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AUDIOVISUAL MISPERCEPTIONS AND OSCILLATORY TIMESCALES:
SYNERGISTIC MARKERS ACROSS THE PSYCHOSIS CONTINUUM?

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Esame finale anno 2026

To Ilenia,
to my beloved family,
and to my grandfather

“All we have to decide is what to do with the time that is given us.”

J.R.R. Tolkien

Abstract

Combining information across senses is a core property of human cognition, largely reliant on temporal binding windows (TBW) that arbitrate the perceptual fate of multisensory events. In audiovisual settings, wider TBW have been associated with misperceptions such as the Sound-Induced Flash Illusion (SIFI), with greater susceptibility reported along the psychosis continuum, often co-varying with the severity of positive-like traits or symptoms, and plausibly reflecting degraded temporal sensitivity to inter-sensory delays. Individual alpha frequency (IAF), an electroencephalographic (EEG) marker proposed to pace the sampling resolution of visual processing, stands among the most compelling neural candidates for scaffolding these computations.

As such, the present thesis offers an overarching view of multisensory perception, the SIFI and alpha rhythms (Chapter 1-3), which furnished a departure point to test two main hypotheses: whether reduced visuo-temporal acuity constitutes the mechanistic fingerprint of enlarged audiovisual TBW toward the upper end of the psychosis continuum, and the extent to which occipital IAF provides a causal handle on these operations. In a first experiment using a revised SIFI paradigm set to dissociate temporal sensitivity from response bias, high-schizotypy individuals displayed broader TBW and reduced visuo-temporal precision relative to low-schizotypy participants, with effects scaling with positive-like subtraits (Chapter 4). A scoping review then mapped recent EEG evidence on alpha-band alterations in schizophrenia-spectrum disorders, highlighting resting-state IAF slowing as a consistent, trait-like EEG feature (Chapter 5). This was followed by a feasibility study showing that artefactual by-products introduced by rhythmic transcranial magnetic stimulation (rhTMS) did not interfere with multisensory performance, thereby validating this protocol as a mechanistic probe of oscillatory contributions to multisensory integration (Chapter 6). Finally, in an rhTMS–EEG co-registered experiment, prestimulus IAF was causally manipulated during a modified SIFI task in participants screened for their positive-like schizotypal traits. Contrary to our predictions, up- or down-pulling IAF did not yield corresponding changes in audiovisual sensitivity under the present task parameters. Rather, faster IAF primarily produced trait-dependent shifts toward a more liberal response criterion, increasing extra-flash illusory reports in individuals with elevated positive-like traits (Chapter 7).

Taken together, these findings argue that positive-like schizotypal traits chiefly index reduced temporal precision, thereby positioning the SIFI as a promising addendum to pre-emptive screening routines. By contrast, the present causal evidence does not provide conclusive support for IAF as a control parameter of audiovisual sensitivity, suggesting that, under specific experimental regimes, IAF manipulation is more readily expressed as trait-gated shifts in decisional policies.

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Chapter 1: A Primer on Multisensory Perception and Misperception

We inhabit a world that constantly floods our sensorium with multiple streams of competing information (Noppeney, 2021). More often than not, such information travels across the environment and reach our senses in different physical forms. For instance, a car's shape and color derive from light reflected within a specific wavelength range, whereas the loud humming of its engine arises from mechanical vibrations propagating through the surrounding air. From an evolutionary perspective, animals (including mammals and humans) have developed a wide set of sensory organs suited to processing diverse signals. Retinal circuitry turns light into neural codes that are then conveyed to thalamic nuclei (Gollisch & Meister, 2010), and in a similar fashion, the cochlear apparatus transduces sound-driven pressure fluctuations (Hudspeth, 2008). Following thalamic relay (Sherman, 2007), primary sensory cortices further refine these signals, which ultimately support perceptual experience. In this context, the neocortex sits on top of the nervous system hierarchy, as it is tasked to resolve perceptual uncertainties idiosyncratic to data collected by peripheral receptors at different temporal latencies, and encoded at the thalamic level, in order to build a faithful representation of the external world (DiCarlo et al., 2012; Felleman & Van Essen, 1991).

While the brain contains several areas specialized for specific sensory modalities, perception most certainly benefits from interactions among these regions, and the exchange of cross-modal information (Angelaki et al., 2009; Ernst & Bühlhoff, 2004; Murray, Lewkowicz, et al., 2016; Noppeney, 2021; Stein & Stanford, 2008). At times, one sense may supply complementary evidence that another does not capture; at others, distinct senses deliver convergent cues that, when pooled, yield a more precise account of the perceived event (Noppeney, 2021; Stein & Stanford, 2008). The wealth of neural computations performed to synergistically combine signals across different competing modalities is known as multisensory integration (Stein & Stanford, 2008). Efficient cross-modal processing is key to adaptive behavior, with many species within the animal kingdom, from humans to non-mammalian vertebrates, possessing biological structures devoted to collect and merge modality-diverse sensory information (Hiramoto & Cline, 2009; King, 2004). The pivotal role played by multisensory integration is also evident at the ontogenetical level, where even newborns have been shown to display rudimentary intersensory abilities (Meltzoff & Borton, 1979). Improved detection of noisy stimuli, and faster response times, are a few examples of behavioral advantages conferred by effective multisensory processing (Stein & Stanford, 2008). Foremost among these is perhaps the synthesis of stimuli encoded under diverging modalities into a unified percept phenomenologically different from the summation

