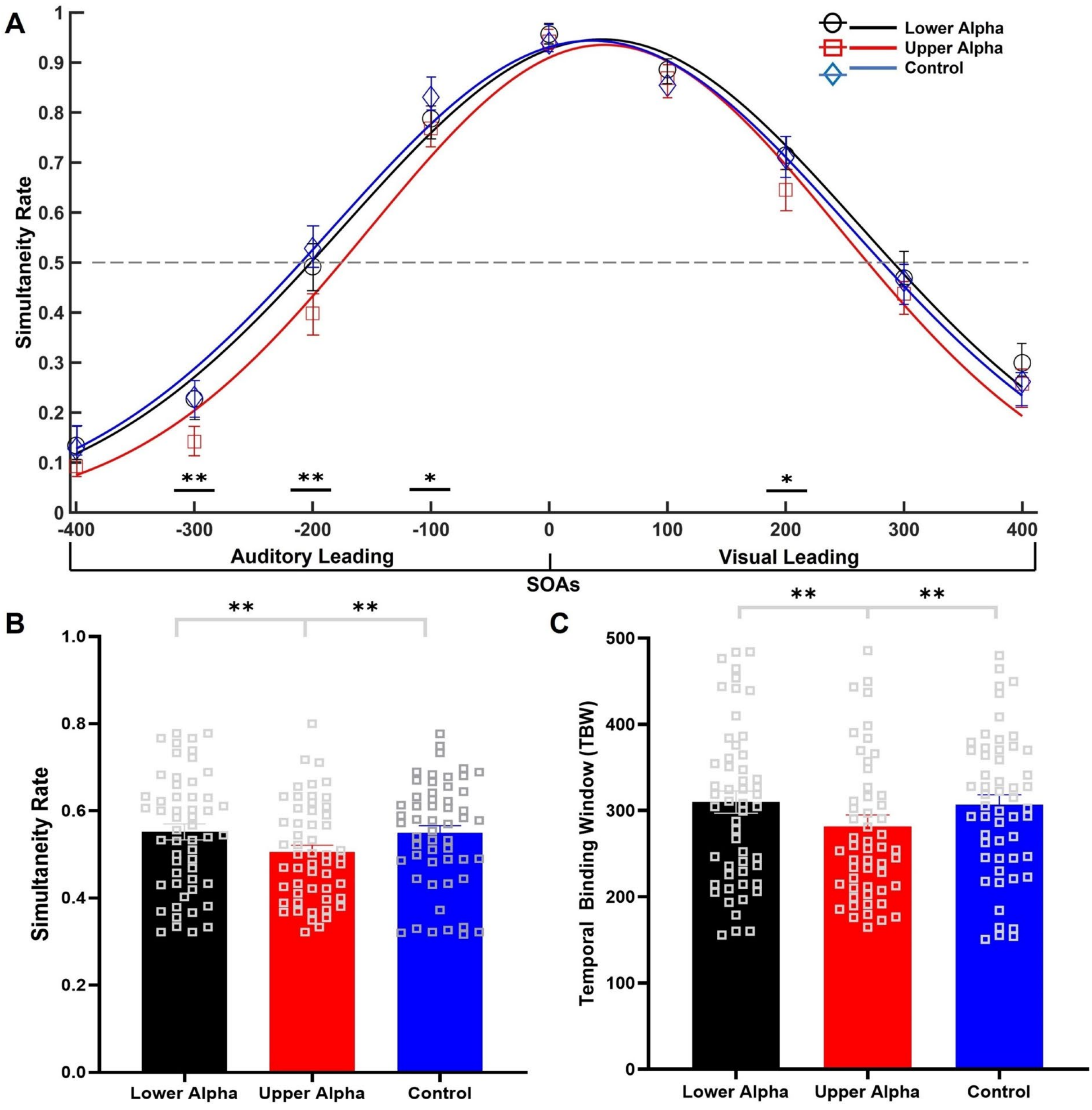

Figure 5. **A)** Gaussian curves obtained across participants in different entrainment conditions. Each individual TBW was derived at a 50% criterion (grey dotted line). Circles, squares and diamonds show simultaneity rates as a function of the SOA in the three experimental conditions, where different types of pre-target entrainment were employed (circle = Lower Alpha; square = Upper Alpha; diamond = Control condition). The asterisks indicate the significant difference in simultaneity rate to specific SOA between the upper alpha entrainment and the lower alpha and control conditions (see the Results section and Table 1 for a detailed description). The error bars indicate the standard error of the mean (SEM). **B)** Bar plots showing the effect of stimulation condition, showing that entrainment modulates the average simultaneity rate reported by participants. The error bars indicate the standard error of the mean (SEM); squares show the individual values. **C)** Bar plots of TBW measures with individual values, showing the modulations induced by different entrainment conditions, with significantly higher AV temporal acuity in the upper alpha condition compared with the lower alpha and control conditions. The error bars indicate the standard error of the mean (SEM); squares show the individual values. *p < .05. **p < .01. (Adapted from: Marsicano et al., 2024).

Descriptive Statistic						
	~12 Hz		~8.5 Hz		Control	
	Auditory Leading (AL)	Visual Leading (VL)	Auditory Leading (AL)	Visual Leading (VL)	Auditory Leading (AL)	Visual Leading (VL)
SOAs	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
100 ms	0.76 (0.29)	0.86 (0.16)	0.78 (0.26)	0.88 (0.14)	0.83 (0.23)	0.85 (0.16)
200 ms	0.38 (0.30)	0.64 (0.27)	0.48 (0.31)	0.71 (0.25)	0.51 (0.30)	0.70 (0.28)
300 ms	0.14 (0.16)	0.43 (0.31)	0.22 (0.31)	0.46 (0.28)	0.22 (0.25)	0.46 (0.31)
400 ms	0.09 (0.14)	0.25 (0.26)	0.13 (0.22)	0.29 (0.23)	0.12 (0.18)	0.26 (0.27)
Paired Sample T-test						
	~12 Hz vs. ~8.5 Hz		~12 Hz vs. Control		~8.5 Hz vs. Control	

SOAs	Auditory Leading (AL)	Visual Leading (VL)	Auditory Leading (AL)	Visual Leading (VL)	Auditory Leading (AL)	Visual Leading (VL)
100 ms	t(53) = -0.977, p = .334	t(53) = -0.750, p = .456	t(53) = -2.531, p = .021*	t(53) = 0.611, p = .728	t(53) = -2.175, p = .983	t(53) = 1.239, p = .33
200 ms	t(53) = -3.807, p = .001**	t(53) = -2.386, p = 0.03*	t(53) = -4.512, p = .001**	t(53) =-2.178, p = .034*	t(53) = -1.624, p = .945	t(53) = 0.148, p = .441
300 ms	t(53) = -3.300, p = .003**	t(53) = -0.892, p = .564	t(53) = -3.473, p = .003**	t(53) =-0.850, p = .564	t(53) = -0.148, p = .558	t(53) = 0.146, p = .564
400 ms	t(53) = -1.422, p = .219	t(53) = -1.419, p = .243	t(53) = -1.472, p = .219	t(53) =-0.144, p = .886	t(53) = 0.235, p = .593	t(53) = 1.058, p = .886

Table 1. Descriptive statistics (mean and standard deviation) of the simultaneity rate averaged across participants reported at each SOA (±-400, ±300, ±200, ±100) and stimulation condition (~12 Hz, ~8.5 and Control), separately for auditory leading (AL) and visual leading (VL) trials. Below the paired sample t-tests (Bonferroni-Holm corrected) showing the differences in simultaneity as a function of the stimulation condition at each SOA. The asterisks indicate the significant difference in simultaneity rate to specific SOA between the upper alpha entrainment and the lower alpha and control conditions. *=p<.05; **=p<.01. (Adapted from: Marsicano et al., 2024).

4.3.2 Gaussian and logistic fitting

The repeated measures ANOVA conducted on the AV TBW confirmed a significant main effect of stimulation condition (F(1.75, 93.03) = 3.946, p = .027, ηp² = 0.069; see Fig. 5). Post hoc comparisons indicated that participants exhibited a narrower TBW, reflecting higher multisensory temporal precision, in the upper alpha entrainment condition (M = 281.75, SD = 97.18) compared to the lower alpha entrainment condition (M = 309.91, SD = 95.21; t(53) = −2.194, p = .016), as well as the control condition (M = 0.549, SD = 82.77; t(53) = −2.718, p = .004). In contrast, the ANOVA conducted on PSS values did not show a significant effect of stimulation condition (F(1.89, 100.16) = 1.610, p = 0.206, ηp² = 0.029). Importantly, the ANOVA performed on the 50% thresholds derived from logistic fitting also did not reveal a significant interaction between stimulation condition and leading sense (F(1.99, 87.60) = 2.329, p = 0.104, ηp² = 0.050), suggesting that the modulation of AV TBWs occurs similarly in both AL and visual-leading VL trials.

4.4 Discussion

The present study aimed to investigate the impact of audiovisual (AV) alpha-band sensory entrainment applied during a short pre-stimulus interval on AV temporal acuity. Our findings represent the first empirical evidence that such rhythmic AV stimulation can effectively induce modulations in the width of the AV TBW. Specifically, we found that upper alpha sensory stimulation (i.e., ~12 Hz) enhances AV temporal acuity by reducing the width of the TBW and decreasing perceived simultaneity compared to lower alpha stimulation (i.e. ~8.5 Hz) and control non-rhythmic conditions. This aligns with existing literature linking alpha oscillations to AV integration and segregation processes, suggesting that alpha rhythm may reflect the temporal unit of AV perception (Bastiaansen et al., 2020; Cecere et al., 2015; Cooke et al., 2019; Ronconi et al., 2023; Venskus & Hughes, 2021). We hypothesize that entrainment of neural oscillations might enhance the temporal sampling capacity of AV perception by synchronizing endogenous oscillatory activity with the frequency of sensory stimulation. However, due to the nature of our web-based behavioral study, we cannot definitively confirm this mechanism, needing future EEG/MEG studies to explore the neural correlates of our findings.

Contrary to our hypothesis, we did not observe a broadening of the TBW or an increase in simultaneity rate following lower alpha stimulation compared to the control condition. Previous research using transcranial alternating current stimulation (tACS) has indicated that rhythmic stimulation at slower alpha frequencies can lead to increased AV sensory integration (e.g., larger TBW) compared to segregation processes (Cecere et al., 2015; Venskus et al., 2021), and this may have resulted in a slowdown of endogenous alpha oscillations (Coldea et al., 2022; Di Gregorio et al., 2022). For example, Venskus et al. (2021) demonstrated that tACS applied at either 14 Hz or 8 Hz during a sound-induced double-flash illusion (DFI) task caused the TBW to narrow or widen, respectively. Similarly, Cecere and colleagues (2015) found that tACS at intrinsic alpha frequency (IAF) or off-peak frequencies produced differing effects on TBW, with lower frequencies (IAF -2 Hz) leading to a widening of the TBW. A potential explanation for the null results at ~8.5 Hz could be that this frequency fell outside the participants' IAF range, thus resulting ineffective in inducing the synchronization of alpha neural oscillation. Indeed, the entrainment of brain oscillations is grounded in the principle of the Arnold Tongue phenomenon (Regan, 1982; Pikovsky et al., 2003; Huang et al., 2021; Notbohm et al., 2016), which suggests that synchronization between different oscillators systems is more likely when the external rhythmic force aligns with the intrinsic endogenous frequency (here: IAF). Since the participants in this study were predominantly young adults, whose IAF is generally faster (Chiang et al., 2011; Scally et al., 2018; Surwillo, 1961), it is plausible that the upper alpha stimulation was within their IAF range, thus effectively synchronizing neural oscillations to the upper alpha rhythmic stimulation. Conversely, lower alpha stimulation may have been outside of their IAF range, thus failing to induce a slowdown of alpha oscillations. However, given the absence of electrophysiological measures in this study, this explanation remains speculative. Additionally, it is noteworthy to consider that different other factors may influence these findings, such as task and stimulus characteristics, which can often affect multisensory integration abilities (Stevenson & Wallace, 2013). Notably, the tACS studies employed different illusory AV integration tasks (i.e., DFI) as compared to the SJ task employed in our study, which could also account for discrepancies in findings. Furthermore, the physiological and behavioral effects of sensory entrainment might differ from those observable in tACS studies, potentially explaining the observed null results following the ~8.5 Hz stimulation. Indeed, sensory entrainment primarily targets the cortical and subcortical sensory pathways, while transcranial stimulation techniques modulate neural activity at the stimulation brain area with potential propagation to connected regions (Albouy et al., 2022; Hanslmayr et al., 2019; Thut et al., 2011b). Additionally, previous tACS studies (Cecere et al., 2015; Venskus et al., 2021) administered continuous alpha-band stimulation while participants performed AV integration tasks to examine “online effects,” whereas the current study delivered trial-by-trial sensory entrainment prior to the target stimulus, thus allowing to investigate AV TBWs modulations observable at the stimulation offset. In this realm, our findings highlight the usefulness of alpha-band sensory entrainment in influencing TBWs for a short period following stimulation offset, which could have significant implications for interventions targeting AV temporal perception abilities in clinical and subclinical populations showing anomalies in sensory information processing (e.g., ASD, SCZ; Zhou et al., 2018).

In line with previous literature (Cecere et al., 2016; Powers et al., 2009; Stevenson et al., 2013), we observed that temporal acuity is typically higher for AL stimulus pairs than for VL conditions. Participants consistently exhibited a higher simultaneity rate in VL trials regardless of stimulation condition. This asymmetry likely stems from the differing neurocognitive mechanisms orchestrating the cross-modal phase reset of neural oscillations (Cecere et al., 2016, 2017; Lakatos et al., 2009; Thorne & Debener, 2014). Interestingly, such differences in neurocomputational processes underlying AL and VL conditions may result in varying degrees of malleability of AV TBWs (Cecere et al., 2016; Powers et al., 2009). Evidence suggests that the AV TBW is less modifiable in AL conditions and more flexible in VL conditions, as demonstrated in perceptual learning training aimed at enhancing AV temporal acuity (Powers et al., 2009; Stevenson et al., 2013; Cecere et al., 2016). However, recent findings indicate a training-dependent symmetrical modulation of AV TBW width that could enhance AV temporal acuity in both leading senses (McGovern et al., 2022). Our results align more closely with these latter findings, as we observed significant improvements in AV temporal acuity in AL trials (SOAs: −300 ms, −200 ms, −100 ms) and a trend toward significance in VL trials (SOA: +200 ms) following upper alpha stimulation before AV stimuli of the SJ task. Additionally, the logistic analysis did not reveal any asymmetries in the modulation of AL and VL thresholds, suggesting that AV temporal acuity was similarly influenced in both conditions. Thus, our findings indicate that the AV rhythmic sensory stimulation effectively maximized the cross-modal phase reset effect between auditory and visual cortices, potentially through neural oscillation entrainment mechanisms, which subsequently modulated both visual-to-auditory and auditory-to-visual temporal acuity. Notably, we observed that the effects induced by sensory stimulation extended across a broader range of SOAs in AL trials compared to VL conditions. This discrepancy may be attributed to the differing temporal resolutions of visual and auditory systems (van Wassenhove, 2013). Given that the auditory system has a higher temporal resolution than the visual system, auditory stimuli driving AV interactions could facilitate the modulatory effects of entrainment, extending its influence on temporal binding of AV information across varying time latencies.

An important methodological aspect of our study regards the successful implementation of the entire experimental procedure through a web-based platform. Our results from the SJ task confirm the feasibility of conducting psychophysical tasks online (Marsicano et al., 2022) and demonstrate that the findings closely resemble those from traditional lab-based studies conducted in less controlled environments (e.g., Zampini et al., 2005; Stevenson et al., 2012; Fenner et al., 2020). Furthermore, in line with recent studies (De Graaf & Duecker, 2022; Kawashima et al., 2022), we demonstrated the successful administration of alpha-band sensory stimulation online, achieving modulations of AV temporal acuity consistent with lab-based studies employing tACS as a neuromodulation technique (Cecere et al., 2015; Venskus et al., 2021). While online experiments facilitate data collection from a larger and more heterogeneous sample with reduced workload (Buhrmester et al., 2016; Mason & Suri, 2012; Reips, 2002; Sauter et al., 2020), they also present methodological limitations that could have impacted our findings. A primary issue may rely on the potential low levels of sustained attention during task execution, which may be less controllable than in lab settings. To mitigate this risk, we implemented various procedures aligned with recent guidelines (Newman et al., 2021; Sauter et al., 2020). Specifically, we conducted rigorous laboratory pilot testing, kept the experiment brief, and provided clear instructions. Another significant challenge in online experiments is achieving accurate timing in stimulus administration, which is particularly relevant for the rapid rhythmic stimulation employed in our study. However, recent findings indicate that studies conducted online using PsychoPy (i.e., the software utilized in our study) achieve high precision in stimulus timing, supporting the reliability of our results (Bridges et al., 2020). Additionally, recent evidence has successfully applied alpha-band sensory stimulation in web-based experiments (De Graaf & Duecker, 2022; Kawashima et al., 2022). In a recent study (Marsicano et al., 2022), we have also demonstrated high overlap in simultaneity judgments of AV events obtained online and in lab-based contexts. Nevertheless, despite these precautions, we cannot entirely rule out the possibility that suboptimal stimulus timing may have influenced our results. Furthermore, logistic fitting analysis of individual data might have introduced a selection bias, particularly toward subjects whose responses did not align with expected simultaneity rate patterns. Other factors, such as the limited number of trials per condition, may also contribute to poor psychometric fitting.

Importantly, recent studies (Buergers & Noppeney, 2022; Di Gregorio et al., 2022) suggest that signal detection theory (SDT) measures (e.g., d' and criterion) may provide more sensitivity to various aspects of visual and AV temporal resolution, such as subjective confidence, prior expectations, and top-down biases. Future studies employing SDT measures will be essential to enhance analytical sensitivity and differentiate how sensory entrainment and other neuromodulatory approaches can influence different aspects of AV temporal perception.

In summary, our findings pave the way for further exploration of rhythmic sensory stimulation protocols aimed at improving AV temporal acuity, both in online and lab-based contexts.

Chapter 5

Individual differences in autistic and schizotypal traits influence audiovisual temporal precision and temporal binding window malleability following alpha-band sensory entrainment

5.1 Introduction

In the previous chapter (i.e., Chapter 4), we discussed the findings of a recent study highlighting the efficacy of AV alpha-band sensory entrainment in modulating AV temporal acuity in the general population. While neural entrainment is an adaptive feature of the human brain, interindividual differences play a significant role in determining individuals' ability to functionally align neural activity with rhythmic sensory patterns. However, these interindividual differences are often overlooked when evaluating neural and behavioural outcomes in entrainment studies. This is a noteworthy aspect, as neural entrainment represents a fundamental mechanism for processing sensory information. A dysfunction in this sensory sampling process can lead to broad impairments in perceptual, cognitive and socio-communicative domains (Riečanský et al., 2010; Ghuman et al., 2017; Northoff, 2018; Noel & Stevenson, 2018; Bharathi et al., 2019; Beker et al., 2021; Black et al., 2024). Employing the same experimental paradigm illustrated in the previous chapter, this section will investigate how different cognitive-perceptual, socio-affective, and communicative individual profiles may influence the modulation of AV temporal acuity following alpha-band sensory entrainment.

As highlighted in the previous section (Chapter 4), a certain degree of temporal tolerance for AV asynchrony is essential for constructing coherent sensory experiences (Zampini et al., 2005; Vatakis & Spence, 2007; Noel et al., 2016). Indeed, even when AV stimuli are not physically synchronous, they are perceived as unified when presented asynchronously within a limited temporal range, a phenomenon conceptualized in the construct of "temporal binding window" (TBW; Colonius & Diederich, 2004; Stevenson et al., 2017a). The TBW's width is commonly employed as a proxy for assessing the temporal resolution of sensory information processing (Colonius & Diederich, 2004;

Wallace & Stevenson, 2014; Marsicano et al., 2022). A narrower TBW indicates higher AV temporal acuity, which has been linked to enhanced performance in higher-level cognitive and socio-affective domains (Lovelace et al., 2003; Powers et al., 2009; Diederich & Colonius, 2015; Zmigrod & Zmigrod, 2016). Conversely, when the tolerance for temporal asynchrony becomes overly liberal (i.e., a broader AV TBW), AV temporal acuity declines, resulting in ambiguous perceptual experiences and potential sensory overload (Martin et al., 2013; Ferri et al., 2018; Marsicano et al., 2022). Reduced temporal precision in synchronizing visual and auditory inputs may impair individuals' ability to interpret and respond to their sensory environment, potentially affecting overall information processing and behavioural responses (Martin et al., 2013; Postmes et al., 2014; Ferri et al., 2018; Marsicano et al., 2022; Ronconi et al., 2023). This scenario is particularly evident in clinical populations, such as those with Schizophrenia Spectrum Disorder (SSD) and Autism Spectrum Disorder (ASD), where cognitive-perceptual and socio-affective anomalies are often associated with reduced temporal precision and wider AV TBWs (Tseng et al., 2015; Balz et al., 2016; Haß et al., 2017; Zhou et al., 2021; Ronconi et al., 2023).

Interestingly, even within the neurotypical population, it can be observable considerable interindividual variability in the temporal resolution of the AV system (Stevenson et al., 2012; Ampollini et al., 2024). The TBW is a dynamic construct that undergoes refinement across development, leading to individual differences in sensory information processing (Ampollini et al., 2024). In this realm, higher ASD- and SSD-like traits in neurotypical individuals have often been associated with perceptual anomalies, which in turn are linked to lower AV temporal acuity and wider TBWs, mirroring the sensory atypicalities often observed in SSD and ASD (Ettinger et al., 2014; Van Laarhoven et al., 2019; Fenner et al., 2020; Muller et al., 2021; Zhou et al., 2021; Marsicano et al., 2022). Despite the similarities in behavioural phenotype, it is hypothesized that the neurocognitive mechanisms underlying these multisensory anomalies can differ between SSD and ASD profiles (Noel & Stevenson, 2018; Jones & Noppeney, 2024). In ASD, broader AV TBWs may be linked to an atypically slowed updating of priors, placing greater emphasis on prediction errors and incoming sensory information (Pellicano & Burr, 2012; Van Boxtel & Lu, 2013; Tarasi et al., 2022). In contrast, SSD-related anomalies in AV temporal perception may result from inflexible prior updating and weakened sensory representations, ultimately leading to dysfunctional integration of sensory inputs (Sterzer et al., 2019; Liddle & Liddle, 2022; Tarasi et al., 2022). More importantly, in both ASD and SSD, these atypicalities are characterized by distinct oscillatory profiles within the alpha-band frequency range (Tarasi et al., 2022). Sensory atypicalities in ASD may emerge from disrupted top-down alpha-band connectivity (Seymour et al., 2019), which is hypothesized to play a key role in transmitting predictive information. This abnormal synchronization of oscillatory neural dynamics typically leads to deficits in both unisensory and multisensory processing, particularly in the temporal integration of sensory stimuli (Van de Cruys et al., 2014; Lawson et al., 2017; Karvelis et al., 2018). In contrast, individuals with high SSD traits may experience sensory encoding anomalies stemming from increased top-down alpha connectivity (Schmack et al., 2013) and aberrant alpha speed (Uhlhaas & Singer, 2015; Ramsay et al., 2021). These atypical oscillatory dynamics lead to abnormal sensory sampling, which biases activity within sensory cortices (Tarasi et al., 2022), ultimately leading to anomalous perceptual experiences frequently observed in individuals with SSD-like features.

A key neural mechanism supporting AV temporal resolution is hypothesized to rely on the speed of parieto-occipital neural oscillations in the alpha frequency band (8-13 Hz; Samaha & Postle, 2015; Cecere et al., 2015; Cooke et al., 2019). According to this framework, visual and auditory inputs are integrated when they coincide within the same alpha cycle, while they are segregated when presented in distinct alpha cycles (Samaha & Postle, 2015; Cecere et al., 2015; Ronconi et al., 2017). Thus, the individual alpha frequency (IAF) may represent the temporal unit of AV perception, with faster IAFs corresponding to narrower AV TBWs and slower IAFs to lower AV acuity. Although the IAF is a relatively stable neurophysiological marker within individuals (Grandy et al., 2013), it exhibits substantial interindividual variability (Haegens et al., 2014), potentially explaining differences in AV temporal resolution across subjects. Notably, individuals with ASD and SSD are often associated with slower alpha oscillations, potentially explaining their larger TBWs (Ippolito et al., 2022). Similarly, neurotypical individuals exhibiting subclinical ASD- and SSD- like traits have been linked to lower AV temporal acuity (Muller et al., 2021; Zhou et al., 2021; Marsicano et al., 2022) and slower IAF (Dickinson et al., 2017; Trajkovic et al., 2021; Ippolito et al., 2022).

As discussed in the previous sections of this thesis, AV temporal perception is highly plastic, with earlier studies showing that rhythmic stimulations at faster or slower alpha frequencies can respectively narrow or widen TBWs (Cecere et al., 2015; Marsicano et al., 2024; Venskus et al., 2021). However, while previous studies have effectively entrained endogenous oscillations and modulated AV TBWs at the group level, these stimulation effects can exhibit substantial interindividual variability in their neural and behavioural outputs (Bachtiar & Stagg, 2014; Schilberg et al., 2017; Janssens & Sacks, 2021). Potential sources of this variability may include different behavioural phenotypes that are associated with specific sub-clinical features. Given that ASD- and SSD-like traits have been shown to drive interindividual differences in AV temporal resolution (e.g., Muller et al., 2021; Zhou et al., 2021; Marsicano et al., 2022) and IAF (Dickinson et al., 2017; Trajkovic et al., 2021; Ippolito et al., 2022; Strang et al., 2022), it is conceivable that the individual traits profile may also influence the malleability of TBWs to external perturbations, such as those induced by rhythmic alpha-band stimulation. Indeed, as previously discussed, individuals with higher ASD and SSD features often exhibit an impaired ability to entrain to rhythmic sequences, resulting in deficits in generating functional temporal predictions from the sensory environment (Ghuman et al., 2017; Northoff, 2018; Bharathi et al., 2019; Beker et al., 2021).

Accordingly, the current study explored interindividual differences in the modulation of AV TBWs by employing the same alpha-band sensory entrainment paradigm used in Chapter 4. AV rhythmic stimulations at slower and faster alpha frequencies, along with a non-rhythmic control condition, were delivered to neurotypical participants before each trial of an AV simultaneity judgment (SJ) task. Importantly, differently from the study discussed in Chapter 4, to investigate potential interindividual differences in the modulation of AV temporal binding windows (TBWs), we collected self-reported data on cognitive, perceptual, socio-affective, and communicative traits using the Autism Spectrum

Quotient (ASQ; Baron-Cohen et al., 2001) and the Schizotypal Personality Questionnaire (SPQ; Raine et al., 1991). These scales quantify subclinical features of ASD and SSD in neurotypical populations (Ettinger et al., 2014; Ronconi et al., 2023).

Through a cluster analysis (Choteau et al., 2016; Abu-Akel et al., 2017), we stratified individuals based on shared characteristics in their personological profiles. This approach was chosen to explore the range of potential phenotypes emerging from the interaction between ASD- and SSD-like traits. The rationale for this strategy is twofold. First, while some personological features associated with ASD and SSD traits may overlap, others diverge. For instance, socio-communicative and affective anomalies are more commonly associated with ASD traits, whereas cognitive-perceptual atypicalities are often linked to the SSD phenotype (Gong et al., 2017; Zhou et al., 2019; Tarasi et al., 2022). Second, past research has typically used a correlational approach, linking total or subscale scores from multidimensional ASD and SSD questionnaires with AV temporal acuity. While this method provides simplicity, it risks overlooking hidden patterns in personological profiles in the general population, where perceptual, cognitive, socio-affective, and communicative styles often interact (Zhou et al., 2020a). Conversely, clustering individuals into homogeneous subgroups based on shared personological features could more effectively uncover the relationship between AV temporal acuity and specific individual trait profiles, as certain dimensions may better predict AV temporal processing (Zhou et al., 2021). We hypothesized that interindividual differences, as indicated by the degree of ASD and SSD-like within cognitive, perceptual, socio-affective and communicative domains, may reveal potential variations in AV temporal acuity and the related flexibility of TBWs size following alpha-band entrainment.

5.2 Methods

5.2.1 Participants

A total of 113 volunteers were recruited among university students. Participants did not receive compensation or course credits. All were volunteers and presented normal or corrected-to-normal vision and hearing. Exclusion criteria were self-reported neurological and attention disorders, epilepsy, and photosensitivity. All subjects performed the web-based version of Simultaneity Judgment (SJ) task and completed the Autism Quotient (AQ; Baron-Cohen et al., 2001) and Schizotypal Personality Questionnaire (SPQ; Raine, 1991). This procedure allowed us to study interindividual differences of entrainment effects on AV temporal acuity. One participant was excluded from subsequent analyses due to inability to do the SJ task, reporting to the investigators the lack of understanding of the instructions of the SJ task. In addition, during data collection, the refresh rate of the monitor/display was recorded for each participant, ensuring a correct timing of AV stimulation at the desired refresh rate (60 Hz). Seven participants were excluded from subsequent analyses since they performed the SJ task using a monitor with different refresh rate with respect to the optimised presentation of the stimuli (i.e., 60 Hz). The final sample included 105 participants (67 females, mean age = 23.4 years, SD = 4.49). All participants were provided with a document containing details about the procedure for correctly completing the web-based experimental paradigm. We underlined the importance of following the instructions we provided for an optimal execution of the online task and for completing the questionnaires (see Marsicano et al., 2024 and Chapter 4 for more details). Following the data-driven stratification of the entire sample into distinct clusters (see Data Analysis), a post-hoc power analysis was conducted to assess the effect size of our findings. This analysis specifically examined the within-between interaction effect in a repeated measures ANOVA (see Results). The research project was approved by the Ethical Committee of the University of Bologna (Prot. n. 0159726), and all participants gave their informed consent.

5.2.2 Apparatus, Stimuli and Experimental Design

The stimuli and experimental paradigm were the same as those used in the experiment presented in Chapter 4 and in Marsicano and colleagues (2024). In summary (Fig. 6A), the task was designed using PsychoPy3 (Peirce, 2007) and implemented via PsychoJS on Pavlovia, a platform for online psychophysics experiments. The stimuli, both audio and visual, were created with Psychtoolbox on MATLAB 2019a and edited using Wondershare Filmora 9. These AV stimuli were generated at different SOAs and were optimized for a 60 Hz monitor refresh rate. The experiment was administered to participants using web browsers (Firefox, Chrome, or Edge), with data on their operating systems (Windows: 74, MacOS: 39) being collected directly from Pavlovia. The experiment employed a web-based AV SJ task, investigating the effects of sensory entrainment at two different alpha frequencies (~8.5 Hz and ~12 Hz) and a non-rhythmic control condition on AV temporal acuity (indexed as TBW size). Entrainment stimuli were rhythmic sequences of white squares (visual) and 500 Hz sinusoidal tones (auditory), while the SJ task used a 6° white circle (visual) and 750 Hz tones (auditory). Stimuli were presented centrally on a black background, with participants sitting approximately 50 cm from the screen. Each trial began with either lower alpha (~8.5 Hz), upper alpha (~12 Hz), or a control condition, lasting 2 seconds. In the lower alpha condition, AV stimuli were presented repeatedly with a SOA of 116.62 ms, while in the upper alpha condition, the SOA was 83.3 ms. The non-rhythmic control condition only presented stimuli for 3 refresh cycles at the beginning and end of the 2-seconds pre-stimulus window.

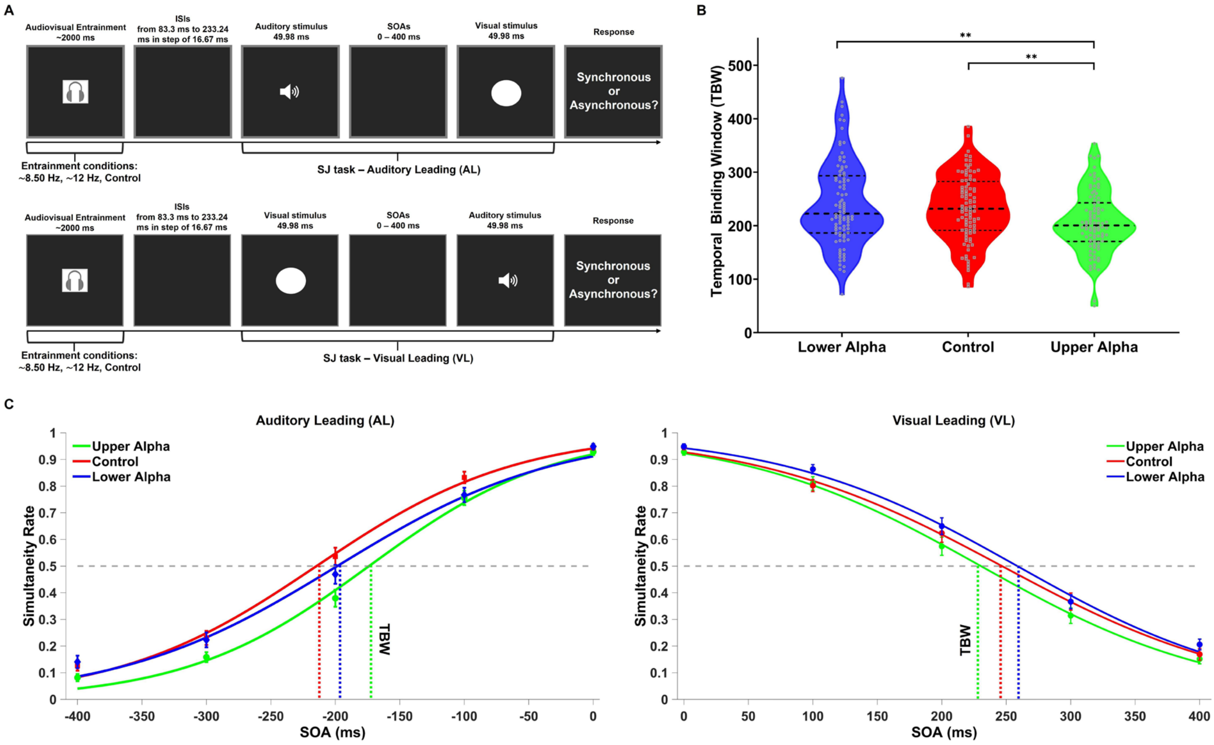

Figure 6. Experimental paradigm and overall results. **A)** Schematic representation of the experimental paradigm, adapted from Marsicano et al., 2024. In the upper panel are represented the Auditory Leading (AL) trials, in which the auditory stimulus was followed by the visual stimulus. In the lower panel are represented the Visual Leading (VL) trials, in which the visual stimulus was followed by the auditory stimulus. Each trial began with the audiovisual entrainment (lower alpha or upper alpha stimulation) or control condition (no stimulation). After a variable time (ISIs) between 83.3 ms and 233.23 ms (in steps of 16.67 ms) the audiovisual target of the Simultaneity Judgment task appears at the centre of the screen. A fixed array of SOAs between the first and second stimulus was used across trials (±400, ±300, ±200, ±100, 0). Trials were counterbalanced between conditions. **B)** Violin plot displaying TBWs modulations as a function of stimulation conditions, showing a narrower TBW following upper alpha entrainment with respect to lower alpha and control conditions, while in contrast no differences emerged between lower alpha and control conditions. Black dotted lines indicate median and quartiles. Grey circles and squares show the individual values. *=p<.05; **=p<.01; ***=p<.001. *=p<.05; **=p<.01; ***=p<.00. **C)** Logistic curves obtained across participants in different entrainment conditions (Upper Alpha, Control, Lower Alpha), separately for Auditory Leading (AL) and Visual Leading (VL) conditions (Left panel: AL; Right panel: VL). Each individual TBW was derived at a 50% criterion (horizontal grey dotted line). Vertical dotted lines show the TBW value following each stimulation condition. Circles show simultaneity rates as a function of the SOA in the three stimulation conditions, where different types of pre-target entrainment were employed (Green Curve = Upper Alpha; Red Curve = Control; Blue Curve = Lower alpha). The error bars indicate the standard error of the mean (SEM).

5.2.3 Autistic Traits

Autistic traits were assessed using the Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001). This self-report questionnaire required participants to respond to various aspects of cognitive style, communicative and socio-affective patterns, and sensory experiences. Specifically, the AQ includes 50 items divided into 5 subscales, each containing 10 items that explore different dimensions of the individual psychological profile: i) attention to detail (assessing abilities in attentional focusing), ii) attention switching (assessing poor attention switching ability/strong focus of attention), iii) imagination (assesses imaginative ability), iv) communication (assessing the weakness in communication skills), v) social skills (assessing the presence of poor social skills). Participants were asked to indicate their level of agreement with each item on a 4-point Likert scale ranging from "definitely agree" to "definitely disagree." Following the original scoring methods (Baron-Cohen et al., 2001), the total scores obtained in each subscale contributed to a global score, with higher values reflecting higher levels of autistic traits.

5.2.4 Schizotypal Traits

Schizotypal traits were assessed using the Schizotypal Personality Questionnaire (SPQ; Raine, 1991). This self-report questionnaire consists of 74 items divided into 9 subscales: ideas of reference, magical thinking, social anxiety, unusual perceptual experiences, constricted affect, no close friends, odd behaviour, odd speech and suspiciousness. These subscales are further organized into 3 main factors: cognitive-perceptual, interpersonal, and disorganization. Participants respond to questions regarding different aspects of their personality, sensory experiences, and beliefs using "Yes" or "No" statements for each item. The original scoring methods (Raine, 1991) were employed, with responses coded in a binary format (no = 0; yes = 1).

5.2.5 Data Analysis

Entrainment modulations of AV Temporal Acuity: Logistic Fitting

In line with our recent study (Marsicano et al., 2024; see Chapter 4), AV TBW was indexed by performing a logistic fitting of the SJ task responses for each participant. This analysis aimed to explore whether AV temporal acuity is influenced by different sensory entrainment sequences and to uncover potential asymmetries in the modulation of AV temporal acuity for AL and VL trials. This methodological approach was essential to investigate potential interindividual differences, as measured by the Autism Spectrum Quotient (AQ) and Schizotypal Personality Questionnaire (SPQ), in the modulation of AV temporal acuity following various entrainment conditions. Consistent with previous literature, participants with poor logistic fitting (adjusted $R^2 < 0.3$) were excluded from the statistical analysis, resulting in a final sample of 92 participants. The adjusted R^2 values were calculated separately for each experimental condition and for each leading sense. The average values obtained for AL trials were as follows: lower alpha adjusted $R^2 = 0.927$; upper alpha adjusted $R^2 = 0.931$; control adjusted $R^2 = 0.935$. For VL trials: lower alpha adjusted $R^2 = 0.901$; upper alpha adjusted $R^2 = 0.928$; control adjusted $R^2 = 0.917$. Psychometric logistic curve fitting was performed for each participant, separately for the AL and VL conditions and across each stimulation condition (i.e., lower alpha, upper alpha, and control). From this analysis, individual 50% threshold values were derived, reflecting the width of the AV TBW. Individual 50% threshold values were used as they provide a more sensitive representation of the simultaneity rate distribution obtained in the current experiment. Specifically, a logistic equation and a non-linear least squares method were utilized to fit the proportion of simultaneity responses to the SJ task as a function of SOAs. The formula used was the following: $y = 1/(1 + \exp(b \times (t - x)))$. In this equation, x represents the SOA between audio and visual stimuli and y represents the proportion of simultaneity responses to the SJ task. The lower y bound was set at 0 and the higher y bound was set at 1 ($y = 0$ indicates that AV stimuli were never perceived as synchronous, and $y = 1$ indicates that they were always perceived as synchronous). The only free parameters of the function were b (the function slope) and t (the 50% threshold), which were restricted to assuming positive values above zero. Both AL and VL curves were also fitted using the data point corresponding to SOA = 0 ms. For AL trials, the absolute value of the threshold, which is typically negative and derived from the left side of the psychometric curve, was determined, while the VL threshold is generally a positive value extracted from the right side of the psychometric curve. The best-fitting parameters were calculated for each participant individually.

Interindividual differences: Cluster Analysis of AQ and SPQ measures

To characterize the multiple phenotypes observable within the ASD-SSD continuum, previous studies implemented factorial (e.g., Principal Component Analysis; Trevisan et al., 2020; Tarasi et al., 2022) and cluster analysis (e.g., k-mean/k-median; Choteau et al., 2016; Abu-Akel et al., 2017) approaches on the measures deriving from the AQ and SPQ questionnaires subscales. In the current study, we decided to implement a cluster analysis technique rather than a factorial approach, as the latter grounds on a variable-centered approach which tends to underestimate the interindividual variability of individuals in a sample (Choteau et al., 2016). On the contrary, cluster analysis is a person-centered approach, unveiling commonalities between individuals, thus identifying group-specific relationships between variables that are typically masked in a globalizing factorial approach. Accordingly, the remaining 92 individuals in our sample following the logistic fitting analysis were stratified using a k-median cluster analysis (Hartigan-Wong method with squared Euclidean distance, maximum number of iterations for finding the optimal clustering solution set to 25) based on participants' z-scored ratings on the 5 subscales of AQ (social skills, attentional switching, attentional to detail, communication, imagination) and the 9 subscales of the SPQ (ideas of reference, social anxiety, odd beliefs/magical thinking, unusual perceptual experiences, eccentric/odd behaviour, no close friends, odd speech, constricted affect, suspiciousness) questionnaires. We calculated the silhouette score of the clusters for values of K ranging from 1 to 10 to determine the best number of clusters (K), selecting the K producing the highest silhouette score. According to the silhouette coefficient (0.23), the optimal clustering solution was 3 K, suggesting a reasonable 3-clusters structure (Kaufman & Rousseeuw, 1990). In addition, in order to evaluate the stability of the clustering model, we used Bayesian Information Criterion (BIC) as optimization method for cluster solution, and identical results were observed (i.e., 3-clusters solution).

Entrainment AV temporal acuity modulations as a function of cluster profile

Finally, we performed a 3 × 2 × 3 repeated-measure analysis of variance (rmANOVA) on the AV TBW with the aim of testing whether performance was influenced by the stimulation condition (within-subjects factor with three levels: lower alpha, upper alpha, control condition), leading sense (within-subjects factor with two levels: AL and VL), and cluster (between-subjects factor with three cluster levels). The Greenhouse–Geisser correction was applied in cases where the sphericity assumption was violated. We performed planned comparisons to investigate AV temporal acuity modulations (i.e., narrowing or broadening of the size of AV TBW) following different entrainment conditions (i.e., lower alpha, upper alpha, control condition) as a function of the clusters and leading sense.

5.3 Results

5.3.1 Interindividual differences: Cluster Analysis

In line with previous evidence describing the ASD-SSD diametrical model using similar methods (Choteau et al., 2016; Abu-Akel et al., 2017; Gong et al., 2017; Zhou et al., 2019; Tarasi et al., 2022), the 3-cluster structure obtained in our analyses (see Fig. 7) described: 1) a first cluster (n=22, 23.9% of participants), named "Socio-affective Traits (SAT)", composed with individuals displaying high scores on the socio-affective dimension (SPQ subscales: no close friends, social anxiety, restricted affect; AQ subscales: social skills, communication, attentional switching), and low scores in the cognitive-perceptual domain (SPQ: ideas of reference, odd beliefs/magical thinking, unusual perceptual experiences, suspiciousness; AQ subscales: attentional to detail, imagination); 2) a second cluster (n=28, 30.4% of participants), called "Cognitive-perceptual Traits (CPT)", was characterized by individuals showing high scores on the cognitive-perceptual dimension (SPQ subscales: ideas of reference, odd beliefs/magical thinking, unusual perceptual experiences, suspiciousness; AQ subscales: attentional to detail, imagination), and low scores in the socio-affective dimension (SPQ subscales: no close friends, social anxiety, restricted affect; AQ subscales: social skills, communication, attentional switching): a third cluster (n=42, 45.6% of participants), called “Low Traits” (LT), composed of individuals with low scores in both AQ and SPQ subscales. The subscales imagination (AQ) and odd speech (SPQ) showed comparable moderate scores in SAT and CPT clusters, and lower scores in LT cluster. Overall, the results from the cluster analysis align with previous findings on the ASD-SSD spectrum (e.g., Tarasi et al., 2022), where individuals with higher scores on the ASD and SPQ subscales exhibit a diametrical pattern of psychological features, with cognitive-perceptual anomalies more closely associated with the schizotypal profile, while higher autistic traits are more related to socio-affective and communicative domains aberrations.

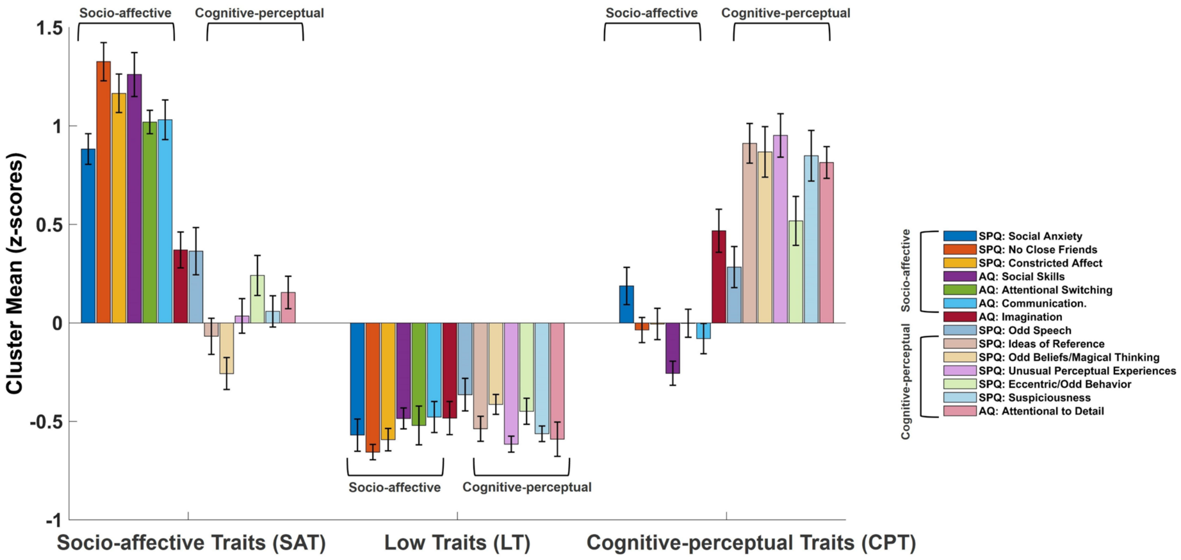

Figure 7. Bar plots illustrating the mean z-scores for each subscale of the Schizotypal Personality Questionnaire (SPQ) and Autism Spectrum Quotient (AQ) questionnaires to highlight the relationship between the three identified clusters: Socio-affective Traits (SAT), Low Traits (LT), and Cognitive-perceptual Traits (CPT). For the cognitive-perceptual domain, the AQ subscales of attentional switching and communication, alongside SPQ subscales such as ideas of reference, odd beliefs/magical thinking, unusual perceptual experiences, eccentric/odd behavior, and suspiciousness, showcase varying degrees of influence across the clusters. In contrast, the socio-affective domain includes AQ subscales of social skills and attention to detail, as well as SPQ subscales such as social anxiety, no close friends, and restricted affect, revealing distinct patterns within each cluster. Notably, both the odd speech and imagination subscales demonstrate comparable moderate mean values within the SAT and CPT clusters, indicating a shared characteristic between these two groups. Error bars in the plots represent the standard error of the mean (SEM).

Regarding power analysis, according to the chosen clustering solution, the input parameters for the interaction effect between condition and stimulation were as follows: effect size = 0.25, significance level = 0.05, total sample size = 92, number of groups = 3, and number of measurements = 3. The resulting output indicated a critical F-value of 2.42, which was lower than the observed F-value for the interaction of interest (F = 3.07; see next sections).

5.3.2 Entrainment AV temporal acuity modulations as a function of cluster profile

First, participants' TBW were indexed from the logistic fitted curves, analyzed separately for each cluster, stimulation condition, and leading sense (Fig. 8). This method facilitated the investigation of how the modulations of AV TBW varied as a function of the individuals' profiles and the specific sensory entrainment conditions they experienced, thus highlighting the interactions between cognitive-perceptual socio-affective and communicative traits within the context of AV temporal acuity.

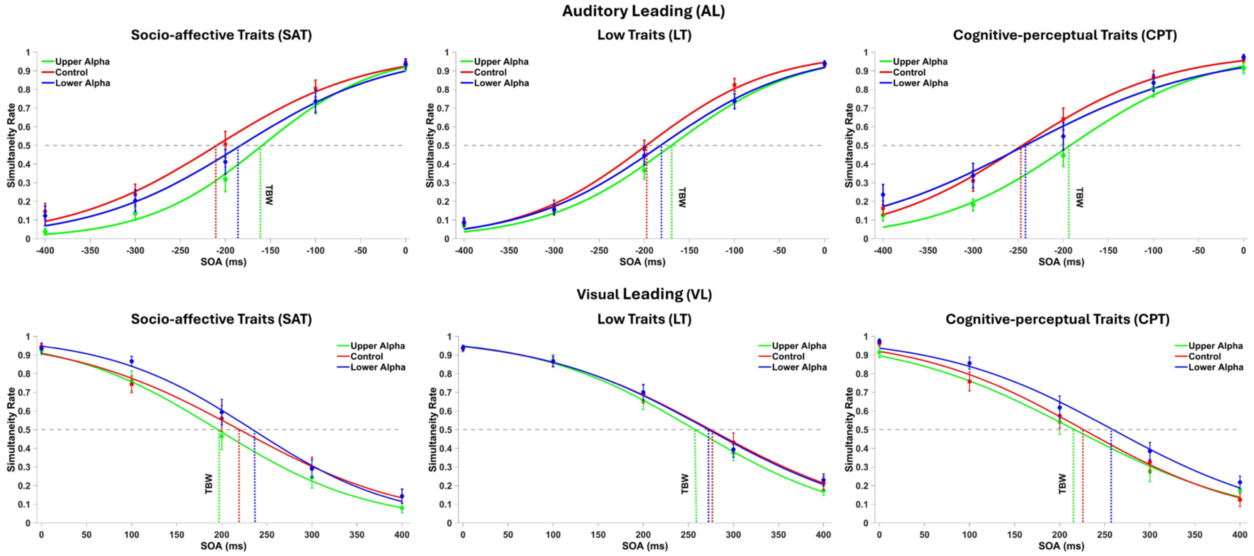

Figure 8. The logistic curves obtained across participants are illustrated for each cluster - Socio-affective Traits (SAT), Low Traits (LT), and Cognitive-perceptual Traits (CPT) - under various entrainment conditions (Upper Alpha, Control, Lower Alpha), analyzed separately for both Auditory Leading (AL) and Visual Leading (VL) conditions. In the upper panel, the AL condition is depicted, while the lower panel shows the VL condition. Each individual temporal binding window (TBW) is derived at a 50% criterion, indicated by a horizontal grey dotted line. The vertical dotted lines represent the TBW value following each stimulation condition. The circles on the curves display the simultaneity rates as a function of the stimulus onset asynchronies (SOAs) across the three different stimulation conditions, utilizing different types of pre-target entrainment (Green Curve = Upper Alpha; Red Curve = Control; Blue Curve = Lower Alpha). The error bars denote the standard error of the mean (SEM).

In line with our recent study (Marsicano et al., 2024), we found that different entrainment conditions modulated AV temporal acuity during the SJ task. The rmANOVA revealed a statistically significant main effect of stimulation ($F(1.63, 145.52) = 16.08$, $p < .001$, $\eta^2p = 0.15$; Fig. 6B) and leading sense ($F(1, 89) = 4.04$, $p = .47$, $\eta^2p = 0.04$; Fig. 6C). In contrast, clusters did not show a statistically significant main effect ($F(2, 89) = 1.90$, $p = .15$, $\eta^2p = 0.04$).

Regarding the stimulation effect, post-hoc comparisons indicated that the upper alpha condition resulted in a significantly narrower TBW reflecting higher AV temporal acuity, compared to the lower alpha condition (M = 207.56, SD = 60.19 vs. M = 240.84, SD = 79.91; t(178) = -5.46, p = .003) and the control condition (M = 233.17, SD = 62.41; t(178) = -4.03, p = .003). Although there was a general trend indicating a broader TBW in the lower alpha condition, the comparison with the control condition did not reach statistical significance (t(178) = 1.43, p = .154).

Additionally, the analysis revealed a statistically significant interaction between stimulation and leading sense (F(1.74, 155.23) = 3.99, p = .02, η^2p = 0.043; Fig. 9A). In the AL condition, participants exhibited a narrower TBW (indicating higher AV temporal precision) following upper alpha entrainment (M = 181.24, SD = 75.89) compared to the lower alpha condition (M = 220.10, SD = 136.23; t(320.41) = -5.24, p < .001) and the control condition (M = 219.20, SD = 93.11; t(320.41) = -4.92, p < .001). However, participants did not show a broader AV TBW in the lower alpha condition compared to the control condition (t(320.41) = 0.31, p = .75). For the VL condition, participants displayed a narrower TBW in the upper alpha entrainment (M = 233.88, SD = 110.25) compared to the lower alpha condition (M = 261.58, SD = 98.66; t(320.41) = -3.68, p < .001), but not compared to the control condition (M = 247.14, SD = 109.39; t(320.41) = -1.66, p = .09). Following lower alpha entrainment, participants showed an enlarged AV TBW compared to the control condition (t(320.41) = 2.02, p = .04). These results are consistent with previous studies (Cecere et al., 2015; Venskus et al., 2021; Marsicano et al., 2024), demonstrating an overall enhancement in AV temporal precision following upper alpha entrainment and a relative decline following lower alpha conditions, with differential modulations observed for AL and VL trials.

Importantly, our analysis revealed statistically significant interactions between leading sense and cluster (F(2, 89) = 3.66, p = .03, η^2p = 0.076; Fig. 9A) as well as stimulation and cluster (F(3.27, 145.52) = 3.07, p = .02, η^2p = 0.06; Fig. 9B).

The interaction between leading sense and cluster factors indicated a broader AV TBW in the LT group during the VL condition (M = 269.25, SD = 91.87) compared to the AL condition (M = 185.09, SD = 75.89; t(89) = -3.67, p < .001). In contrast, the SAT (VL: M = 221.59, SD = 91.85; AL: M = 197.86, SD = 98.66; t(89) = 0.75, p = .45) and CPT (VL: M = 235.35, SD = 102.61; AL: M = 246.54, SD = 104.26; t(89) = -0.39, p = .69) groups did not demonstrate statistically significant differences between leading senses. In the AL condition, the CPT cluster exhibited lower AV temporal precision (M = 246.54, SD = 104.26) compared to the LT group (M = 185.09, SD = 75.89; t(165.87) = -2.7, p = .036). No other significant effects emerged when comparing the AV TBW between AL and VL conditions across different clusters (all p-values > .068).

On the other hand, the interaction between stimulation condition and cluster indicated increased AV temporal precision (i.e., narrower AV TBW) following upper alpha entrainment compared to the control condition in each cluster: SAT upper alpha (M = 182.43, SD = 51.45) vs. SAT control (M = 221.69, SD = 65.19; t(178) = -2.89, p = .004), CPT upper alpha (M = 212.85, SD = 69.05) vs. CPT control (M = 238.29, SD = 54.12; t(178) = -2.11, p = .036), and LT upper alpha (M = 210.39, SD = 48.61) vs. LT control (M = 235.77, SD = 57.04; t(178) = -3.25, p < .001). In contrast, lower alpha entrainment was effective in broadening AV TBWs compared to the control condition only in the CPT cluster (CPT lower alpha: M = 271.69, SD = 92.58; t(178) = 2.77, p = .006), but not in SAT (SAT lower alpha: M = 225.05, SD = 80.05; t(178) = 0.24, p = .85) or LT clusters (LT lower alpha: M = 228.54, SD = 65.63; t(178) = -0.73, p = .46). Additionally, the statistical comparison between groups based on the size of TBW after different stimulation conditions indicated that in the lower alpha condition, the CPT cluster exhibited an enlarged AV TBW (M = 271.69, SD = 92.58) compared to SAT (M = 225.05, SD = 80.05; t(166.17) = -2.43, p = .016) and LT clusters (M = 228.54, SD = 65.63; t(166.17) = -2.63, p = .009). Furthermore, there was a trend toward a narrower AV TBW in the SAT cluster (M = 182.43, SD = 51.45) compared to the LT cluster during the upper alpha condition (M = 217.20, SD = 55.61; t(166.17) = -1.96, p = .051). No other significant effects emerged when comparing AV TBW among the different entrainment conditions as a function of the different clusters (all p-values > .11). This analysis did not reveal a statistically significant interaction between stimulation condition, leading sense, and cluster factors (F(3.48, 155.23) = 1.53, p = .20, $\eta^2p = 0.03$).

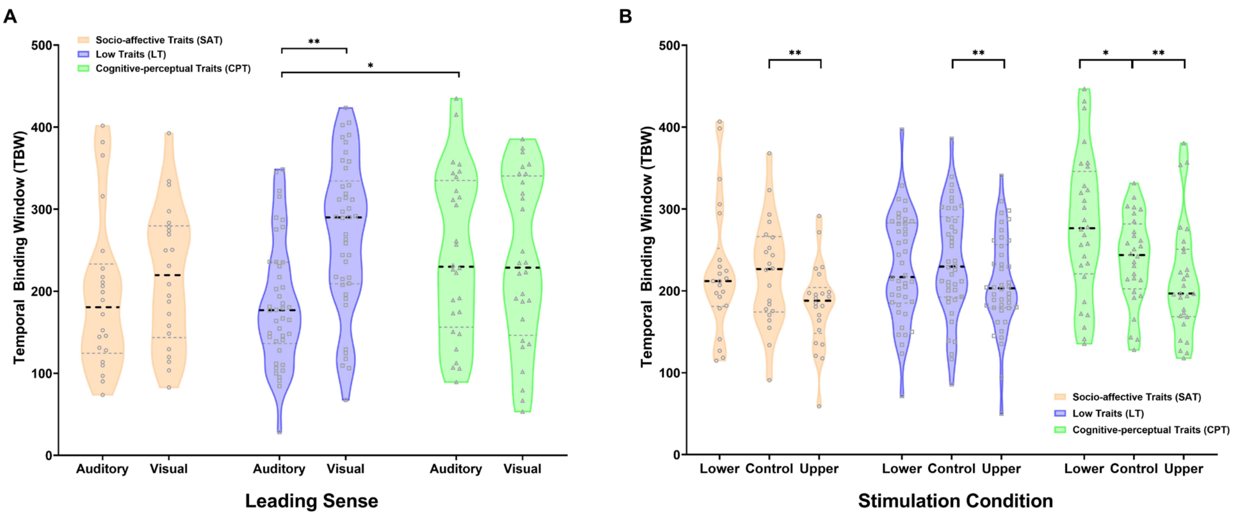

Figure 9. Violin plots illustrating the modulation of temporal binding windows (TBWs) based on stimulation condition, cluster, and leading sense. **A)** Violin plots indicating the interaction between cluster and leading sense. In the Visual Leading (VL) condition, the Low Traits (LT) cluster exhibited a significantly enlarged AV TBW compared to the Auditory Leading (AL) condition. In contrast, the Socio-affective Traits (SAT) and Cognitive-perceptual Traits (CPT) clusters did not reveal statistically significant differences between leading senses. Additionally, the CPT cluster demonstrated a narrower TBW in the AL condition relative to the LT group. The black dotted lines indicate the median, while the grey dotted lines represent the quartiles. Individual values are denoted by grey circles, squares, and triangles. Asterisks indicate significance levels: *=p<.05; **=p<.01; ***=p<.001. **B)** Violin plots highlighting the interaction between stimulation condition and cluster. It reveals that AV temporal acuity significantly increased following the upper alpha condition compared to the control condition across all clusters (SAT, LT, CPT). Conversely, lower alpha entrainment led to a broadening of AV TBW in the CPT cluster when compared to the control condition, while no significant changes were observed in the SAT and LT clusters. Black dotted lines indicate the median, and grey dotted lines show the quartiles, with individual values represented by grey circles, squares, and triangles. Asterisks indicate significance levels: *=p<.05; **=p<.01; ***=p<.001.

5.4 Discussion

5.4.1 Audiovisual TBW modulations following alpha-band sensory entrainment

The main purpose of the current study was to investigate how trait-dependent features of the individual's perceptual, cognitive, and socio-affective profile may impact audiovisual (AV) temporal acuity, inspecting the effects induced by alpha-band AV entrainment on the malleability of the temporal resolution of the AV system. The overall pattern of results, considering the total sample, aligns with those observed in the study presented in the previous section (Chapter 4; Marsicano et al., 2024), as well as with previous alpha-band tACS (Cecere et al., 2015; Venskus et al., 2021), supporting the idea that the speed of alpha oscillatory activity can reflects the temporal unit of AV binding processes (Cecere et al., 2015; Cooke et al., 2019; Bastiaansen et al., 2020; Venskus & Hughes, 2021; Ronconi et al., 2023). By applying AV alpha-band sensory entrainment for a brief period (~2 seconds) during the pre-stimulus interval of an AV Simultaneity Judgment (SJ) task, we found that upper alpha sensory stimulation (i.e., ~12 Hz) enhanced AV temporal perception, similarly for both AL and VL conditions, by shrinking TBWs width and reducing perceived simultaneity, compared to the non-rhythmic control condition and lower alpha entrainment (i.e., ~8.5 Hz).

5.4.2 Interindividual differences: Cognitive-Perceptual Traits (CPT), Low Traits (LT) and Socio-Affective Traits (SAT)

Importantly, we investigated whether certain trait-dependent features of the individual personological profile could affect the temporal resolution of the AV system, and its associated malleability following alpha-band stimulations. Accordingly, to index interindividual differences, we first stratified our sample by performing a cluster analysis on measures derived from the Autism Quotient (AQ; Baron-Cohen et al., 2001) and the Schizotypal Personality Questionnaire (SPQ; Raine, 1991). The rationale behind this approach is grounded on recent findings demonstrating a diametrical relationship between ASD- and SSD-like traits within the general population (e.g., Tarasi et al., 2022), as well as an atypical resolution of the AV system in individuals exhibiting higher traits (Fenner et al., 2020; Muller et al., 2021; Zhou et al., 2021; Marsicano et al., 2022). Importantly, individuals with marked ASD- and SSD- like features often exhibit difficulties in generating temporal predictions from rhythmic sequences in the sensory environment (Riečanský et al., 2010; Ghuman et al., 2017; Northoff, 2018; Noel & Stevenson, 2018; Bharathi et al., 2019; Beker et al., 2021), thus potentially resulting in a diminished neural and behavioural entrainment to sensory input. Despite such anomalies in ASD and SSD often presenting with similar behaviours, the underlying causes are hypothesised to be of different nature (Noel & Stevenson, 2018; Tarasi et al., 2022). In line, several evidence identified diametrically opposed phenotypes in the general population: individuals exhibiting subclinical anomalies in the socio-affective domain (ASD-like) displayed intact abilities in the cognitive-perceptual dimension (SSD-like) and vice versa, while lower atypicalities in both domains indicated the absence of ASD- and SSD- like subclinical features (Gong et al., 2017; Zhou et al., 2019; Tarasi et al., 2022). In line with this framework, our results revealed a three-cluster structure of individuals sharing common personological features. Each cluster was distinguished by pronounced atypicalities in either the socio-affective domain (Socio-affective Traits; SAT), the cognitive-perceptual domain (Cognitive-perceptual Traits; CPT), or by low traits across both dimensions (Low Traits; LT). Accordingly, we explored the potential differences among the observed clusters in the modulation of AV TBWs as a function of the nature of cross-modal interaction (i.e. leading sense) and of the different rhythmicity embedded in the sensory stream (i.e. sensory entrainment).

5.4.3 Interindividual differences and AV leading sense differences

Regardless of the stimulation condition, our results revealed a significant asymmetry in the width of AV TBWs between AL and VL sequences within the LT group, but not in the SAT or CPT groups. Specifically, a broader TBW was observed in the VL condition for the LT group. This pattern is consistent with previous research showing that, in the general population, AV multisensory processes typically exhibit larger TBWs for VL sequences compared to AL sequences (Bushara et al., 2001; Grant et al., 2004; van Wassenhove et al., 2007; Kaganovic & Schumaker, 2016; Marsicano et al., 2022, 2024). The higher temporal resolution of the auditory system, compared to the visual system, has been proposed as a possible explanation for this asymmetry (van Wassenhove, 2013; Cecere et al., 2016, 2017), with the differences potentially rooted in the distinct neural mechanisms that orchestrate cross-modal phase resetting of brain oscillations (Lakatos et al., 2009; Thorne & Debener, 2014; Cecere et al., 2016, 2017).

In contrast, both the SAT and CPT groups did not show this typical leading sense asymmetry. The absence of differences in TBW sizes between AL and VL sequences may indicate that individuals with pronounced anomalies in cognitive-perceptual or socio-affective domains tend to perceive AL pairs as more simultaneous, possibly due to less reliable auditory temporal processing compared to visual processing (Donohue et al., 2012; Stevenson et al., 2017a, 2017b; Zhou et al., 2020a; Foucher et al., 2007; Muller et al., 2020). Regarding the CPT group, previous research has linked perceptual anomalies to slower sensory information sampling in auditory brain areas (Foucher et al., 2007; Muller et al., 2020). These findings align with evidence that cognitive-perceptual anomalies (e.g., unusual perceptual experiences, odd beliefs, magical thinking) are often associated with atypical AV temporal binding (Ferri et al., 2017, 2018; Muller et al., 2021; Dalal et al., 2021; Marsicano et al., 2022). Such characteristics, central to the structure of the CPT group, likely contribute to the atypical AV temporal processing observed in our study. Similarly, individuals with socio-affective and communicative atypicalities (i.e., SAT group), which resemble ASD-like traits, tend to prioritize visual processing and exhibit slower auditory processing (Donohue et al., 2012; Stevenson et al., 2017a; Zhou et al., 2020b; Aykan et al., 2020; Seymour et al., 2020). A recent study by Ronconi and colleagues (2023) found that in individuals with ASD, AV integration/segregation processes were primarily driven by auditory processing, suggesting that over-encoding auditory information might contribute to their atypical AV temporal processing. Another noteworthy result is that the CPT group exhibited lower temporal acuity in AL trials compared to the LT group, while no significant differences emerged between the LT and SAT groups. This aligns with the idea that individuals with higher cognitive-perceptual atypicalities have lower auditory temporal resolution than LT participants (Foucher et al., 2007; Muller et al., 2020). This pattern in the CPT group may also reflect a more general AV multisensory deficit, leading to more pronounced atypicalities in AV temporal binding compared to individuals with high socio-affective traits (Zhou et al., 2021). Indeed, ASD-like traits are often linked to selective AV temporal processing anomalies for stimuli with social and communicative value (e.g., speech stimuli), while SSD-like traits are associated with more generalized sensory processing deficits, affecting both speech and nonspeech stimuli (Zhou et al., 2020b; 2021). These generalized deficits may help explain the CPT group's more pronounced AV temporal processing anomalies during the flash-beep SJ task, which involved AV stimuli without socio-communicative content. Overall, our findings suggest that individual differences in cognitive-perceptual and socio-affective traits may influence cross-modal audiovisual interaction mechanisms, affecting the typical asymmetry between AL and VL sequences observed in the general population.

5.4.4 Interindividual differences shape TBW modulations following alpha-band sensory entrainment

Finally, we explored whether the size of AV TBWs was modulated differently depending on AV stimulation conditions and individual trait profiles.

First, after non-rhythmic pre-stimulus stimulation (i.e., the control condition), no significant differences in TBW width were found among the groups. This suggests that the groups showed comparable AV temporal acuity under natural temporal sampling conditions. This finding enriches prior research, where the link between broader AV TBWs and traits resembling SSD or ASD within the general population has been inconsistent (Donohue et al., 2012; Noel & Stevenson, 2018; Zhou et al., 2019, 2022; Weiland et al., 2022). More recent evidence, however, suggests that by analyzing ASD- and SSD-like traits as distinct dimensions, certain domain can selectively predict AV temporal processing anomalies (Yaguchi & Hidaka, 2018; Ferri et al., 2017; Fenner et al., 2020; Dalal et al., 2021; Marsicano et al., 2022; Ainsworth & Bertone, 2023). However, our stratification approach, based on varying degrees of ASD- and SSD-like traits across cognitive-perceptual and socio-affective domains, also confirmed no differences in natural AV temporal acuity between groups.

Despite the absence of between-group differences in the control condition, our findings highlight that interindividual differences can drive distinct modulations of AV TBWs following alpha-band entrainment. Specifically, all participants exhibited narrower TBWs following upper alpha stimulation, compared to the control condition, suggesting that faster alpha stimulation enhanced the AV system's temporal capacity across all groups. This is consistent with similar results in the general population (Marsicano et al., 2024; see Chapter 4).

On the other hand, after lower alpha stimulation, only the CPT group showed a significant widening of AV TBWs, while the LT and SAT groups did not exhibit any modulations. These group-specific differences in TBW malleability following alpha-band stimulation align with prior research indicating consistent interindividual variability in processing rhythmic sensory sequences (Ghuman et al., 2017; Northoff, 2018; Bharathi et al., 2019; Beker et al., 2021; Black et al., 2024). Neural entrainment, the mechanism through which brain rhythms align with external rhythmic inputs, is considered an adaptive feature in the general population (Thut et al., 2011a, 2011b; Lakatos et al., 2019). Rhythmic stimulation can optimize sensory encoding by synchronizing endogenous brain activity with external rhythmic streams, ensuring sensory information is processed within optimal temporal windows (De Graaf et al., 2013; Spaak et al., 2014; Ronconi et al., 2018; Marsicano et al., 2024). The atypical behavioural responses in the CPT group following the lower alpha stimulation might be explained by previous findings highlighting that individuals with higher SSD-like features typically show anomalies in encoding rhythmic sensory patterns (Riečanský et al., 2010; Ghuman et al., 2017; Northoff, 2018; Bharathi et al., 2019; Beker et al., 2021; Black et al., 2024). These sensory processing anomalies may stem from disruptions in bottom-up perceptual processes, where individuals give more weight to prior expectations than to incoming sensory inputs, leading to difficulties in integrating sensory information into coherent models of the sensory environment (Sterzer et al., 2019; Liddle & Liddle, 2022; Tarasi et al., 2022). In other words, individuals exhibiting marked atypicalities in structuring their perceptual experience tend to quickly generate models of the sensory environment and adhere to them inflexibly, giving less weight to sensory prediction errors. In line with this framework, our findings may suggest that, in the CPT group, the difficulties in organizing incoming sensory information into coherent representations (Sterzer et al., 2019; Tarasi et al., 2022) may lead to an increased rigidity in adhering to probabilistic representations generated from rhythmic sensory sequences, which could promote synchronization to various alpha-band stimulations, ultimately impacting AV TBWs.

Alternatively, it is possible that the observed differences between groups could also be attributed to interindividual variations in IAF speed and different levels of synchronization between endogenous neural oscillations and stimulation frequency during entrainment (Ippolito et al., 2022). However, due to the lack of M/EEG data in this study, these interpretations remain speculative. Indeed, other factors, such as task characteristics and stimulus properties (Stevenson & Wallace, 2013), may also play a role in explaining the observed group differences.

5.4 Conclusion and future perspectives

Our findings indicate that interindividual differences within the general population significantly impact AV temporal processing abilities and their adaptability following rhythmic entrainment, specifically within the alpha-band frequencies. By employing a clustering procedure and stratifying our sample into three distinct subgroups based on ASD- and SSD-like traits across cognitive-perceptual, socio-affective, and communicative domains, we uncovered behavioural patterns that would otherwise remain hidden without considering these individual differences. This highlights how specific characteristics of individual profiles can predict AV sensory encoding capacities. The results demonstrated that, in contrast to the LT and SAT groups, individuals with pronounced cognitive-perceptual traits (i.e., CPT group) exhibited atypical AV temporal acuity, both across different leading sense modalities and in response to various alpha-band stimulations. This suggests that the CPT group's temporal processing abilities may be influenced by their cognitive-perceptual atypicalities. Overall, our data-driven clustering approach underscores the importance of analyzing individual trait profiles when assessing AV temporal sampling abilities and entrainment mechanisms. Since each individual's profile is shaped by interactions among multiple domains (e.g., cognitive-perceptual, socio-affective, and communicative), a deeper understanding of how personological features such as incoherent perception, communicative dysfunction, and social cognition contribute to AV multisensory processing is essential. Indeed, these behavioral patterns are rooted in the effectiveness of multisensory integration, further emphasizing the importance of individual profiles in predicting sensory processing capabilities.

Chapter 6

Prolonged modulations of alpha-band visual entrainment on EEG resting-state alpha oscillations

6.1 Introduction

Among all spontaneous neural rhythms, converging evidence suggests that the neural rhythmicity observable in the alpha-band (~7-13 Hz) may be responsible for sampling visual information in discrete cycles, playing an active role in the timing of neural processing (VanRullen, 2016; Cuello et al., 2022; Fakche & Duguè, 2024; Wutz, 2024; Benwell et al., 2022; Gallina et al., 2024). Indeed, alpha oscillatory measures (i.e., phase, power, and frequency) have been consistently linked to various aspects of visual performance, with outcomes depending on the momentary phase of ongoing oscillatory activity as a function of its power (Mathewson et al., 2009; Busch et al., 2009; Samaha et al., 2017; Ronconi & Melcher, 2017; Cuello et al., 2022; Di Gregorio et al., 2022; Benwell et al., 2022). Variations in alpha oscillatory parameters have been consistently associated with fluctuations in the excitability of the visual cortex, leading to rhythmic modulations in both visual and attentional performance, ultimately affecting the probability of processing perceptual inputs (Jensen et al., 2010; Spaak et al., 2014; Boncompte et al., 2016; Samaha et al., 2017; Di Gregorio et al., 2022; Benwell et al., 2022; Tarasi & Romei, 2024).

Importantly, alpha activity in the occipital-parietal regions has been demonstrated to predict the excitability of the visual system in both healthy individuals (Klimesch et al., 2007; Sadaghiani & Kleinschmidt, 2016) and clinical populations (Pietrelli et al., 2019; Allaman et al., 2021; Gallina et al., 2022), indicating that alpha rhythms may reflect a reliable neurophysiological signature for the functionality of the visual system (Romei et al., 2008). However, neural oscillatory activity is not an invariant feature of the neural system, but it is highly plastic and influenced by task demands and neurocognitive states (Klimesch et al., 2007; Mathewson et al., 2009; Mathewson et al., 2011; Samaha et al., 2017; Alamia & VanRullen, 2024). Interestingly, variations in endogenous neural rhythmicity are frequently shaped by the rhythmic patterns inherent in environmental sensory streams through the phase synchronization of their oscillatory systems, a phenomenon commonly referred to as the "entrainment" of neural oscillations (for recent reviews, see: Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024). Neural entrainment, as discussed in the previous chapters, refers to the temporal synchronization of endogenous neural activity to an external driving rhythm, resulting in an alignment of phase and frequency, as well as an enhancement in the power of ongoing neural oscillations (Lakatos et al., 2019). Building on this entrainment mechanism, previous studies employing rhythmic stimulation have consistently demonstrated effective synchronization of brain oscillations with the external stimulation frequency, suggesting that spontaneous alpha oscillatory activity can be externally modulated (Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024).

In this context, evidence from sensory entrainment (e.g., visual, auditory, and audiovisual modalities) has yielded significant insights into the mechanisms underlying the entrainment of neural oscillations. Notably, alpha-band sensory entrainment has emerged as a valuable tool for modulating alpha oscillations by specifically targeting visual oscillatory networks (e.g., Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2024). In this regard, the application of brief sequences of alpha-band visual rhythmic stimulation (~0.5–5 seconds) has been consistently demonstrated to entrain brain oscillations, leading to phase alignment and an enhancement in the power of ongoing alpha oscillations (Mathewson et al., 2011; Spaak et al., 2014; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Szaszkó et al., 2024; Fakche & Duguè, 2024), with the most pronounced effects typically observed at frequency-sensitive occipito-parietal scalp sites (Mathewson et al., 2012; Spaak et al., 2014; Gray & Emmanouil, 2019), ultimately supporting the idea that neural oscillatory populations can be functionally entrained when the stimulation is aligned with their resonant preferential frequency (Regan, 1982; Pikovsky et al., 2003; Thut et al., 2012). Importantly, the transient effects induced by alpha-band sensory entrainment do not return to baseline power immediately following the stimulation offset. Rather, they have been shown to persist for ~3-5 alpha cycles (~500 ms; Spaak et al., 2014; Wiesman & Wilson, 2019), leading to a corresponding modulation of the temporal resolution within the sensory system and influencing visual performance, either in-phase or out-of-phase with the stimulation frequency (De Graaf et al., 2013; Spaak et al., 2014).

However, despite its promising potential, several aspects regarding the effects of sensory entrainment on neural oscillations remain under debate. Firstly, it is still unclear whether prolonged sensory entrainment can induce persistent modulations of alpha oscillatory parameters. Prior research has largely focused on short-duration sequences of rhythmic sensory stimulation (~0.5–5 seconds) administered on a trial-by-trial basis, which have yielded transient neural and perceptual effects that typically persist for only a brief interval following the end of the entrainment (~100–550 milliseconds; Mathewson et al., 2012; Spaak et al., 2014; Kizuk & Mathewson, 2017; Wiesman & Wilson, 2019; Gray & Emmanouil, 2019), raising the question of whether prolonged alpha-band sensory stimulation can effectively promoting long-lasting modulations of brain oscillatory activity.

Relatedly, it is still unclear which properties of rhythmic stimulation are most effective for inducing functional modulations of alpha oscillatory activity. Neural entrainment is inherently frequency-dependent and relies on the interplay between the stimulation frequency and the intrinsic oscillatory characteristics of the targeted brain regions (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022). For sensory entrainment to be effective, the stimulation frequency must fall within a specific bandwidth and align with the preferential neural rhythm of the targeted oscillatory system (Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022). Previous studies have consistently demonstrated that sensory entrainment, when tuned to the preferential frequency band of the visual system (i.e., alpha band), results in specific modulations of alpha oscillatory parameters in occipito-parietal brain areas, which are associated with concurrent fluctuations in visual performance (Mathewson et al., 2011; Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019). While earlier research frequently employed fixed frequencies within the alpha band for sensory entrainment across all participants, it has been posited that entrainment effects may be maximal when the stimulation frequency corresponds to the IAF (Thut et al., 2011a; Zaehle et al., 2010; Notbohm et al., 2016). Nevertheless, it remains uncertain whether deviations from the spontaneous IAF during stimulation can yield distinct functional oscillatory and perceptual outcomes.

Importantly, the question of whether the effects of entrainment on alpha oscillations are focal or distributed across various brain regions remains unresolved. Previous studies employing short-term entrainment have demonstrated that these effects are predominantly localized to posterior brain areas contralateral to the site of stimulation (Thut et al., 2011a; Spaak et al., 2014). However, it has yet to be investigated whether prolonged alpha-band entrainment, in contrast to short-term stimulation, may induce more widespread effects that strengthen alpha traveling waves across the scalp, with effects that could be potentially observable in neural regions ipsilateral to the stimulation site as well as in more centro-frontal neural sources (Zhang et al., 2018; Alamia & VanRullen, 2019, 2024; Fakche & Duguè, 2024).

To address these questions, we acquired EEG oscillatory signals both before and after blocks of prolonged visual entrainment (i.e., 1 minute of duration) to investigate whether visual rhythmic stimulation, presented in the right or left hemifields across different experimental sessions and at various frequencies within the alpha band (IAF, IAF -2 Hz, and IAF +2 Hz), could induce persistent effects on ongoing alpha oscillatory spectral measures (i.e., power, phase, and IAF within the 7–13 Hz range) immediately following the entrainment period over a 1-minute of eyes-closed resting state. This was accomplished by comparing eyes-closed resting-state oscillatory activity recorded before and after the entrainment stimulation. Furthermore, we examined which alpha stimulation frequency was most effective in inducing maximal effects on post-entrainment resting-state activity and whether these effects were diffuse rather than topographically focal, considering neural activity in both posterior and anterior scalp regions. Given that alpha-band entrainment has been shown to selectively modulate alpha oscillatory activity (e.g., Spaak et al., 2014; Keitel et al., 2018, 2019), we also assessed theta-band oscillatory parameters (3–6 Hz), further implementing a control entrainment condition with a fixed theta frequency (i.e., 4.5 Hz) to ensure the specificity of frequency dependency in the sensory entrainment's effects on neural oscillatory activity.

6.2 Methods

6.2.1 Participants

A total of 25 healthy young adults (14 females; mean age = 22.8, SD = 2.74) were recruited from university students as volunteers, without receiving compensation or course credits. All participants had normal or corrected-to-normal vision and hearing. Exclusion criteria included self-reported neurological or attention disorders, epilepsy, and photosensitivity. Participants were fully informed about the study's procedures and purpose and provided written informed consent. The determination of the sample size was informed by previous entrainment studies (e.g., Spaak et al., 2014; Gray & Emmanouil, 2019). The study was conducted in accordance with the ethical principles of the Declaration of Helsinki and received approval from the ethical committee of the Department of Psychology "Renzo Canestrari" at the University of Bologna (Prot. 42483).

6.2.2 Apparatus and Stimuli

Participants were seated in a soundproof room and positioned with a chin rest at a viewing distance of 57 cm from a 24-inch LED monitor (Acer) with a resolution of 1080 × 980 pixels and a vertical refresh rate of 144 Hz. The visual entrainment stimuli were displayed for three refresh cycles (21 ms each), with the intervals between stimuli varying based on the specific stimulation frequency (see next section for details). Throughout the experiment, eye movements were tracked using a pan-tilt ASL 6000 eye-tracking system operating at a 60 Hz sampling rate. Simultaneously, electroencephalographic (EEG) data were continuously recorded using a BrainAmp DC amplifier (BrainProducts GmbH, Germany) and Ag/AgCl electrodes (Acticap Slim, BrainProducts GmbH, Germany) placed at 63 scalp locations (Fp1, AF3, AF7, F1, F3, F5, F7, FC1, FC3, FC5, FT7, FT9,

C1, C3, C5, T7, CP1, CP3, CP5, TP7, TP9, P1, P3, P5, P7, PO3, PO7, O1, Fp2, AF4, AF8, F2, F4, F6, F8, FC2, FC4, FC6, FT8, FT10, C2, C4, C6, T8, CP2, CP4, CP6, TP8, TP10, P2, P4, P6, P8, PO4, PO8, O2, Fz, CPz, Pz, POz, Oz). AFz served as the reference electrode, and Cz as the ground. The EEG was recorded with a band-pass filter from 0.01 to 100 Hz and a sampling rate of 1000 Hz, with electrode impedances kept below 25 KΩ. All visual stimuli were presented against a middle-grey background. The rhythmic visual stimulation, or visual entrainment, involved flickering white squares (6 × 6 cm) displayed 15 cm lateral to a central black fixation cross (0.5 × 0.5 cm). For each participant, visual entrainment was administered to either the left or right visual hemifield in separate, randomized sessions.

6.2.3 Experimental Procedure

The experimental session (for a schematic representation, see Fig. 10) began with the acquisition of baseline eyes-closed resting-state EEG signals, consisting of nine separate 1-minute blocks. Following these baseline EEG recordings, each participant's individual alpha frequency (IAF) was calculated and visually inspected (for details on the IAF processing and computation, see the next section) to quantify their baseline brain oscillatory activity and determine the alpha-band stimulation frequencies for the subsequent visual entrainment. After computing the IAF, the visual entrainment protocol commenced. Participants underwent visual entrainment at four different frequencies: one corresponding to their IAF, two frequencies higher (IAF +2 Hz) and lower (IAF -2 Hz) relative to their IAF, and a control condition outside the alpha band, in the theta band (4.5 Hz). Each stimulation condition (IAF, IAF +2 Hz, IAF -2 Hz, and Theta) began with 1 minute of visual entrainment, immediately followed by 1 minute of eyes-closed resting state. This design allowed for the assessment of the effects of visual entrainment on post-entrainment eyes-closed resting EEG activity compared to baseline resting activity. The procedure (i.e., 1 minute of entrainment followed by 1 minute of eyes-closed resting state) was repeated nine times for each of the four stimulation conditions, resulting in nine blocks of entrainment and nine blocks of resting state per condition. Visual entrainment to the right and left hemifields was presented in separate experimental sessions, with the order of presentation randomized across participants. Similarly, the sequence of stimulation conditions was randomized. Participants were instructed to maintain their gaze on a central fixation cross during visual entrainment and to keep their head positioned on the chin rest throughout the entire experimental session.

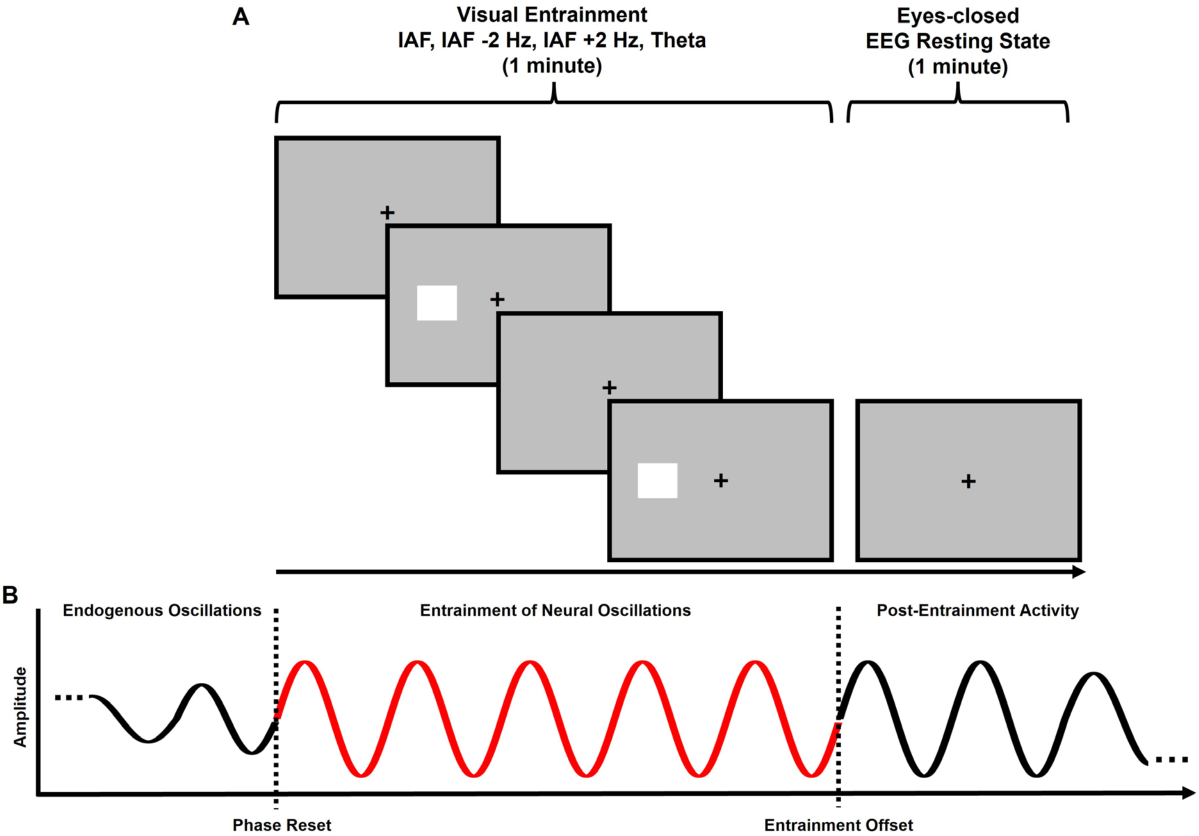

Figure 10. Schematic representation of the experimental paradigm. **A)** The experiment began with the acquisition of baseline EEG signals during eyes-closed resting state, comprising nine distinct 1-minute blocks. Following these baseline recordings, each participant's individual alpha frequency (IAF) was computed and visually examined to quantify baseline brain oscillatory activity and to establish the alpha-band stimulation frequencies for subsequent visual entrainment. After determining the IAF, the visual entrainment protocol began. Specifically, participants were administered with visual entrainment at four different frequencies: IAF, two frequencies above (IAF +2 Hz) and below (IAF -2 Hz), and a control condition outside the alpha band, within the theta range (4.5 Hz). Each condition (IAF, IAF +2 Hz, IAF -2 Hz, and theta) consisted of 1 minute of visual entrainment followed by 1 minute of eyes-closed resting. This procedure (1 minute of entrainment followed by 1 minute of rest) was repeated nine times for each condition, resulting in nine entrainment and nine resting blocks per condition. Visual entrainment was applied separately to the right and left hemifields in randomized order across participants, with randomized stimulation sequences. Participants fixated on a central cross during throughout the experimental session. **B)** Graphical representation depicting alpha-band visual entrainment. A visual rhythmic stimulation administered at a specific frequency induces a phase reset of the endogenous brain oscillations in targeted brain areas, with a subsequent phase synchronization and an increase in amplitude. At the entrainment offset, the stimulation effects can persist for several cycles.

6.2.4 Individual Alpha Frequency (IAF) Computation

The EEG signals recorded during the baseline condition were pre-processed and analyzed offline using EEGLAB (v.2022; Delorme & Makeig, 2004) and custom scripts developed in MATLAB (R2022a; The Mathworks Inc., USA). Data from all electrodes were re-referenced to the average of all scalp electrodes and filtered with a band-pass filter ranging from 1 to 100 Hz. Continuous EEG data were then segmented into 1-second epochs. Dimensionality reduction was performed using Principal Component Analysis (PCA), which reduced the data to 32 components. Independent Component Analysis (ICA) was subsequently applied, allowing for the visual identification and removal of components corresponding to horizontal and vertical eye movement artifacts. A Fast Fourier Transform (FFT) was then computed on the artifact-free EEG data, yielding a frequency resolution of 0.5 Hz. To determine the appropriate stimulation frequencies for the alpha-band entrainment conditions (i.e., IAF, IAF +2 Hz, IAF -2 Hz), the individual alpha frequency (IAF) for each participant was identified over two distinct parieto-occipital regions of interest (ROIs). These ROIs comprised seven electrodes located over the left (P1, P3, P5, P7, PO3, PO7, O1) and right (P2, P4, P6, P8, PO4, PO8, O2) scalp regions, representing the contralateral and ipsilateral ROIs relative to the stimulated hemifield. The mean stimulation frequencies for the IAF, IAF +2 Hz, and IAF -2 Hz conditions were 10.39 ± 0.57 Hz, 12.67 ± 0.58 Hz, and 8.47 ± 0.57 Hz, respectively, while the theta stimulation frequency was fixed at 4.5 Hz.

6.2.5 Alpha- and Theta-band activity: power, inter-trial phase coherence, and IAF

The EEG signals from all electrodes, acquired during the baseline condition and following the four entrainment conditions (IAF, IAF +2 Hz, IAF -2 Hz, and Theta), were re-referenced to the average of all scalp electrodes and filtered with a 1-100 Hz band-pass filter. The EEG data, consisting of nine separate 1-minute blocks of eyes-closed resting-state recordings, were combined and segmented into 1-second epochs, resulting in 540 epochs for each experimental condition. Dimensionality reduction was performed using Principal Component Analysis (PCA), reducing the data to 32 components, and Independent Component Analysis (ICA) was applied to identify and remove components corresponding to horizontal and vertical eye artifacts. A Fast Fourier Transform (FFT) was performed on each of the 540 artifact-free epochs, yielding a frequency resolution of 0.5 Hz. Individual Alpha Frequency (IAF) and alpha power were calculated for each epoch as the peak and mean power (in dB), respectively, within the 7–13 Hz range for each electrode. Additionally, inter-trial phase coherence (ITPC), a neural oscillatory measure reflecting evoked brain responses to rhythmic stimuli (Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019), was computed. As a control analysis, theta power and ITPC were calculated in the 3-6 Hz range using the same procedure. Power, ITPC, and IAF values for each epoch were averaged across blocks, yielding 60 epochs for each experimental condition. To evaluate the duration of entrainment effects on subsequent 1-minute resting-state activity, the averaged 60 epochs were divided into three segments, each containing 20 epochs. For statistical analysis, separate repeated measures ANOVAs were conducted to assess whether prolonged visual entrainment induced persistent modulations with widespread, rather than localized, effects on neural oscillatory activity. Two posterior parieto-occipital regions of interest (ROIs) - the left hemisphere (P1, P3, P5, P7, PO3, PO7, O1) and the right hemisphere (P2, P4, P6, P8, PO4, PO8, O2) - and one anterior ROI (Fp1, Fp2, AF3, AF4, AF7, AF8, F1, F2, Fz, AFz) were selected. To examine differential effects of the four entrainment conditions on resting EEG activity in the posterior ROIs compared to baseline, repeated measures ANOVAs were performed on alpha and theta measures (i.e., power, ITPC, IAF) with factors including Condition (Baseline, post-IAF, post-IAF +2 Hz, post-IAF -2 Hz, Theta), Temporal Segment (1, 2, 3), Hemisphere (Left and Right ROIs), and Stimulated Hemifield (Left or Right). Similarly, separate ANOVAs were conducted for the anterior ROI, with factors including Condition, Temporal Segment, and Stimulated Hemifield, for both alpha and theta measures. The Greenhouse–Geisser correction was applied in cases where the sphericity assumption was violated, and all post-hoc comparisons were performed using Tukey's HSD test.

6.3 Results

6.3.1 Entrainment-induced effects on oscillatory power

Alpha-band (7-13 Hz) power

For the posterior ROIs, the ANOVA conducted on alpha power revealed significant main effects of Temporal Segment ($F(2, 48) = 12.35$, $p < .001$), Hemisphere ($F(1, 24) = 4.81$, $p = 0.038$), and Condition ($F(4, 96) = 15.84$, $p < 0.001$; see Fig. 11A), with no significant effect of Stimulated Hemifield ($F(1, 24) = 0.19$, $p = 0.66$). Post-hoc comparisons for Temporal Segment indicated that alpha power was higher in the first segment ($M = 6.20$ dB, $SD = 4.58$) compared to the second ($M = 5.76$ dB, $SD = 4.36$; $p = 0.036$) and third segments ($M = 5.35$ dB, $SD = 4.07$; $p < 0.001$), with a further decrease in alpha power observed from the second to the third segment ($p = 0.049$). For Hemisphere, post-hoc comparisons showed that alpha power was higher in the right hemisphere ($M = 6.25$ dB, $SD = 4.82$) compared to the left ($M = 5.30$ dB, $SD = 4.25$; $p = 0.038$).

Regarding the Condition main factor (Fig. 10A), post-hoc comparisons revealed that alpha power was significantly higher following IAF ($M = 6.69$ dB; $SD = 5.14$; $p < 0.001$), IAF -2 Hz ($M = 6.16$ dB, $SD = 4.89$; $p < 0.001$), and IAF +2 Hz ($M = 5.92$ dB, $SD = 4.66$; $p = 0.045$), compared to the baseline condition ($M = 4.8$ dB, $SD = 4.07$). However, alpha power following Theta stimulation ($M = 5.29$ dB, $SD = 4.58$) did not significantly differ from baseline ($p = 0.34$), indicating that only entrainment in the IAF range effectively increased alpha power. The Theta condition exhibited lower alpha power compared to IAF ($p < 0.001$) and a marginally non-significant difference compared to IAF -2 Hz ($p = 0.11$). Importantly, no significant interactions were found between the main factors (p-values > 0.42), suggesting that the effects induced by alpha-band entrainment on alpha power were independent of the temporal segment, hemisphere, and stimulated hemifield. Consequently, these effects appeared to be sustained over time and distributed both ipsilaterally and contralaterally to the stimulated hemifield.

To further investigate the differential effects elicited by the different stimulation frequencies administered within the alpha-band (i.e., IAF, IAF -2 Hz, IAF +2 Hz), we calculated the power differences observed between the post-entrainment conditions and baseline activity. An additional repeated measures ANOVA was performed on these power differences, with factors including Condition Differences (IAF – Baseline, IAF -2 Hz – Baseline, IAF +2 Hz – Baseline), Temporal Segment, Hemisphere, and Stimulated Hemifield. This analysis revealed a significant main effect of Condition Differences (F(2, 48) = 11.16, p < 0.001; see Fig. 11C), indicating stronger entrainment modulations (greater power differences between baseline and post-entrainment activity) following IAF stimulation (M = 1.89, SD = 1.08) compared to both the IAF -2 Hz (M = 1.36, SD = 0.89; p = 0.007) and IAF +2 Hz conditions (M = 1.11, SD = 0.96; p < 0.001). No significant power differences were observed between the IAF -2 Hz and IAF +2 Hz conditions (p = 0.31). These findings align with previous evidence suggesting that rhythmic stimulation at participants' IAF can induce stronger resonance phenomena in neural oscillatory activity (Regan, 1982; Pikovsky et al., 2003; Thut et al., 2012).

For the anterior ROI, the ANOVA performed on alpha power did not reveal a significant main effect of Stimulated Hemifield (F(1, 24) = 0.45, p = 0.5), but significant main effects of Temporal Segment (F(2, 48) = 5.77, p = 0.005) and Condition (F(4, 96) = 5.20, p < .001; see Fig. 11B). Post-hoc comparisons for Temporal Segment indicated that alpha power was higher in the first segment (M = 2.17 dB, SD = 1.23) compared to the third segment (M = 2.0 dB, SD = 1.33; p = 0.004). For the Condition main factor (Fig. 11B), post-hoc comparisons revealed that alpha power was significantly increased following IAF (M = 2.39 dB; SD = 1.33; p = 0.003) and IAF +2 Hz (M = 2.3 dB, SD = 2.28; p = 0.019) compared to the baseline condition (M = 1.76 dB, SD = 1.13), with a significant power difference between IAF and Theta stimulation condition (M = 1.85 dB, SD = 1.27; p = 0.016). Furthermore, alpha power following Theta entrainment did not significantly differ from baseline (p = 0.98), suggesting that only IAF and IAF + 2 Hz stimulation modulated alpha power. Importantly, consistent with the findings in the posterior ROIs, the ANOVA revealed no significant interactions between the main factors (p-values > 0.107), indicating that the modulations of alpha power induced by the entrainment do not vary across temporal segments or the stimulated hemifield.

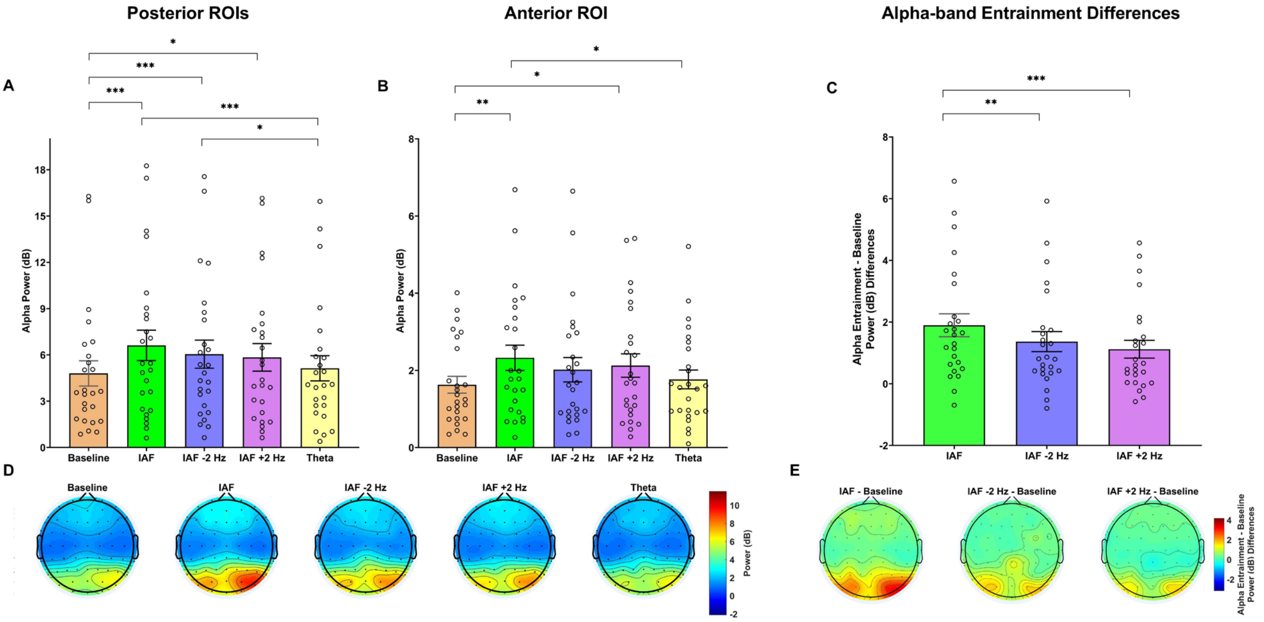

Figure 11. The figure highlights alpha-band (7-13 Hz) power results following baseline and the different entrainment conditions. **A)** Bar plot showing the effect of stimulation condition on posterior region of interests (ROIs). The results revealed that entrainment increase alpha power following alpha-band (IAF, IAF -2 Hz, IAF +2 Hz), but not theta stimulation, as compared to baseline condition. **B)** Bar plot showing the effect of stimulation condition on anterior ROI. The results revealed that entrainment increase alpha power following IAF and IAF +2 Hz, but not IAF -2 Hz and theta stimulations, as compared to baseline condition. **C)** Bar plot showing the power differences observed between the post-entrainment conditions in the alpha-band and baseline activity. The results showed that that entrainment delivered at the participants' IAF can induces stronger power modulations as compared to other alpha frequencies (i.e., IAF -2 Hz, IAF +2 Hz). **D)** Topographic scalp maps depicting alpha power over the scalp for each stimulation condition. **E)** Topographic scalp maps depicting alpha power differences between each alpha-band entrainment condition and baseline power. The error bars indicate the standard error of the mean (SEM); black circles show the individual values. $^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

Theta-band (3-6 Hz) power

In contrast to the findings for alpha power, the control ANOVA conducted on theta power revealed a significant main effect of Hemisphere (F(1, 24) = 5.91, p = 0.022), indicating that higher theta power was observed in the right hemisphere (M = 0.76 dB, SD = 0.034) compared to the left hemisphere (M = 0.72 dB, SD = 0.41; p = 0.013). However, no other significant main effects or interactions were found (p-values > 0.117). Similarly, in the anterior ROI, the analysis revealed no significant main effects or interactions (p-values > 0.136). These results suggest that the entrainment administered within both the alpha and theta bands did not induce any significant modulation of theta power in either the posterior or anterior ROIs (see Fig. 12). This finding indicates that while alpha power was effectively modulated by the specific entrainment conditions, theta power remained stable across the experimental conditions, highlighting a distinct response pattern in the neural oscillatory activity associated with these frequency bands.

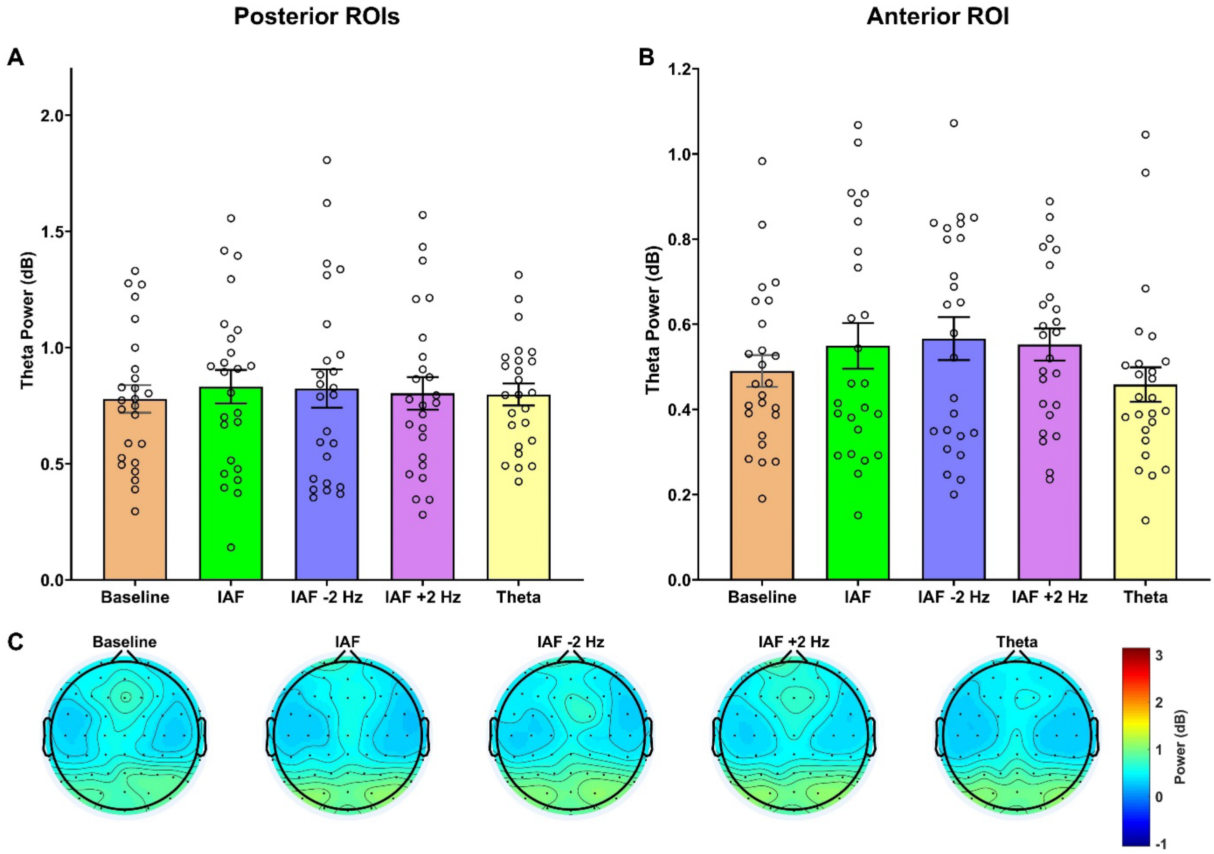

Figure 12. The figure highlights theta-band (3-6 Hz) power results following baseline and the different entrainment conditions. **A)** Bar plot showing the effect of stimulation condition on posterior region of interests (ROIs). The results did not reveal any entrainment-induced modulations on theta power over the posterior ROIs. **B)** Bar plot showing the effect of stimulation condition on anterior ROI. The results did not show significant power modulations. **C)** Topographic scalp maps depicting theta power over the scalp for each stimulation conditions. The error bars indicate the standard error of the mean (SEM); black circles show the individual values.

6.3.2 Entrainment-induced effects on oscillatory ITPC

Alpha-band (7-13 Hz) ITPC

For the posterior ROIs, the repeated measures ANOVA performed on ITPC indicated significant main effects of Temporal Segment (F(2, 48) = 4.79, p = 0.012) and Condition (F(4, 96) = 3.51, p = 0.01; see Fig. 13). However, there were no significant effects observed for Stimulated Hemifield (F(1, 24) = 0.72, p = 0.4) or Hemisphere (F(1, 24) = 0.95, p = 0.33).

Post-hoc comparisons regarding the Temporal Segment revealed that alpha ITPC was significantly higher in the first segment (M = 0.5 dB, SD = 0.14) compared to the third segment (M = 0.47 dB, SD

= 0.16; p = 0.01); all other comparisons were not statistically significant (p-values > 0.11). Notably, post-hoc comparisons for the Condition factor showed that alpha ITPC was significantly greater following individual alpha frequency (IAF) stimulation (M = 0.52, SD = 0.16; see Fig. 13A) compared to the baseline condition (M = 0.46, SD = 0.12; p = 0.004), while no other comparisons reached significance (p-values > 0.09). This indicates that only IAF entrainment resulted in an increase in alpha ITPC. No significant interactions were found between the main factors (p-values > 0.07), suggesting that the effects of IAF stimulation on alpha ITPC were consistent across temporal segments, hemispheres, and stimulated hemifields, demonstrating sustained effects over time that were topographically distributed both ipsilaterally and contralaterally to the stimulated hemifield.

Conversely, in the anterior ROI, the ANOVA conducted on alpha ITPC revealed no significant main effects or interactions (p-values > 0.067; see Fig. 13B), indicating that none of the entrainment conditions modulated ITPC in the anterior scalp region.

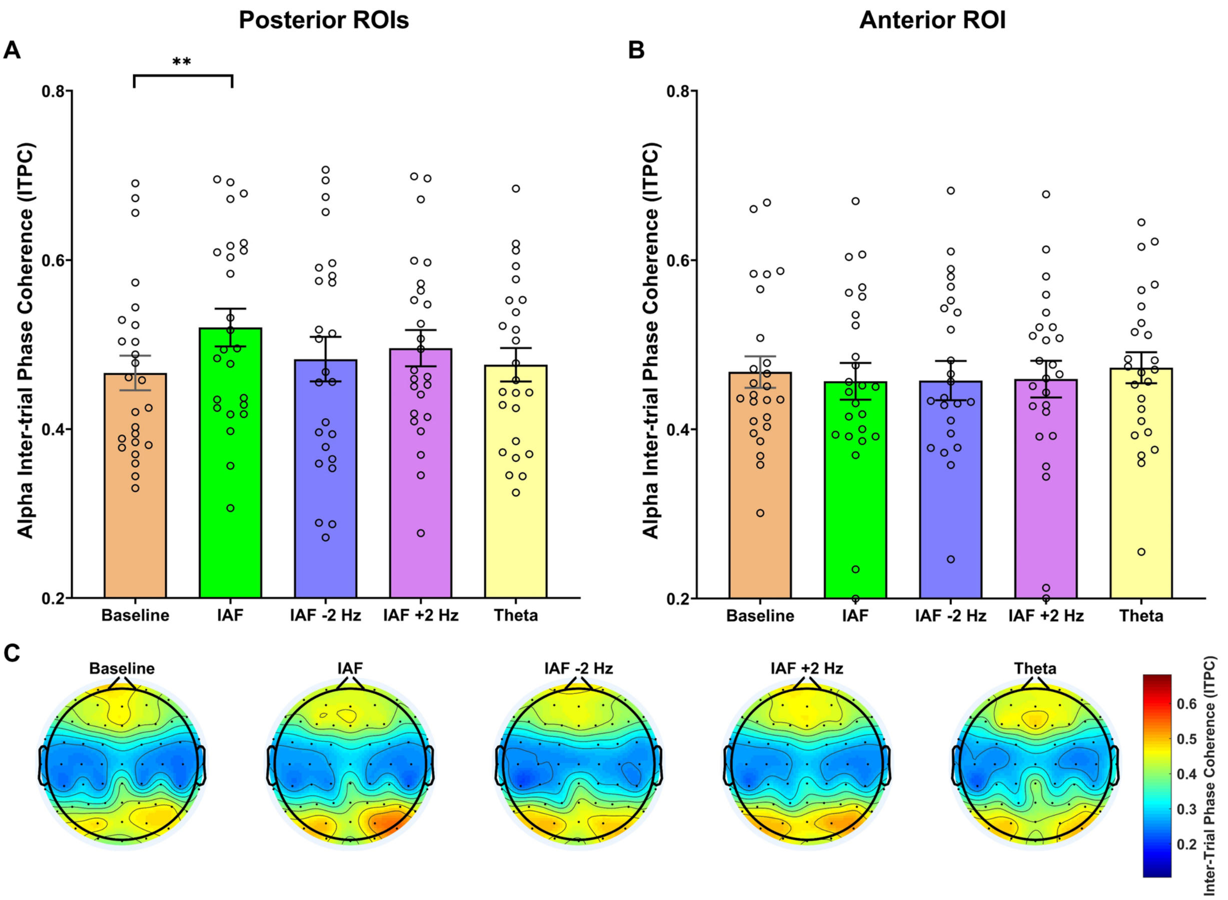

Figure 13. The figure highlights alpha-band (7-13 Hz) Inter-Trial Phase Coherence (ITPC) results following baseline and the different entrainment conditions. **A)** Bar plot showing the effect of stimulation condition on posterior region of

interests (ROIs). The results revealed that entrainment increase alpha power following IAF entrainment, with respect to baseline condition. **B)** Bar plot showing the effect of stimulation condition on anterior ROI. The results revealed that entrainment did not induces any significant modulation of alpha ITPC following stimulation conditions. **C)** Topographic scalp maps depicting alpha ITPC over the scalp for each stimulation condition. The error bars indicate the standard error of the mean (SEM); black circles show the individual values. *p < .05. **p < .01. ***p < .001.

Theta-band (3-6 Hz) ITPC

The repeated measures ANOVA conducted on theta ITPC revealed a significant main effect of Stimulated Hemifield (F(1, 24) = 4.81, p = 0.038) and Condition (F(4, 96) = 2.72, p = 0.033; see Fig. 14). However, no significant effects were observed for Hemisphere (F(1, 24) = 3.20, p = 0.086) and Temporal Segment (F(2, 48) = 2.77, p = 0.072). Post-hoc comparisons indicated that theta ITPC was significantly higher following stimulation delivered to the right hemifield (M = 0.49, SD = 0.13) compared to the left hemifield (M = 0.44, SD = 0.18; p = 0.038). Regarding the main effect of Condition (Fig. 14A), post-hoc analyses did not reveal any significant comparisons among the different stimulation conditions (p-values > 0.08). Furthermore, no significant interactions were found between the main factors (p-values > 0.058).

In the anterior ROI, the ANOVA performed on alpha ITPC did not show significant main effects for Stimulated Hemifield (F(1, 24) = 0.99, p = 0.32) and Condition (F(4, 96) = 1.33, p = 0.26). However, there was a significant main effect of Temporal Segment (F(2, 48) = 3.55, p = 0.036). Post-hoc comparisons indicated that alpha ITPC was significantly higher in the first segment (M = 0.72, SD = 0.24) compared to the second segment (M = 0.70, SD = 0.21; p = 0.037). All other comparisons, including those related to the Condition factor (Fig. 14B), were not statistically significant (p-values > 0.13). No significant interactions were found between the main factors (p-values > 0.51).

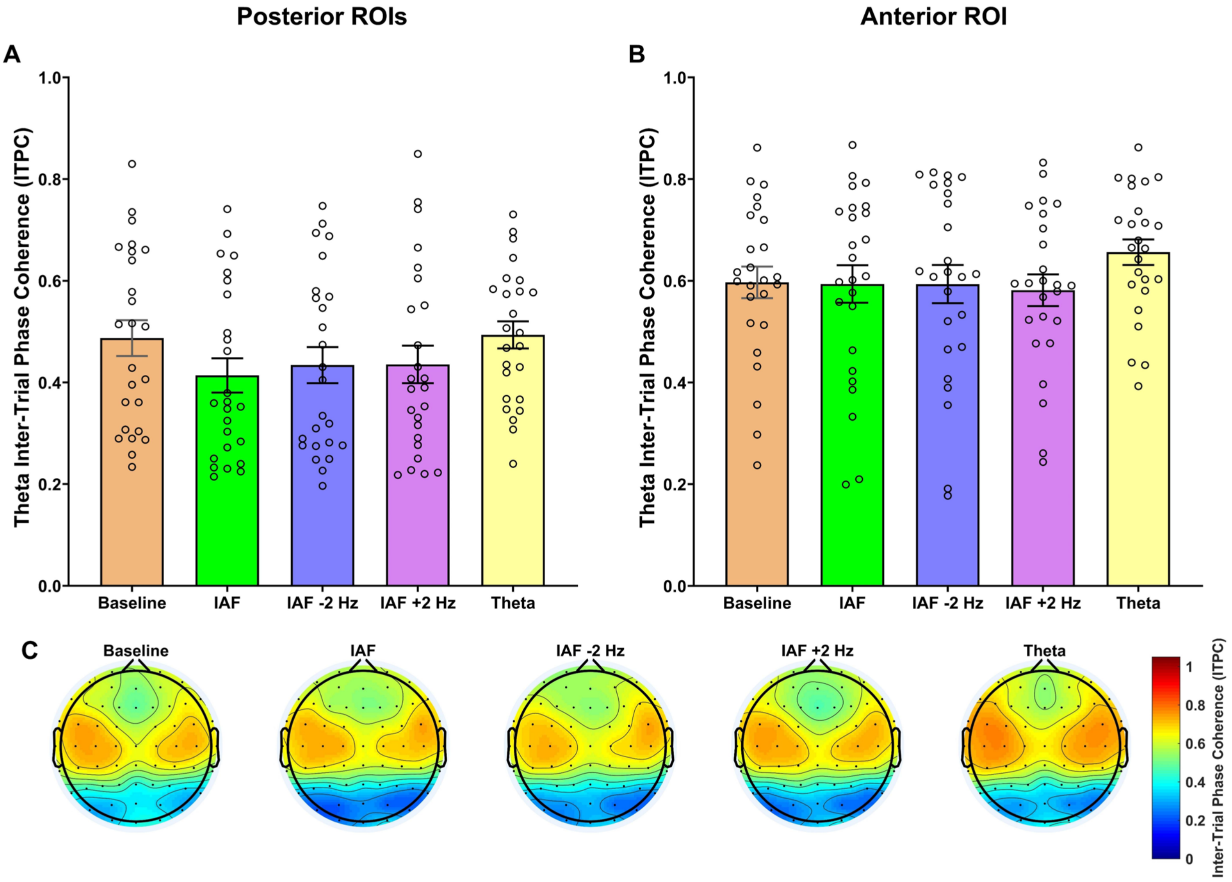

Figure 14. The figure highlights theta-band (3-6 Hz) Inter-Trial Phase Coherence (ITPC) results following baseline and the different entrainment conditions. **A)** Bar plot showing the effect of stimulation condition on posterior region of interests (ROIs). The results did not reveal any entrainment-induced modulations on theta ITPC over the posterior ROIs. **B)** Bar plot showing the effect of stimulation condition on anterior ROI. The results did not show significant power modulations. **C)** Topographic scalp maps depicting theta ITPC over the scalp for each stimulation conditions. The error bars indicate the standard error of the mean (SEM); black circles show the individual values.

6.3.3 Entrainment-induced effects on IAF

We also analyzed potential shifts in the frequency peak, which were separately identified as the highest peaks in both the power spectrum (i.e., IAF) and inter-trial phase coherence (ITPC), induced by the different stimulation frequencies within the alpha band (i.e., IAF, IAF +2 Hz, and IAF -2 Hz) in comparison with one another and the baseline condition (see Fig. 15). This analysis aimed to determine whether rhythmic visual entrainment at specific frequencies would lead to systematic changes in the peak frequency of oscillatory activity.

The ANOVA conducted on the individual alpha frequency (IAF) observed in the power spectrum over the posterior ROIs revealed a significant main effect of Temporal Segment ($F(2, 48) = 29.96$, $p < 0.001$). No other significant main effects or interactions were identified (p-values > 0.12). Post-hoc comparisons for the Temporal Segment indicated that the IAF was faster in the first segment (M = 10.41 Hz, SD = 0.81) compared to the second (M = 10.23 Hz, SD = 0.77; $p < 0.001$) and third segments (M = 10.25 Hz, SD = 0.68; $p < 0.001$). This finding suggests that the speed of IAF decreases over time, regardless of stimulation conditions, stimulated hemifield, or hemisphere. All other comparisons were not statistically significant (p-values > 0.13).

Similarly, the ANOVA performed on the anterior ROI demonstrated a significant main effect of Temporal Segment ($F(2, 48) = 37.84$, $p < 0.001$), indicating a faster IAF in the first segment (M = 10.18 Hz, SD = 0.89) compared to the second (M = 10.35 Hz, SD = 1.11; $p < 0.001$) and third segments (M = 10.20 Hz, SD = 0.97; $p < 0.001$). No other significant main effects or interactions were found (p-values > 0.14).

The ANOVA examining the frequency peak observed in the ITPC over the posterior ROIs revealed no significant main effects or interactions (p-values > 0.063). Likewise, the ANOVA conducted on the anterior ROI also did not show significant main effects or interactions (p-values > 0.19).

Overall, these results suggest that while a relative decrease in IAF speed was observed over time, none of the entrainment conditions induced a significant change in the frequency peak, either speeding it up or slowing it down.

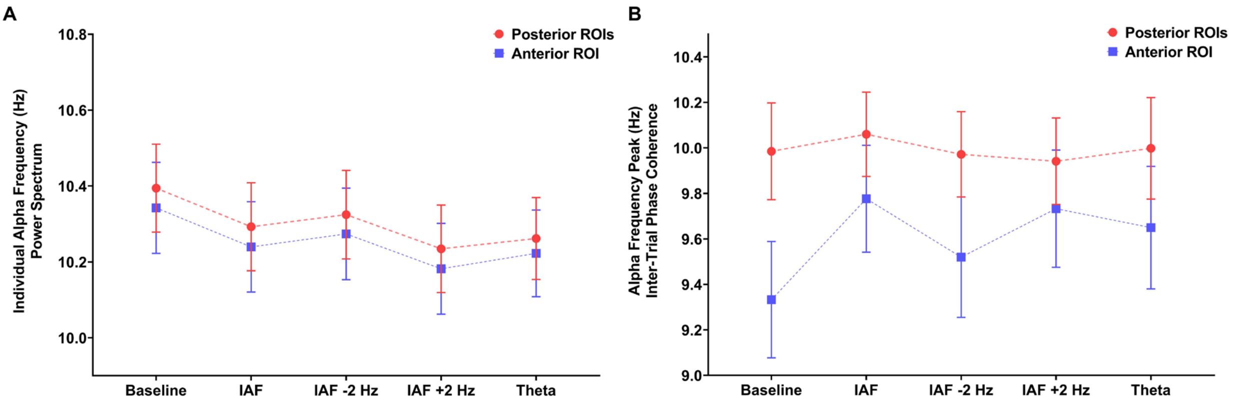

Figure 15. The figure depicts the alpha frequency peak identified on power **(A)** and Inter-Trial Phase Coherence (ITPC; **B)** spectrums following each stimulation condition, separately for posterior (red lines) and anterior (blue lines) Region of Interests (ROIs). However, such analysis did not reveal any significant modulations of alpha peak frequency both in power and ITPC spectral measures. The error bars indicate the standard error of the mean (SEM).

6.3.4 Correlation between baseline and post-entrainment Alpha Power and ITPC

Based on the significant modulations of alpha power and inter-trial phase coherence (ITPC) induced by entrainment administered within the alpha band, we hypothesized that baseline oscillatory activity might influence the strength of the observed post-entrainment activity modulations, as previously reported (Helfrich et al., 2014). Accordingly, we performed Pearson correlational analyses separately for alpha power and ITPC measures, distinguishing between posterior and anterior ROIs. This analysis aimed to link baseline activity to the differences observed between the various entrainment conditions (i.e., IAF, IAF -2 Hz, and IAF +2 Hz) and baseline. By examining these correlations, we aimed to investigate how individual variations in baseline oscillatory activity could predict the effectiveness of visual entrainment in modulating neural oscillations.

Regarding alpha power, we found that in the posterior ROIs, higher baseline power was associated with a greater difference following IAF entrainment ($r = 0.424$, $p = 0.035$; Fig. 16A). In contrast, no significant correlations were observed after IAF -2 Hz ($r = 0.353$, $p = 0.084$) or IAF +2 Hz ($r = 0.265$, $p = 0.2$). This indicates that the stronger resonance phenomena following IAF stimulation were specific to neural activity in the posterior scalp regions. In the anterior ROI, however, no significant correlations emerged ($p > 0.65$), suggesting that the relationship between baseline alpha power and changes following stimulation does not extend to more frontal brain regions. On the other hand, when examining alpha ITPC (Fig. 16B), the results did not reveal significant correlations for either the posterior (p-values > 0.38) or anterior ROIs (p-values > 0.62).

Overall, these correlational results suggest that increased alpha power following IAF stimulation may be predicted by higher alpha power during the baseline condition, particularly in the posterior scalp areas. Importantly, no significant associations were found for the ITPC measure, indicating that the effects of IAF stimulation on alpha power do not extend to phase coherence in the analyzed scalp regions.

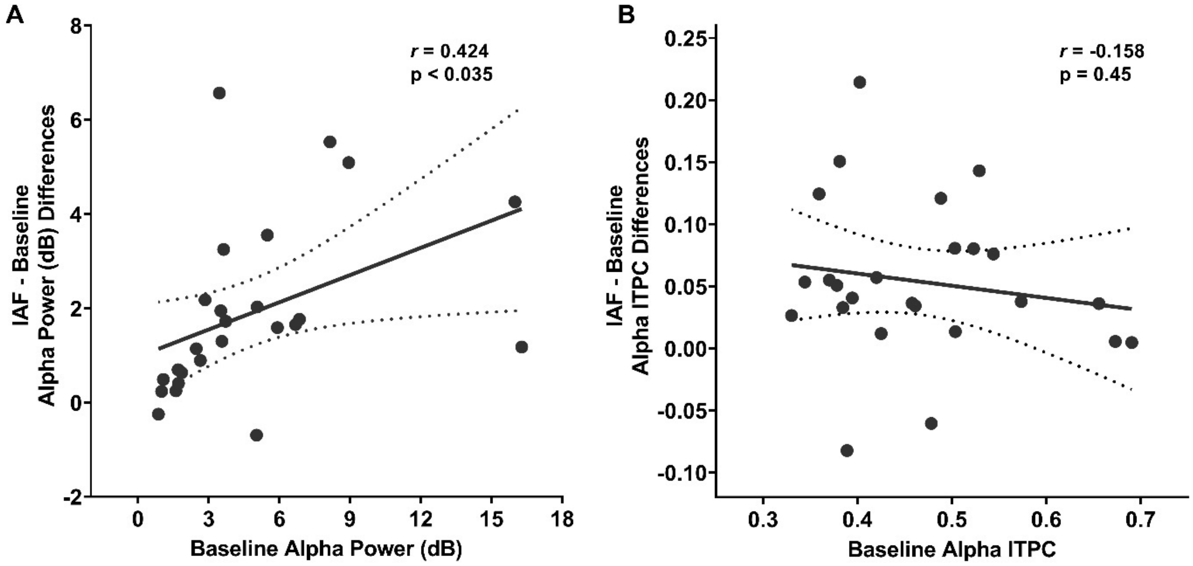

Figure 16. The figure highlights the relationships revealed by the Pearson correlation coefficient between baseline Alpha Power **(A)** and Inter-Trial Phase Coherence (ITPC; **B**) and the differences observed between post-IAF entrainment and the baseline activity. A positive association was found only for the alpha power (*r* = 0.424; p < 0.035).

6.4 Discussion

The main purpose of the current study was to investigate whether prolonged alpha-band visual entrainment can induce persistent and frequency-specific modulations of resting-state alpha oscillatory activity following the offset of stimulation, with potential differential outcomes depending on the stimulation frequency (i.e., IAF, IAF -2 Hz, IAF +2 Hz, Theta). Additionally, we explored whether these entrainment-induced effects were diffuse rather than topographically focal on the scalp, examining neural activity across both posterior and anterior brain areas.

Overall, our findings indicate that, compared to baseline oscillatory activity, prolonged alpha-band visual entrainment selectively enhanced both power and inter-trial phase coherence (ITPC) in the alpha frequency band, while no significant effects were observed in the theta frequency band. Notably, these enhancements persisted throughout the 1-minute post-entrainment resting-state period, suggesting that the effects of entrainment were not only significant but also sustained over time. This highlights the potential of alpha-band entrainment as a method for modulating neural oscillations and enhancing perceptual performance. Furthermore, the entrainment of neural oscillations at participants' individual alpha frequency (IAF) resulted in stronger modulations of alpha spectral measures compared to IAF -2 Hz, IAF +2 Hz, and theta stimulation frequencies. These effects were comparable in both posterior scalp areas, contralateral and ipsilateral to the stimulated hemifield, and even led to a further increase in alpha oscillatory spectral measures that extended across the anterior scalp region. While this overall pattern of results aligns with previous studies and provides further evidence of the efficacy of alpha-band visual entrainment in enhancing ongoing alpha oscillatory activity (Thut et al., 2011a; Mathewson et al., 2012; Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019; Wiesman & Wilson, 2019; Szaszkó et al., 2024; Fakche & Duguè, 2024; for a recent review, see: Gallina et al., 2023), our findings also reveal significant aspects of sensory entrainment that can extend its potential applications, by highlighting how prolonged visual rhythmic stimulation can impact the activity of different oscillatory spectral measures across various neural circuits.

First, our findings highlighted that the effects of alpha-band visual stimulation on resting-state alpha power can be persistently observed (i.e., ~1 minute) following prolonged trains of rhythmic stimulation. Specifically, we found that after alpha-band stimulation (i.e., IAF, IAF -2 Hz, and IAF +2 Hz), but not after theta entrainment, there was a sustained increase in alpha power in posterior scalp areas. This effect was topographically diffuse, affecting both ipsilateral and contralateral regions to the stimulated hemifield, when compared to baseline brain oscillations and following theta entrainment. Importantly, when considering the potential differential effects of various stimulation frequencies within the alpha band, our results indicated that stronger entrainment modulations (characterized by greater power differences between baseline and post-entrainment activity) were specifically observed following IAF stimulation. Additionally, we noted an increase in alpha power in the anterior scalp area following IAF stimulation, but not after theta stimulation, when compared to baseline and theta entrainment alpha power. These results are consistent with previous evidence suggesting that rhythmic stimulation tuned to IAF induces stronger resonance phenomena in the neural oscillatory activity of the visual system (e.g., Regan, 1982; Pikovsky et al., 2003; Thut et al., 2012; Vossen et al., 2015; Notbohm et al., 2016), underscoring the importance of tailoring rhythmic stimulation to individuals' neural rhythms to maximize the effectiveness of sensory entrainment.

Importantly, our findings suggest that the effects of alpha-band visual entrainment on alpha power can be topographically diffuse and distributed, rather than being focal and confined to the contralateral posterior areas, as previously reported (Mathewson et al., 2012; Spaak et al., 2014). The widespread effect on alpha power observed in this study may arise from the fact that previous research typically employed short trains of rhythmic entrainment (i.e., ~0.5–5 seconds; Mathewson et al., 2011; De Graaf et al., 2013; Spaak et al., 2014; Kizuk & Mathewson, 2017; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019). While these brief sessions effectively induced transient modulations of alpha oscillatory power, they were likely too short to produce the more widespread aftereffects we observed over the scalp. In contrast, our findings indicated increased alpha power not only in the contralateral posterior area but also ipsilateral to the stimulation and in anterior regions. This suggests that more distributed entrainment aftereffects can emerge when rhythmic stimulation is delivered in a sustained manner, potentially engaging widespread cortical networks, leading to a broad increase in alpha power and involving mechanisms of neural plasticity both within and beyond the occipito-parietal cortices, ultimately resulting in the wiring of reverberating neural circuits and in a diffuse modulations of cortical excitability (Vossen, 2015; Otero et al., 2022).

Interestingly, it is possible to speculate that these widespread effects of entrainment can also be understood within the framework that describes alpha oscillations as traveling waves orchestrating information flow across different brain areas (Zhang et al., 2018; Lozano-Soldevilla and VanRullen, 2019; Alamia & VanRullen, 2019, 2024; Fakche & Duguè, 2024). Indeed, while alpha activity is predominantly distributed over the occipito-parietal cortices (e.g., Williamson et al., 1997; Rosanova et al., 2009), alpha oscillations also extend to more centro-frontal neural sources, propagating in various directions - both forward (from anterior to posterior areas) and backward (from posterior to anterior areas) - depending on brain states and task demands (Alamia & VanRullen, 2024; Fakche & Duguè, 2024). In the presence of lateralized visual stimulation, alpha-band oscillations have been shown to propagate across the topographic space from occipital to frontal regions, as well as to areas ipsilateral to the visual inputs (Alamia & VanRullen, 2024). Accordingly, the observed alpha power modulations following rhythmic stimulation in both ipsilateral and anterior scalp regions may rely on a reverberation of entrainment-induced modulations in the contralateral posterior scalp area, propagating forward through alpha waves across the scalp (Alamia & VanRullen, 2024; Fakche & Duguè, 2024), underscoring the potential of prolonged alpha-band visual stimulation not only to enhance local oscillatory activity but also to facilitate communication across broader neural networks. Future empirical research is needed to investigate this hypothesis by evaluating the effects of alpha-band sensory entrainment on alpha traveling waves.

Interestingly, when we investigated how baseline alpha power might impact the strength of post-entrainment aftereffects on resting-state oscillatory activity, we found a significant positive correlation between higher baseline alpha power and a stronger increase in alpha power following entrainment administered at participants' IAF selectively in posterior, but not in anterior scalp regions. Such a finding supports the hypothesis that stimulation rhythms resonant with the individual frequency of the occipito-parietal system (i.e., IAF) may effectively synchronize endogenous alpha-band oscillatory activity in posterior regions, with propagating and diffused effects extending to the anterior scalp regions.

In contrast to alpha power, we observed a sustained increase in alpha inter-trial phase coherence (i.e., ITPC) over the 1-minute resting-state period, but this effect was selectively obtained following IAF stimulation in the posterior scalp areas, affecting both ipsilateral and contralateral regions relative to the stimulated hemifield. Notably, there were no significant modulations of alpha ITPC in the anterior scalp areas across the different stimulation conditions, potentially indicating that the effects of entrainment on alpha ITPC were localized to the posterior regions and were significantly sensitive to the stimulation frequency (i.e., IAF entrainment).

While our findings align with previous research indicating that phase synchronization between alpha oscillations and external rhythmic stimuli occurs when the stimulation frequency is matched to the preferred frequency of the visual oscillatory system (Pikovsky et al., 2003; Thut et al., 2012), they also underscore the differential impacts of entrainment on oscillatory spectral measures of power and phase coherence. Prior studies employing brief rhythmic (e.g., Spaak et al., 2014; Gray & Emmanouil, 2019) and quasi-rhythmic stimulations (e.g., Keitel et al., 2018, 2019) have offered insights into how distinct populations of endogenous neural oscillations synchronize with external rhythmic inputs, showing the varying effects of rhythmic visual stimulation on spectral measures of alpha oscillatory activity. Indeed, research on rhythmic visual stimulation in the alpha band has demonstrated that power and ITPC may represent two distinct yet interrelated functional populations of alpha activity within the visual system. Here, alpha power is thought to reflects self-sustained endogenous oscillatory activity, while ITPC captures evoked responses that are phase-locked to visual stimulation (Makeig et al., 2002; Spaak et al., 2014; Keitel et al., 2019). When rhythmic visual stimulation is applied, it generally enhances intrinsic alpha power by synchronizing ongoing, self-generated neural oscillations and increasing the consistency of oscillatory phase (i.e., ITPC) across trials due to continuous evoked responses to the rhythmic input (Spaak et al., 2014; Keitel et al., 2019; Gray & Emmanouil, 2019). Furthermore, power and ITPC have been shown to be interrelated, with the amplification of endogenous neural oscillations in response to rhythmic stimuli depending on the initial phase-locking of ongoing neural activity to the external stimulation (Mathewson et al., 2009). Thus, the differing effects on alpha oscillatory measures observed in our study may be attributed to the modulation of self-sustained endogenous alpha oscillations by alpha-band visual entrainment, which persisted independently after the stimulation ended, showing widespread and generalized effects across the range of alpha-band stimulations (i.e., IAF, IAF -2 Hz, IAF +2 Hz). In contrast, alpha ITPC, which reflects stimulus-related activity primarily generated in the brain regions where endogenous alpha oscillations occur (i.e., posterior brain areas), indicated that the persistent increase in this spectral parameter was confined to stimulation at the IAF in the posterior scalp areas, likely suggesting a reverberation of the evoked responses to visual rhythmic stimulation during the 1-minute of resting state alpha oscillatory activity (Keitel et al., 2018, 2019). Overall, these findings highlight that while alpha power was consistently increased across both posterior and anterior scalp regions following all alpha-band entrainment frequencies, ITPC was specifically enhanced in the posterior areas when the stimulation frequency matched participants' IAF, thus supporting the idea that two distinct neural mechanisms - reflected in evoked responses to rhythmic stimulation (i.e., ITPC) and ongoing endogenous oscillations (i.e., power) - may underlie the entrainment effects associated with alpha oscillatory activity synchronization (Keitel et al., 2018, 2019; Gray & Emmanouil, 2019).

Notably, our findings did not reveal a synchronization of the IAF peak with the external stimulation frequencies, aligning with previous research that demonstrated significant changes in both power and ITPC spectral measures, while showing no shift in IAF (Spaak et al., 2014; Keitel et al., 2018, 2019; Wiesman & Wilson, 2019; Gray & Emmanouil, 2019; but also see: Ronconi & Melcher, 2017). The lack of modulation in IAF following alpha-band visual entrainment may be attributed to the notion that IAF represents a stable characteristic of spectral activity (e.g., Grandy et al., 2013). Rather than being influenced by bottom-up sensory stimulation, IAF appears to reflect neural mechanisms that internally regulate perceptual processing, remaining unaffected by external environmental perturbations (Grandy et al., 2013; Gray & Emmanouil, 2019).

Crucially, although our study observed persistent post-entrainment effects, it remains unclear which neural mechanisms enable the sustained impact of entrainment-driven signals over time. It has been proposed that both online and offline transient modulations of neural oscillatory activity, observable after brief periods of rhythmic entrainment, may depend on long-term potentiation (LTP) mechanisms of neural plasticity, which facilitate the enhancement of neural oscillatory activity (Vossen, 2015). Consequently, we can hypothesize that the long-lasting increases in alpha spectral measures (i.e., power and ITPC) identified in our study might also be influenced by LTP mechanisms, believed to sustain the aftereffects of entrainment. Further support for this hypothesis comes from computational studies that have simulated the effects of entrainment on neural systems, indicating that the strongest entrainment effects occur when the driving stimulation frequency aligns with the resonance frequency of the simulated neural system (Jansen et al., 1993; Otero et al., 2022). While these findings connect models of neural oscillations with empirical observations and provide insights into the mechanisms driving neural entrainment, future research that combines both empirical and computational approaches is essential to elucidate these mechanisms further.

Overall, our findings provide the first empirical evidence that alpha-band visual entrainment can lead to long-lasting modulations of alpha oscillatory activity across a wide range of scalp areas, especially when the stimulation frequency aligns with participants' IAF. An intriguing area for future investigation is the exploration of how alpha-band sensory entrainment could functionally enhance alpha oscillatory activity. Since alpha oscillations are closely associated with various aspects of visual perception and serve as a reliable indicator of perceptual processing (Klimesh et al., 2007; Sadaghiani & Kleinschmidt, 2016), our findings suggest that prolonged entrainment paradigms could selectively enhance sensory encoding and influence visual awareness through the plastic reorganization of the underlying oscillatory systems. Such prolonged sensory entrainment methods may hold significant therapeutic promise for patients with posterior brain damage and visual field deficits (Pietrelli et al., 2019; Allaman et al., 2021; Gallina et al., 2022), as well as for individuals with neurodevelopmental disorders characterized by atypical alpha oscillatory activity (for a recent review, see: Ippolito et al., 2022).

Chapter 7

Prolonged effects of alpha-band visual entrainment on visual detection performance

7.1 Introduction

In the previous chapter (i.e., Chapter 6), we discussed empirical findings highlighting the efficacy of visual alpha-band sensory entrainment in inducing persistent modulations of endogenous alpha oscillatory activity observable in the minute following the entrainment offset. These findings suggest that visual alpha-band entrainment, but non theta stimulation, can induce prolonged changes in alpha spectral measures, particularly when the stimulation is tuned to alpha-band frequencies, with stronger effects observed following IAF stimulation. In the current chapter, the efficacy of visual entrainment administered in the alpha frequency band (i.e., IAF, IAF -2 Hz, IAF +2 Hz) will be examined to evaluate its ability in inducing persistent effects, observable over 1 minute after the stimulation offset, on visual performance in a simple visual detection task (for a similar experimental paradigm, see: Gallina et al., 2024).

As highlighted in previous sections, alpha oscillations have consistently been associated with various aspects of visual information processing, demonstrating differential behavioral outcomes depending on the momentary phase and power of ongoing oscillatory activity (Mathewson et al., 2009; Busch et al., 2009; Samaha et al., 2017; Ronconi & Melcher, 2017; Cuello et al., 2022; Di Gregorio et al., 2022; Benwell et al., 2022).Within this framework, prior studies consistently showed that transient reductions in alpha power preceding stimulus presentation enhances visual detection, highlighting the role of alpha desynchronization in optimizing the timing of visual information processing (Ergenoglu et al., 2004; Klimesch et al., 2007; van Dijk et al., 2008; Mathewson et al., 2009; Di Gregorio et al., 2022). Relatedly, visual stimuli presented during the positive phase of the alpha cycle elicit stronger neural responses, improving visual detection and perceptual sensitivity (Hanslmayr et al., 2007; Spaak et al., 2014; Samaha et al., 2016, 2017). Interestingly, alpha oscillations also influence decision criterion in perceptual judgments, with a higher alpha power associated with a more conservative decision criterion, reflecting heightened attentional inhibition of visual information processing (Samaha et al., 2016, 2017; Di Gregorio et al., 2022).

Furthermore, using a methodological approach known as "dense-sampling", rhythmic patterns at alpha frequencies have been also observed in perceptual performance (Balestrieri et al., 2022; de Graaf et al., 2013; Drewes et al., 2015; Landau & Fries, 2012; Ronconi et al., 2018; Ronconi & Melcher, 2017; Gallina et al., 2024). In this regard, by densely sampled in time visual performance, previous evidence has documented an intrinsic rhythmic pattern in behavioral performance that fluctuate within the alpha frequency band when individuals process visual information (~10 Hz; Dugué et al., 2011; McLelland et al., 2016; VanRullen, 2016; Ronconi & Melcher, 2017; Gallina et al., 2024), corresponding to the neural oscillatory activity of alpha oscillations observable over parieto-occipital brain areas (Dugué et al., 2011; McLelland et al., 2016).

Overall, these findings highlight the intrinsic importance of alpha-band oscillatory activity in orchestrating visual information processing. Importantly, by synchronizing endogenous oscillatory activity to external alpha-band rhythmic stimulation through the mechanisms of neural entrainment (see previous sections), it has been revealed that spontaneous alpha oscillations can be externally modulated, providing insight into the relationship between visual perception and neural rhythms via phase-locking, and promoting functional modelling of alpha brain activity (Lakatos et al., 2019; Gallina et al., 2023). In this context, alpha-band sensory entrainment has proven particularly effective in enhancing visual performance by modulating oscillatory networks and facilitating intra- and cross-modal sensory interactions (e.g., Ronconi & Melcher, 2017; Ronconi et al., 2018; Marsicano et al., 2024). A key feature of this approach is its ability to amplify sensory inputs aligned with rhythmic stimuli, generating temporal regularities that enhance subsequent visual information processing (Busch et al., 2009; Mathewson et al., 2010). For instance, brief trains of alpha-band visual entrainment administered trial-by-trial before a visual cueing task have been shown to improve visual detection when targets were presented in-phase with the rhythmic sensory stream (Mathewson et al., 2010; De Graaf et al., 2013; Spaak et al., 2014; Wiesman & Wilson, 2019), further revealing that the effects induced by alpha-band visual entrainment do not revert to baseline levels immediately following the end of the stimulation, but instead these effects can persist for ~3-5 alpha cycles (~300-500 ms; Spaak et al., 2014; Wiesman & Wilson, 2019; De Graaf et al., 2013; Marsicano et al., 2024). However, some aspects of the effects of alpha-band visual entrainment on visual performance remain to be clarified. In this regard, it remains unknown whether prolonged alpha-band stimulation can induce long-lasting, persistent modulations of visual performance. Previous studies have predominantly used short-duration trains of rhythmic sensory stimulation (~0.5–5 seconds) on a trial-by-trial basis, yielding transient perceptual effects that typically persist only briefly after the entrainment period (~100–550 milliseconds; Mathewson et al., 2012; Spaak et al., 2014; Kizuk & Mathewson, 2017; Wiesman & Wilson, 2019; Gray & Emmanouil, 2019), thus leaving unresolved whether extended alpha-band sensory stimulation can produce sustained modulations of visual information processing. Additionally, it remains debated which properties of alpha-band rhythmic stimulation are most effective in modulating neural oscillatory activity. Neural entrainment is frequency-dependent, relying on the relationship between the stimulation frequency and the intrinsic oscillatory properties of the targeted brain regions (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016; Huang et al., 2021; Otero et al., 2022). Evidence shown that entrainment tuned to alpha band frequencies induces specific modulations of alpha oscillatory activity in occipito-parietal regions, affecting visual performance, with more pronounced effects when the stimulation frequency matches the neural system's preferential rhythm (i.e., IAF; Mathewson et al., 2011; Spaak et al., 2014; Keitel et al., 2018, 2019), but whether deviations from IAF during stimulation yield different perceptual outcomes remains currently unclear.

Importantly, to effectively reveal the impact of alpha-band sensory entrainment on visual performance, it is essential to identify the behavioural measures that best capture the modulated perceptual and cognitive mechanisms underlying visual information processing. Most studies investigating the effects of alpha-band sensory entrainment on visual performance have primarily focused on response accuracy and detection rate, consistently documenting an increase in visual detection following alpha-band rhythmic stimulation (e.g., De Graaf et al., 2013; Spaak et al., 2014). However, although accuracy has proven to be an effective measure for revealing the effects of alpha-band entrainment on visual performance, this approach might obscure specific modulations that cannot be addressed through the analysis of this behavioral index alone, as alpha oscillatory activity influences various aspects of perceptual performance, modulating both visual information processing and the decision-making mechanisms underlying perceptual judgments (Samaha et al., 2016, 2017; Di Gregorio et al., 2022). In this regard, measures derived from the signal detection theory framework (SDT; Green & Swets, 1966), such as perceptual sensitivity (*d'*) and decision criterion (*c*), have been shown to be more sensitive in revealing different aspects of visual information processing (Samaha et al., 2016, 2017; Buergers & Noppeney, 2022; Di Gregorio et al., 2022). Thus, adopting measures derived from SDT framework would allow for disentangling how alpha-band sensory entrainment differentially affects various aspects of visual performance by evaluating modulations in perceptual sensitivity while accounting for shifts in decision criterion.

To address these questions, in the current study participants performed a visual detection task before and after blocks of prolonged visual entrainment (i.e., 1 minute of duration) to investigate whether visual rhythmic stimulation, presented in the right or left hemifields (across different experimental sessions) at various frequencies within the alpha band (i.e., IAF, IAF -2 Hz, and IAF +2 Hz), could induce persistent effects on different aspects of visual performance (i.e., hit rate, perceptual sensitivity and decision criterion) observable after the stimulation offset, by modulating the underlying alpha-band oscillatory activity. This was achieved by comparing visual detection performance before and after the entrainment, separately for each stimulation condition and hemifield. Additionally, we explored which alpha-band stimulation frequency was most effective in inducing maximal effects on visual performance.

7.2 Methods

7.2.1 Participants

A total of 16 healthy young adults (9 females, mean age = 24.2 years, SD = 3.28) were recruited among university students. Participants did not receive compensation or course credits. All were volunteers and presented normal or corrected-to-normal vision and hearing. Exclusion criteria were self-reported neurological and attention disorders, epilepsy, and photosensitivity. Participants were informed about the procedure and the purpose of the study and gave written informed consent. The determination of the sample size was informed by previous entrainment studies (e.g., Spaak et al., 2014; Di Gregorio et al., 2022). The study was designed and performed in accordance with the ethical principles of the Declaration of Helsinki and was approved by the ethical committee of the Department of Psychology “Renzo Canestrari” of the University of Bologna (Prot. 42483).

7.2.2 Apparatus and Stimuli

Participants were seated in a soundproof room, positioned with a chin rest at a viewing distance of 57 cm in front of a 24-inch LED monitor (Acer) with a resolution of 1080 × 980 pixels and a vertical refresh rate of 144 Hz (32-bit depth; gamma value was set to +1). The duration of the visual entrainment stimuli was set to three refresh cycles (21 ms), with each stimulus being separated by different cycles of a blank screen, depending on the stimulation frequency (see next section). The rhythmic visual stimulation (i.e., visual entrainment) consisted of flickering white squares (6 × 6 cm) presented 15 cm lateral to a central black fixation cross (0.5 × 0.5 cm). For each participant, visual entrainment was presented to the right or left hemifield relative to the central fixation cross in separate, randomized sessions. All stimuli in the visual detection task were delivered on a middle grey background and consisted of vertically oriented Gabor patches (.5 × .5°), appearing at 15° at the right or the left to a black central fixation cross (.5 × .5°), on the midline. To ensure that stimuli were presented at threshold (contrast detection threshold was set at 75% of accuracy; Drewes et al., 2015; Lesmes et al., 2015), the contrast of the Gabor patches was adjusted individually before the experiment, through a Bayesian QUEST procedure (Watson & Pelli, 1983; for a detailed description of the QUEST procedure, see section 7.2.3). The experiment was developed in MATLAB (R2018a; The Mathworks Inc., USA) using customized routines implemented with the PsychToolbox (Brainard & Vision, 1997). Throughout the experimental procedure, eye movements were tracked and recorded using a pan-tilt ASL 6000 eye-tracking system, operating at a sampling rate of 60 Hz.

7.2.3 Experimental Procedure

The experimental session (for a graphical representation, see Fig. 17), began with the acquisition of baseline eyes-closed resting-state EEG signals, consisting of 9 separate 1-minute blocks. Following the baseline EEG recordings, each participant's individual alpha frequency (IAF) was calculated and visually inspected (for the details of the IAF processing and computation see the next section) to determine the alpha-band stimulation frequencies for the subsequent visual entrainment. Following EEG baseline blocks, 9 separate blocks of 1-minute visual detection task began, in order to identify the participant’s visual detection baseline. In this task (see also Gallina et al., 2024), each trial began with the presentation of a full-sized black screen for 21 ms, designed to induce a phase reset of functionally relevant oscillations within sensory modalities (e.g., from visual stimuli to visual areas; Landau & Fries, 2012). This phase reset allowed for the measurement of behavioral fluctuations over time, aligned with a reset point (Fiebelkorn et al., 2011; Landau & Fries, 2012). Immediately after the black screen's offset, target stimuli in the form of Gabor patches appeared for 42 ms in either the left or right hemifield, in different experimental session, at varying stimulus onset asynchronies (SOAs). Participants were required to focus their attention on a single hemifield, deploying their endogenous attentional resources to one specific location without the guidance of an exogenous spatial cue. To sample rhythmic perceptual activity, SOAs were randomly distributed across 17 time points, ranging from 56 ms to 292 ms in steps of 14 ms, in line with the dense sampling procedure (Fiebelkorn et al., 2011; Landau & Fries, 2012). After the Gabor patch disappeared, a black central question mark (.5 × .5 cm) replaced the central fixation cross, prompting participants to respond (no time limit). Participants were instructed to report whether they detect the Gabor or not, by pressing two different buttons on a keyboard, and to keep their gaze on the central fixation cross, for the entire duration of the experimental session. Once a response was given, the central fixation cross reappeared for a randomly varying intertrial interval (ITI) between .5 and 1.5 seconds before the next trial began. Each experimental block consisted of 6 trials per SOA for target-present conditions (a total of 102 trials) and 17 catch trials (target absent), resulting in 119 trials per block. Before the task, the contrast of the Gabor patches was individually adjusted using a QUEST procedure for both the left and right hemifields. The QUEST method, an adaptive psychometric approach, places each trial at the current Bayesian estimate of the threshold, leveraging the human psychometric function's invariance in form when expressed in log intensity (Watson & Pelli, 1983). Target Gabor patches were presented at the individual's 75% contrast detection threshold. In the QUEST procedure, participants completed 4 target presentations per SOA (68 trials), with no catch trials. After the baseline estimation procedure, the visual entrainment protocol started. In detail, participants underwent the visual entrainment protocol at three different frequencies: one corresponding to their IAF, and two frequencies higher (IAF +2 Hz) and lower (IAF -2 Hz) relative to the IAF. Each stimulation condition (i.e., IAF, IAF +2 Hz, IAF -2 Hz) started with 1 minute of visual entrainment, which was immediately followed by 1 minute of the visual detection task described above. This design allowed for the assessment of the effects of visual entrainment on post-entrainment visual detection performance compared to the baseline condition. This procedure (i.e., 1 minute of entrainment followed by 1 minute of a visual detection task) was repeated 9 times for each of the three stimulation conditions, resulting in a total of 9 blocks of entrainment and 9 blocks of visual detection task per condition. The presentation of visual entrainment to the right and left hemifields occurred in separate experimental sessions, with the order of presentation randomized across participants. Similarly, the sequence of stimulation conditions was randomized. Participants were instructed to maintain their gaze on a central fixation cross during the visual entrainment and to keep their head positioned on the chin rest throughout the entire experimental session.

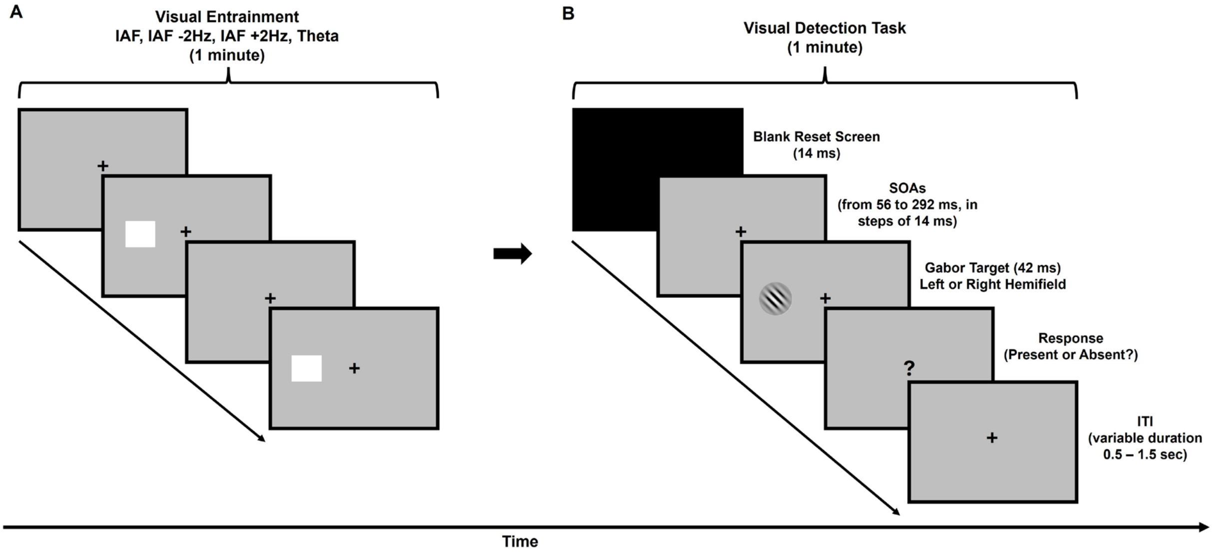

Figure 17. Schematic representation of the experimental procedure. The experimental session began with the acquisition of baseline eyes-closed resting state EEG signal, recorder over nine separate 1-minute block to determine individual alpha frequency (IAF). Following EEG baseline blocks, 9 separate blocks of 1-minute visual detection task began, in order to evaluate the participant's visual detection baseline. **A)** The visual entrainment consisted of three stimulation conditions (i.e., IAF, IAF -2 Hz, IAF+2 Hz). Each stimulation condition began with 1 minute of visual entrainment, immediately followed by 1 minute of visual detection task (B). This cycle (1 minute of entrainment followed by 1 minute of visual detection task) was repeated nine times per stimulation condition, in separate session for left and right visual stimuli presentation, resulting in a total of nine entrainment blocks and nine visual detection task for each stimulation condition and hemifield. The order of condition was randomized. Participants were instructed to focus on a central fixation cross during visual entrainment and to keep their heads on a chin rest throughout the session. **B)** Each trial began with the presentation of a blank reset screen (14 ms). Different stimulus onset asynchronies (SOAs; from 56 to 292 ms, in steps of 14 ms) preceded the appearance of lateralized Gabor target stimuli (42 ms) presented at the participants' contrast threshold. Target stimuli were delivered to the right or left hemifield in separate experimental blocks. At the Gabor target offset, participants had to report whether the target stimulus was perceived as present or absent. After the participants' response, the central fixation cross appeared again at a randomly varying duration (Intertrial Interval, ITI; ranging from .5 to 1.5 s) before the subsequent trial. (Adapted from: Gallina et al., 2024).

7.2.4 Data processing and analysis

Eye-movement recordings from all participants were processed offline. Trials where participants' gaze deviated from the central fixation cross were excluded from the analysis. The remaining trials were analyzed separately for each experimental session (i.e. different hemifield) and each participant. Signal Detection Theory (SDT) was implemented to obtain *d'* and *c* measures from the visual detection task responses for each hemifield and stimulation condition, using *Statilite* software (Version 1.05, developed by Chris Rorden). The measure *d'* quantifies a participant's sensitivity to stimuli, with higher *d'* values indicating greater sensitivity to detecting stimuli. On the other hand, *c* represents the participant's decision criterion, with a *c* value different from 0 indicating a bias in choice (i.e., a positive value implies a conservative bias, while a negative value implies a liberal bias). These measures were calculated using the proportion of hit rate (i.e., correct detections) and false alarms (incorrect detections when no stimulus was present). Importantly, to evaluate how alpha-band visual entrainment influenced visual detection, perceptual sensitivity, and decision criterion, we computed hit rates, *d'*, and *c* separately for the baseline condition and for the blocks of the visual detection task preceded by IAF, IAF -2 Hz, and IAF +2 Hz stimulations. These measures were computed separately for the visual task presented to the left and right hemifield. To statistically examine the effect of entrainment stimulations on hit rate, *d'* and *c*, we conducted separated repeated-measures ANOVA, having as within-subject factors stimulation conditions (four level: baseline, IAF, IAF -2 Hz, IAF +2 Hz), and hemifield (two levels: left and right stimuli presentation). Significant main effects and interactions where subsequently explored with post-hoc paired sample t-tests analysis using Tukey HSD test.

7.3 Results

As hypothesized, entrainment stimulation modulated visual detection performance. The repeated measures ANOVA on hit rate revealed a significant main effect of Condition ($F(3, 45) = 8.76$, $p < 0.001$; $\eta^2p = 0.369$; Fig. 18A). In contrast, this analysis did not reveal a statistically significant main effect of hemifield ($F(1, 15) = 0.25$, $p = 0.619$, $\eta^2p = 0.017$) or an interaction between the main factors ($F(3, 45) = 1.07$, $p = .369$, $\eta^2p = 0.067$). Regarding the stimulation effect, post-hoc comparisons indicated an increased hit rate following IAF stimulation ($M = 0.779$ dB; $SD = 0.142$) compared to the baseline ($M = 0.691$; $SD = 0.159$; $p < 0.001$; Fig. 18A). Other stimulation conditions did not show significant differences from baseline (all p-values > 0.34).

The repeated measures ANOVA on perceptual sensitivity (i.e., *d'*) did not reveal significant main effects of Condition ($F(3, 45) = 1.39$, $p = 0.25$; $\eta^2p = 0.085$; Fig. 18B) and Hemifield ($F(1, 15) =$

0.006, p = 0.939; η^2p = 0.001) or a significant interaction between main factors (F(3, 45) = 2.38, p = .0.082, η^2p = 0.137), suggesting that participants' perceptual sensitivity remained unchanged across entrainment conditions. In contrast, the repeated measures ANOVA on decision criterion (i.e., *c*) revealed a significant main effect of Condition (F(3, 45) = 6.03, p = 0.002; η^2p = 0.287; Fig. 18C). In contrast, this analysis did not reveal a statistically significant main effect of hemifield (F(1, 15) = 1.64, p = 0.22, η^2p = 0.099) or an interaction between the main factors (F(3, 45) = 0.24, p = 0.24, η^2p = 0.088). Regarding the stimulation effect, post-hoc comparisons indicated a lower c values following IAF stimulation (M = -0.013; SD = 0.436) compared to the baseline (M = 0.21; SD = 0.461; p = 0.005; Fig. 18C). Other stimulation conditions did not show significant differences from baseline (all p-values > 0.32).

Overall, these results suggest that while IAF stimulation did not enhance perceptual sensitivity, it influenced decision criterion without altering perceptual sensitivity.

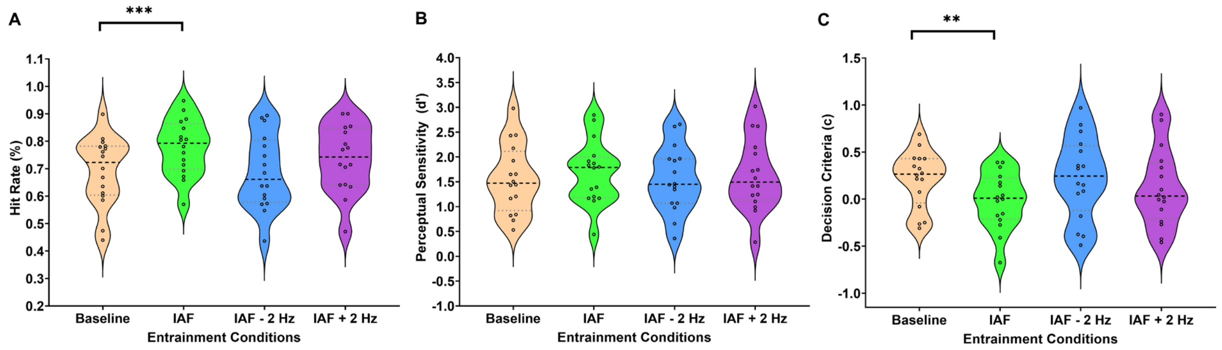

Figure 18. Violin plots showing the effects of entrainment conditions on hit rate (**A**), perceptual sensitivity (**B**) and decision criterion (**C**). **A**) The results revealed that only the entrainment administered at IAF increase hit rate as compared to baseline condition. However, employing measures derived from the Signal Detection Theory (STD) framework, the results showed that entrainment delivered at IAF did not enhance perceptual sensitivity (**B**), but induced a modulation of decision criterion (**C**). Black dotted lines indicate the median, while grey dotted lines indicate quartiles. Grey circles show individual values. *=p<0.005; **=p<0.01; ***=p<.001.

7.4 Discussion

The main purpose of the current study was to explore whether prolonged alpha-band visual entrainment can induce persistent modulations of visual detection performance at the stimulation offset, with potential differential outcomes depending on the stimulation frequency (i.e., IAF, IAF -2 Hz, IAF +2 Hz). In details, it has been investigated whether visual entrainment could modulate specific aspects of perceptual performance, influencing both visual information processing (i.e., detection rate and perceptual sensitivity) and higher-level dimensions of perceptual judgments (i.e., decision criterion).

First, the results demonstrated that prolonged alpha-band visual entrainment selectively enhanced visual detection rates specifically following IAF visual entrainment, while stimulation at IAF -2 Hz and IAF +2 Hz did not yield similar improvements. This pattern of results is consistent with prior research and further supports the effectiveness of alpha-band visual entrainment in enhancing visual detection performance when the stimulation frequency aligns with the preferential rhythm of the targeted brain area (Thut et al., 2011a; Mathewson et al., 2012; for a recent review, see: Gallina et al., 2023), further highlighting that the effects of alpha-band visual stimulation on visual detection performance can be persistently observed (i.e., ~1 minute) when followed by prolonged trains of rhythmic stimulation.

However, by evaluating measures derived from the Signal Detection Theory (STD; Green & Swets, 1966) framework, our findings revealed that alpha-band visual entrainment differentially impacted various aspects of visual performance. Indeed, while IAF stimulation enhanced participants' detection rates, this stimulation did not improve perceptual sensitivity (i.e., *d'*) but lowered decision criterion (i.e., *c*), thus influencing perceptual judgments without affecting sensitivity. However, while these findings align with previous literature indicating that alpha oscillatory activity can differentially orchestrate both the sensitivity thresholds of visual information processing and decision-making processes underlying perceptual judgments (Samaha et al., 2016, 2017; Di Gregorio et al., 2022), it has been previously documented that a more conservative decision criterion (i.e., higher *c*) may be associated with increased alpha power, which indicates a higher level of attentional inhibition, leading to a more rigorous evaluation of sensory evidence before making a perceptual decision (Samaha et al., 2016, 2017; Di Gregorio et al., 2022). Therefore, based on previous findings, since neural entrainment typically leads to the phase alignment of endogenous oscillatory activity accompanied by a power increase, if in the current study IAF stimulation effectively synchronized the ongoing oscillations and enhanced alpha power, we could have expected a more conservative response bias (i.e., high decision criterion; Samaha et al., 2016, 2017; Di Gregorio et al., 2022).

However, our results stem from a different experimental design compared to the existing literature, which has primarily used correlational or 'online stimulation' approaches to explore the relationship between alpha oscillatory measures and various aspects underlying perceptual judgments. Indeed, differently from previous literature (Samaha et al., 2016, 2017; Di Gregorio et al., 2022), in our study, we investigated the modulatory effects of alpha-band sensory entrainment on the observable changes in visual performance for an extended period following the stimulation offset. Accordingly, the increased decision criterion after IAF stimulation may indicate a different neural state, where post-stimulation effects on alpha oscillatory activity could have impacted different alpha oscillatory networks (Lockley et al., 2006; Dockree et al., 2007; Sadaghiani et al., 2010), leading to more balanced perceptual decision-making. Within this perspective, while alpha oscillations over occipito-parietal brain areas have often been associated with an increased decision criterion reflecting mechanisms of attentional inhibition (Samaha et al., 2016, 2017; Di Gregorio et al., 2022), alpha oscillatory activity over more diffuse brain networks (e.g., prefrontal and cingulo-insular-thalamic networks; Sadaghiani et al., 2010) has been identified as a reliable electrophysiological signature of tonic alertness and sustained vigilance (Makeig & Inlow, 1993; Makeig & Jung, 1995; Lockley et al., 2006; Dockree et al., 2007; Sadaghiani et al., 2010). Thus, we may speculate that the prolonged visual entrainment administered at the participants' IAF might have induced persistent modulations of alpha oscillatory activity over different neural circuits, increasing alpha power and enhancing tonics alertness and physiological arousal across diffuse alpha oscillatory networks (Lockley et al., 2006; Dockree et al., 2007; Sadaghiani et al., 2010), ultimately leading to a less conservative response strategy. In support of this hypothesis, as also highlighted by the findings observed in the previous section (Chapter 6), IAF visual entrainment can induce effects on alpha power that are topographically diffuse and distributed rather than focal and confined to the posterior brain areas (Thut et al., 2011a; Mathewson et al., 2012), and in the presence of lateralized visual stimulation, alpha-band oscillations propagate across the topographic space both forward and backward from occipital to frontal regions (Alamia & VanRullen, 2024; Fakche & Duguè, 2024). Thus, it is conceivable that, in the current study, the visual entrainment effects might have increased alpha power following IAF stimulation in different neural circuits, boosting visual attentional readiness and lowering the decision threshold, potentially explaining the differences between the present study and the previous literature (Samaha et al., 2016, 2017; Di Gregorio et al., 2022). Future studies investigating the specific oscillatory networks where alpha power is modulated following alpha-band visual stimulation might clarify whether the increase in alpha power affects low-level sensory areas, as well as decision-making neural regions that orchestrate perceptual judgments. This approach could help determine whether the modulation of alpha power serves as a mechanism for enhancing sensory processing or if it primarily impacts higher-order cognitive functions involved in decision-making.

Importantly, our findings highlighted that, while prolonged alpha-band visual entrainment can improve visual detection performance (i.e., detection rates) and lower decision criterion, it does not necessarily modulate perceptual sensitivity to the visual stimuli. In line with these findings, it has been demonstrated that changes in decision criteria can occur independently of sensitivity (Green & Swets, 1966), and increased alpha power might indeed enhance processing efficiency without necessarily affecting discrimination thresholds (Haegens et al., 2011). Relatedly, the prolonged IAF stimulation, by increasing visuo-attentional readiness and tonic alertness through alpha power modulations (Lockley et al., 2006; Dockree et al., 2007; Sadaghiani et al., 2010), may have made participants feel more confident in their ability to detect the visual target, leading them to adopt a less conservative response strategy. Thus, the possibility that the stimulation enhanced participants' confidence in their perceptual judgments, as reflected in a lowering of decision criterion, could also explain the higher hit rates without a corresponding increase in perceptual sensitivity (i.e., d'), as participants became more willing to report detections without actual improvements in perceptual accuracy. Since it has recently been shown that alpha power can predict subjective confidence (e.g., Di Gregorio et al., 2022), future alpha-band entrainment studies are needed to disentangle whether the lower decision criterion following IAF stimulation observed in this study stems from increased confidence rather than changes in perceptual sensitivity, by assessing participants' confidence levels alongside their visual performance measures.

In prior research, alpha-band visual entrainment effects on different aspects of perceptual performance have been reported in the study by Mathewson and colleagues (2010). Specifically, they assessed visual detection rates and perceptual sensitivity (i.e., d') on a trial-by-trial basis following a brief period (i.e., 574 ms) of entrainment stimulation at 12 Hz. Their findings demonstrated improved visual performance for targets presented in phase with the preceding alpha-band visual stimulation. However, in contrast to the current study, the authors administered the entrainment for only a few time period before the stimulus presentation and did not analyze variations in performance related to response strategy biases stemming from changes in decision criterion. In addition, differently from Mathewson and colleagues (2010), due to the methodological constraints of our experimental paradigm, we did not analyze visual performance measures as a function of stimulus presentation in-phase and anti-phase relative to the rhythmic visual stimulation. This limitation may have affected our ability to draw comparisons regarding the phase-dependent effects of alpha-band entrainment on visual performance, which could be an important aspect to consider in future studies exploring the relationship between rhythmic stimulation and different aspects of perceptual judgments. As a result, these methodological differences likely contributed to the divergent behavioural outcomes observed in the present study compared to those reported by Mathewson and colleagues (2010).

Another potential explanation for our results may rely on the possibility that the effects of visual entrainment dissipated at the onset of the visual detection task, as the visual stimuli can induce a phase reset of endogenous alpha oscillations in the visual system (Lakatos et al., 2009; Thorne & Debener, 2014; Cecere et al., 2016, 2017). Although we highlighted in the previous chapter (see Chapter 6) that the effects of alpha-band visual entrainment can persist over extended periods following stimulation offset on ongoing resting-state oscillatory activity (i.e., alpha power and inter-trial phase coherence), in the absence of M/EEG measures in the current study, it is not possible to disentangle whether the effects of the stimulation on the neural oscillatory substrate were observable at its offset during the visual detection task.

Overall, our findings revealed that prolonged alpha-band visual entrainment can differentially impact various aspects of visual performance observed in an extended period following stimulation offset. When the visual stimulation was aligned with the preferential rhythm of the targeted brain area (i.e., IAF; for a recent review, see Gallina et al., 2023), participants exhibited a higher detection rate and a lower decision criterion compared to baseline visual performance. This suggests that the effects of alpha-band visual stimulation on visual detection performance can be observed persistently when followed by prolonged trains of rhythmic stimulation. Such results underscore the importance of aligning stimulation frequency with individual neural rhythms to optimize perceptual outcomes and highlight the potential of alpha-band entrainment as a tool for enhancing visual processing in both experimental research and clinical settings (Lakatos et al., 2019; Gallina et al., 2023). Future investigations will be necessary to disentangle how alpha-band visual entrainment can differentially affect perceptual sensitivity, subjective confidence, and perceptual decision-making by modulating the underlying alpha oscillatory activity. Understanding these interactions will provide valuable insights into the mechanisms by which alpha oscillatory activity influences perceptual and cognitive processes and could pave the way for targeted interventions in clinical and non-clinical populations showing anomalous alpha activity (for a review, see: Ippolito et al., 2022).

Chapter 8

General Discussion

Neural oscillatory activity in the alpha band (~7-13 Hz) has been consistently shown to serve as a crucial mechanism in orchestrating sensory sampling processes and regulating optimal phases of information processing (VanRullen, 2016; Cuello et al., 2022; Wutz, 2024; Gallina et al., 2024). Although alpha activity was historically considered an "idling" rhythm (e.g., Pfurtscheller et al., 1996), the current perspective suggests that alpha oscillations may be responsible for processing sensory information through a periodic sampling mechanism, organized in sequences of perceptual cycles reflected by the underlying alpha oscillations (Klimesch et al., 2007; Cuello et al., 2022; Wutz et al., 2024; Schoffelen et al., 2024).

Within this framework, as extensively discussed throughout this thesis, alpha spectral measures have consistently been associated with various aspects of visual performance, actively contributing to inhibitory control and the timing of neural processing, with outcomes influenced by the instantaneous phase of ongoing oscillatory activity as a function of its power and frequency (Samaha et al., 2017; Cuello et al., 2022; Benwell et al., 2022). Interestingly, prior research has shown that the contribution of alpha oscillatory activity to information processing is not confined to visual information, but can assume a pivotal role in shaping perceptual performance both within and across different sensory modalities (Bastiaansen et al., 2020; Cecere et al., 2015; Keil & Senkowski, 2018; Cooke et al., 2019; Ronconi et al., 2023). Indeed, several studies have underscored the involvement of alpha oscillations in coordinating cross-modal audiovisual (AV) interaction mechanisms, determining the temporal integration of different sensory information (Bastiaansen et al., 2020; Cecere et al., 2015; Keil & Senkowski, 2018). In line with this perspective, it is currently hypothesized that the individual alpha frequency (IAF) may reflects the temporal unit of visual and AV perception, where sensory inputs are integrated when falling within the same alpha cycle, but segregated when occurring in different alpha cycles (Samaha & Romei, 2024).

Overall, the picture emerging from these findings underscores that alpha oscillations represent a fundamental mechanism shaping unimodal and cross-modal perceptual performance. However, alpha oscillatory activity is highly plastic and dynamically modulated by internal and external stimulations (Klimesh et al., 2007; Mathewson et al., 2009; Mathewson et al., 2011; Alamia & VanRullen, 2024). Leveraging the mechanisms of neural plasticity, a recent framework seeks to modulate endogenous alpha oscillatory activity through the entrainment mechanisms of neural oscillations to directly investigate the relationship between alpha activity and visual/AV information processing (Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024).

Neural entrainment, as extensively discussed throughout this work, refers to the temporal synchronization of endogenous neural activity with an external driving rhythm, leading to phase and frequency alignment as well as an increase in the power of endogenous oscillations (Lakatos et al., 2019; Gallina et al., 2023; Duecker et al., 2024). Building on the entrainment mechanism, research utilizing transcranial non-invasive brain stimulation techniques (NIBS; Lakatos et al., 2019; Duecker et al., 2024), as well as rhythmic sensory stimulation (Gallina et al., 2023), has consistently demonstrated the synchronization of brain oscillations with the external stimulation frequency, revealing resonance phenomena in neural activity, accompanied by corresponding fluctuations in visual and AV perceptual performance (Lakatos et al., 2019; Gallina et al., 2023). In this regard, as previously discussed (see Chapter 3), sensory entrainment approaches - such as visual, auditory, and audiovisual rhythmic stimulation - have provided valuable insights into the mechanisms of alpha-band entrainment in shaping sensory information processing (Lakatos et al., 2019; Gallina et al., 2023). Specifically, alpha-band visual and AV entrainment has proven to be a valuable tool for probing and enhancing visual and AV performance by engaging alpha oscillatory networks and promoting intra- and cross-modal interactions between sensory systems (Spaak et al., 2014; et al., 2018; Marsicano et al., 2023). However, several key aspects of the effects induced by alpha-band sensory entrainment on neural oscillations and perceptual performance remain unexplored (Gallina et al., 2023; Duecker et al., 2024). In the present thesis, the mechanisms of alpha-band sensory entrainment, administered through unisensory (i.e., visual entrainment) and multisensory (i.e., audiovisual entrainment) modalities, were thoroughly investigated to explore how rhythmic stimulation shapes alpha oscillatory activity, ultimately leading to both short- and long-lasting functional modulations in perceptual performance.

In Chapter 4, the effects of AV alpha-band entrainment on AV temporal binding mechanisms were investigated. Although the efficacy of AV entrainment in shaping visual temporal integration and segregation processes has been demonstrated (Ronconi & Melcher, 2017; Ronconi et al., 2018), it remained under debate whether alpha-band sensory stimulation could similarly influence the temporal resolution of the AV temporal binding system, given that distinct neurocomputational mechanisms may orchestrate uni- and multisensory perception (Senkowski et al., 2008; Lakatos et al., 2009; Cecere et al., 2016, 2017; Bauer et al., 2020). In this study (Chapter 4), each trial of an AV Simultaneity Judgment task was preceded by AV entrainment at either slower (~8.50 Hz) or faster (~12 Hz) alpha frequencies, or by a control non-rhythmic condition, in order to measure individuals' baseline AV temporal sampling. Since AV temporal perception has been linked to the speed of the alpha rhythm (Cecere et al., 2015; Bastiaansen et al., 2020; Cooke et al., 2019), it was hypothesized that trials of the SJ task following the upper alpha (~12 Hz) condition of sensory stimulation would exhibit a lower simultaneity rate and a narrower AV TBW, a probabilistic measure that reflects the likelihood of perceiving two sensory stimuli as a single percept across a range of stimulus onset asynchronies (SOAs; Stevenson et al., 2017a). On the other hand, trials following AV rhythmic stimulation delivered at the slower alpha frequency (~8.5 Hz) would show an enlargement of the TBW. The results emerging from this study demonstrated that AV entrainment can effectively induce modulations in the width of the AV TBW as a function of the alpha stimulation frequency. Specifically, we found that upper alpha sensory stimulation (~12 Hz) enhances AV temporal acuity by narrowing the width of the TBW and decreasing perceived simultaneity compared to lower alpha stimulation (~8.5 Hz) and control non-rhythmic conditions. These findings align with previous research linking alpha oscillations to AV integration and segregation processes, suggesting that neural entrainment may enhance the temporal sampling capacity of AV perception by synchronizing endogenous oscillatory activity with the frequency of the external rhythmic stimulation, supporting the idea that the alpha rhythm may reflects the temporal unit of AV perception (Bastiaansen et al., 2020; Cecere et al., 2015; Cooke et al., 2019; Venskus & Hughes, 2021).

Importantly, while these findings demonstrated the efficacy of AV alpha-band sensory entrainment in modulating AV temporal acuity (Chapter 4), interindividual differences can play a crucial role in determining an individual's capacity to functionally align neural activity with rhythmic sensory streams (Lakatos et al., 2019). However, interindividual differences are often overlooked when assessing neural and behavioural outcomes in entrainment studies, despite the fact that neural entrainment is a fundamental mechanism for processing sensory information, and dysfunction in this sensory sampling process can lead to significant impairments across perceptual, cognitive, and socio-communicative domains (Northoff, 2018; Noel & Stevenson, 2018; Black et al., 2024). This is particularly evident in individuals with Autism Spectrum Disorder (ASD) and Schizophrenia Spectrum Disorder (SSD), as well as neurotypical individuals in the general population with higher ASD- and SSD-like traits, where individuals often show a diminished ability to entrain to rhythmic sensory patterns (Riečanský et al., 2010; Black et al., 2024). Additionally, interindividual differences in ASD and SSD traits contribute to variations in AV temporal perception, with higher atypicality in cognitive-perceptual and socio-communicative domains often linked to reduced AV temporal precision, as these multisensory abilities strongly depend on the efficiency of neural oscillatory systems in integrating sensory information (Haß et al., 2017; Zhou et al., 2019; Van Laarhoven et al., 2019; Fenner et al., 2020; Zhou et al., 2021; Ronconi et al., 2023). Accordingly, in Chapter 5, using the same experimental paradigm described in Chapter 4, we explored how interindividual differences in cognitive-perceptual, socio-affective, and communicative profiles may influence AV temporal acuity and its malleability following alpha-band sensory entrainment, administering brief AV rhythmic stimulations at slower and faster alpha frequencies before each trial of an AV SJ task. The overall pattern of results observed in the total sample aligns with the findings presented in Chapter 4, as well as with previous alpha-band entrainment studies (Cecere et al., 2015; Venskus et al., 2021; Marsicano et al., 2024), indicating that participants exhibited higher AV temporal acuity following faster alpha stimulation. Crucially, to examine potential interindividual differences in the modulation of AV TBWs, self-reported data regarding cognitive-perceptual and socio-communicative traits were collected using the Autism Spectrum Quotient (ASQ; Baron-Cohen et al., 2001) and the Schizotypal Personality Questionnaire (SPQ; Raine et al., 1991). By implementing cluster analysis on these measures (Choteau et al., 2016), participants were grouped according to shared characteristics within their personological profiles: one cluster was characterized by distinct atypicalities in the socio-affective domain (Socio-affective Traits; SAT), another by atypicalities in the cognitive-perceptual domain (Cognitive-perceptual Traits; CPT), while the third cluster showed low traits across both domains (Low Traits; LT). Participants in the LT group demonstrated a significant leading sense asymmetry, exhibiting wider TBWs for Visual Leading trials compared to Auditory Leading sequences, which is consistent with prior research attributing this asymmetry to the auditory system's enhanced temporal resolution (van Wassenhove, 2013; Cecere et al., 2016). In contrast, the SAT and CPT groups did not exhibit the typical asymmetry, suggesting that individuals with cognitive-perceptual or socio-affective anomalies may perceive AL pairs as more simultaneous due to impaired auditory temporal processing (Donohue et al., 2012; Stevenson et al., 2017a, 2017b). Finally, the investigation focused on whether the size of AV TBWs was modulated differently based on the AV entrainment conditions and the individual trait profiles. In the control non-rhythmic condition, no significant differences in TBW width were found among groups, indicating comparable AV temporal acuity under natural conditions. This supports previous research suggesting inconsistent links between broader AV TBWs and traits resembling ASD and SSD profiles (Donohue et al., 2012; Zhou et al., 2019). However, following alpha-band stimulation, all participants exhibited narrower TBWs after upper alpha stimulation, suggesting enhanced AV temporal acuity. Conversely, only the CPT group demonstrated a significant widening of AV TBWs after lower alpha stimulation, highlighting group-specific differences in TBW modulation (Ghuman et al., 2017; Zhou et al., 2021). These atypical responses observed in the CPT group following lower alpha entrainment may stem from difficulties in encoding rhythmic sensory patterns, reflecting impairments in bottom-up perceptual processes (Riečanský et al., 2010; Sterzer et al., 2019).

Overall, the findings from Chapters 4 and 5 suggest that alpha-band sensory entrainment can effectively modulate AV temporal acuity, and that individual differences within the general population significantly affect AV temporal processing abilities and their malleability following rhythmic entrainment. However, while these significant effects were observable immediately after the offset of stimulation, whether alpha-band stimulation can induce long-lasting effects on neural activity and perceptual performance remains an unresolved question (Gallina et al., 2023). Relatedly, while previous studies using short-term rhythmic stimulations have shown that entrainment effects are mainly localized in occipito-parietal brain areas contralateral to the stimulation (Thut et al., 2011a; Spaak et al., 2014), it remains unclear whether prolonged alpha-band entrainment, in contrast to short-term stimulation, could induce more widespread effects, enhancing alpha activity across diffused brain regions (Zhang et al., 2018; Alamia & VanRullen, 2019, 2024). In the current thesis, to address these questions, both EEG and psychophysical measurements were employed to investigate whether alpha-band visual entrainment could induce long-lasting, persistent modulations of alpha oscillatory activity (Chapter 6) and functional changes in visual detection performance (Chapter 7).

In Chapter 6, EEG oscillatory signals were recorded before and after 1-minute blocks of visual entrainment to investigate whether rhythmic stimulation, presented in the right or left hemifields at various alpha-band frequencies (IAF, IAF -2 Hz, and IAF +2 Hz), could induce long-lasting effects on alpha oscillatory spectral measures. These effects were assessed immediately after the entrainment period during a 1-minute eyes-closed resting state, considering alpha activity in both posterior and anterior scalp regions. Given that alpha-band entrainment has been shown to selectively modulate alpha oscillations (e.g., Spaak et al., 2014; Keitel et al., 2018, 2019), theta-band activity (3-6 Hz) was also analyzed, and a control condition with a fixed theta frequency (4.5 Hz) was introduced to determine the specificity of frequency-dependent effects on neural oscillatory activity. The findings observed in this study indicated that, compared to baseline oscillatory activity, prolonged alpha-band visual entrainment selectively enhanced both power and inter-trial phase coherence (ITPC) within the alpha frequency band, while no significant effects were observed in the theta frequency band. Notably, these enhancements persisted throughout the 1-minute post-entrainment resting-state period, suggesting that the effects of entrainment were not only significant but also sustained over time, highlighting the potential of alpha-band sensory entrainment as a technique for inducing long-lasting modulations of neural oscillations. Furthermore, entrainment of neural oscillations at participants' IAF resulted in stronger modulations of alpha spectral measures compared to IAF -2 Hz and IAF +2 Hz stimulations. This result aligns with previous evidence suggesting that rhythmic stimulation tuned to participants' IAF induces stronger resonance phenomena in the neural oscillatory activity of the visual system (Regan, 1982; Pikovsky et al., 2003; Notbohm et al., 2016). Notably, the effects of alpha-band entrainment were comparable in both posterior scalp regions, whether contralateral or ipsilateral to the stimulated hemifield, and further resulted in an increase in alpha oscillatory activity that spread to the anterior scalp region. Thus, unlike previous studies that employed brief entrainment stimulation (e.g., Spaak et al., 2014; Gray & Emmanouil, 2019), the sustained rhythmic stimulation in the current study led to widespread increases in alpha power, suggesting that more distributed entrainment after-effects can emerge with prolonged stimulation. Consequently, it is conceivable that prolonged alpha entrainment engaged widespread cortical areas, promoting information flow through oscillatory networks both within and beyond the occipito-parietal cortices (Vossen, 2015; Otero et al., 2022; Alamia & VanRullen, 2019, 2024; Fakche & Duguè, 2024). Interestingly, in contrast to alpha power, we observed a sustained increase in alpha ITPC selectively following IAF stimulation in the posterior scalp areas. Prior research using alpha-band visual stimulation has demonstrated that power and ITPC may represent two distinct functional populations of alpha activity (Spaak et al., 2014; Keitel et al., 2018, 2019; Gray & Emmanouil, 2019). Indeed, alpha power is thought to reflects self-sustained endogenous oscillatory activity, while ITPC captures evoked responses that are phase-locked to visual stimulation (Spaak et al., 2014; Keitel et al., 2019). Thus, the varying effects on alpha oscillatory measures observed in this study may be attributed to the modulation of self-sustained endogenous alpha oscillations, persisting independently after the stimulation offset, showing generalized effects across the range of alpha-band stimulations. In contrast, alpha ITPC, which reflects stimulus-related activity primarily generated in the visual cortex, revealed that the sustained increase in this spectral parameter was limited to IAF stimulation in posterior scalp regions, suggesting a prolonged reverberation of the evoked responses to visual rhythmic stimulation (Keitel et al., 2018, 2019). Thus, the current findings support the idea that two distinct neural mechanisms (i.e., power and ITPC) may underlie the entrainment effects associated with the synchronization of alpha oscillatory activity (Keitel et al., 2018, 2019; Gray & Emmanouil, 2019). Overall, this study provides the first empirical evidence that alpha-band visual entrainment can induce long-lasting modulations of endogenous alpha oscillatory activity across a broad spectrum of scalp regions, particularly when the stimulation frequency is aligned with participants' IAF.

Chapter 7 examined whether visual entrainment administered at alpha frequencies (i.e., IAF, IAF -2 Hz, and IAF +2 Hz) would induce comparable long-lasting effects on visual performance. Accordingly, participants performed a visual detection task (for a similar experimental paradigm, see Gallina et al., 2024) before and after blocks of prolonged visual entrainment (i.e., 1 minute) to explore whether visual rhythmic stimulation presented in the right or left hemifields (across various experimental sessions) at different frequencies within the alpha band (i.e., IAF, IAF -2 Hz, and IAF +2 Hz) could induce long-lasting effects on multiple aspects of visual performance (i.e., hit rate, perceptual sensitivity, and decision criterion) that could be observed after the stimulation offset, by comparing visual detection performance before and after the entrainment. Overall, the results indicated that prolonged alpha-band visual entrainment improved visual detection performance, as evidenced by increased detection rates, selectively following IAF stimulation. In contrast, stimulation at IAF -2 Hz and IAF +2 Hz did not produce similar enhancements. This finding aligns with prior research that underscores the efficacy of alpha-band visual entrainment in enhancing visual detection performance when the stimulation frequency corresponds with the visual system's preferred rhythm

(Mathewson et al., 2012; Spaak et al., 2014; Wiesman & Wilson, 2019). Importantly, these findings suggest that the effects of alpha-band visual stimulation on visual performance can be persistently observed (~1 minute) when followed by prolonged rhythmic stimulation. Notably, the investigation also focused on how alpha-band visual entrainment could modulate specific aspects of perceptual performance. By evaluating measures from Signal Detection Theory (SDT; Green & Swets, 1966), the findings indicated that while alpha-band visual entrainment improved participants' detection rates, it did not enhance perceptual sensitivity (i.e., *d'*), instead resulting in a lowering of decision criterion (i.e., *c*). However, a more conservative decision criterion has often been associated with increased alpha power, suggesting a greater level of attentional inhibition (Samaha et al., 2016, 2017). Therefore, if the IAF stimulation in the current study effectively synchronized ongoing oscillations and enhanced alpha power, based on these previous studies, we might have expected a more conservative response strategy. However, our results arise from a distinct experimental design, differing from prior correlational or online stimulation studies. Accordingly, the decreased decision criterion following IAF stimulation may reflect a different neural state, where post-stimulation effects might have induced persistent modulations in widespread alpha oscillatory networks involved in the regulation of tonic alertness and sustained vigilance (e.g., Dockree et al., 2007; Sadaghiani et al., 2010), ultimately leading to a decreased criterion during perceptual decision-making. Alternatively, the prolonged IAF stimulation, by increasing visuo-attentional readiness, may have enhanced participants' confidence in detecting visual targets, leading them to adopt a less conservative response strategy, even in the absence of a corresponding increase in perceptual sensitivity. Overall, the findings from Chapters 6 and 7 indicated that prolonged alpha-band visual entrainment can lead to long-lasting modulations of endogenous alpha oscillatory activity and visual perceptual performance, particularly when the rhythmic stimulation is aligned with the visual system's preferential rhythm (i.e., IAF).

Future Directions and limitations

Taken together, the findings from the experimental studies presented in this work serve as proof-of-concept that endogenous alpha oscillatory activity can be externally modulated, with both short- and long-lasting effects observable at the stimulation offset. Importantly, these findings also suggest that rhythmic stimulation can be applied to investigate the relationship between perceptual performance and alpha oscillations through the phase-locking of their oscillatory systems, as well as to functionally model alpha neural activity through the plastic reorganization of the underlying oscillatory networks (Vossen et al., 2015). Thus, such prolonged sensory entrainment technique may hold significant potential for patients with posterior brain damage and visual field deficits (Pietrelli et al., 2019; Allaman et al., 2021; Gallina et al., 2022), as well as for individuals with neurodevelopmental disorders characterized by atypical alpha oscillatory activity and anomalous sensory processing (Ippolito et al., 2022). Furthermore, given the interindividual variability in entrainment effects observed in the studies presented (e.g., Chapter 5), these findings underscore the importance of aligning the stimulation frequency with individual neural rhythms to optimize perceptual outcomes and effectively apply alpha-band sensory entrainment as a tool for enhancing perceptual processing (Lakatos et al., 2019; Gallina et al., 2023).

In the present work, we primarily employed sensory entrainment administered through audiovisual (Chapters: 4, 5) and visual (Chapters: 6, 7) modalities. However, sensory entrainment can be extended to other sensory modalities. Existing literature strongly suggests that, while the neural circuits involved in different forms of sensory entrainment may vary depending on the sensory modality employed, the fundamental mechanisms underlying alpha-band sensory entrainment (i.e., phase resetting and synchronization of endogenous neural oscillations) remain consistent across modalities (e.g., visual, auditory, tactile, audiovisual), thus suggesting that findings observed within a specific sensory modality may be generalizable to others (Gallina et al., 2023). Nonetheless, it is important to acknowledge that certain sensory modalities may preferentially and more effectively entrain specific oscillatory circuits (e.g., visual entrainment engaging the visual system). In this context, previous research has proposed that the modulatory effects of sensory entrainment may differ based on the sensory modality of the rhythmic sensory stream employed and its potential interaction with the perceptual and cognitive processes under investigation (Gallina et al., 2023; Duecker et al., 2024). Despite these insights, current literature remains limited in disentangling potential dissociable effects of sensory entrainment across multiple sensory modalities. Future research is therefore necessary to clarify whether the functional modulation of sensory entrainment mechanisms is contingent upon the sensory modality employed.

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