of all cues it arose from, such as flavor perception or heading estimates (Fetsch et al., 2010; Small & Prescott, 2005). Although these operations do appear to occur effortlessly, to reconcile (either by combining or integrating) cross-modal signals, our brain accomplishes many sophisticated and moment-to-moment computations, some of which following well-characterized neurophysiological rules, and associated with specific behavioral outcomes (Stein & Stanford, 2008).

1.1 Principles of Multisensory Perception

Seminal attempts to chart the physiological dynamics underlying multisensory processing entailed the study of electrical activity in response to exogenous stimulation through in vivo single-unit recording in non-human animals (Meredith & Stein, 1983; Newman & Hartline, 1981). Whereas a preliminary work showed non-linear interactions in bimodal neurons of the rattlesnake optic tectum driven by visual and infrared inputs (Newman & Hartline, 1981), the basic neurocomputational principles of cross-modal integration were for the first time detailed in anesthetized cats (Meredith & Stein, 1983). The authors focused on neurons of the superior colliculus, an evolutionarily conserved midbrain hub whose deep layers host converging visual, auditory, and somatosensory inputs. Beside their polymodal properties, these neurons exhibited response profiles to combined stimuli that differed systematically from those to unisensory inputs. Depending on neuronal tuning and stimulation parameters, it was possible to identify two distinct activation regimes. On the one hand, the combined response to multimodal stimulation could be associated with an amplified signal that exceeded either the strongest unisensory response (i.e., *multisensory enhancement*), or even the sum of all unisensory activations, pointing to *superadditive* effects. On the other hand, the integrated response could display a sharp suppression as compared either to the best unisensory response (i.e., *multisensory depression*), if not the sum of all unisensory responses, implying *subadditive* effects. These and other statistical regularities concerning how neurons behave in response to stimulation paved the way to the further formalization of what are known as the three principles of multisensory perception:

- 1) *Inverse Effectiveness* – First witnessed as the foundational mechanism driving both *superadditive* and *subadditive* effects (Meredith & Stein, 1983), it posits that when single-modality cues are near-threshold, their cross-modal combination engenders a massive response boost, often larger than the one likely elicited by their sum. The converse holds as well: single-modality signals exceeding the threshold level, when combined, yields little additional benefit and can suppress any incremental gain. In brief, multisensory integration amplifies weak stimuli and tapers strong ones. This principle also applies to behavior, as shown in cats and monkeys displaying increased

attentional orienting when near-threshold visual cues are coupled with faint auditory clicks (Stein et al., 1988; Wallace et al., 1996)

- 2) *Spatial Congruence* – First observed in the superior colliculus of anesthetized cats, and further confirmed in rhesus monkeys, this principle states that cross-modal enhancement is contingent on the topographical organization of polysensory neurons, such that a response increase may occur as long as multisensory stimuli fall within overlapping receptive fields (Meredith & Stein, 1986; Stein et al., 1975; Wallace et al., 1996). The closer cross-modal pairs spatially align with portions of a neuron's receptive field where visuotopic, somatotopic, or tonotopic maps overlap, the greater the enhancement. Conversely, spatially misaligned signals provide little additional gain, if not even a response suppression (Meredith & Stein, 1996).
- 3) *Temporal Coincidence* – Akin to the *spatial congruence* rule, this principle provides that neural responses to cross-modal stimulation are strongest when sensory cues fall within a short temporal window (Meredith et al., 1987). Near-simultaneity is key: stimuli occurring slightly outside such critical window typically fail to elicit a response facilitation, and might even induce effects compatible with *multisensory depression*. In addition, greater temporal alignment shortens response onset latency, driving membrane potentials more rapidly toward threshold (B. A. Rowland et al., 2007). Crucially, these neuronal dynamics are mirrored behaviorally, with increased attentional orienting and faster reaction times in alert cats exposed to co-occurring cross-modal cues (Stein et al., 1988; Wallace et al., 1998).

All in all, multisensory integration appears to be instantiated in biological structures acting as coincidence detectors (Stanford et al., 2005). Weak and modality-diverse signals that converge into overlapping receptive fields within a shared temporal window, cause a summation of synaptic inputs, which in turn drives amplified and earlier population bursts in a superadditive fashion (B. A. Rowland et al., 2007).

1.2 Multisensory Properties of the Neocortex

Although the above principles governing cross-modal interplay were initially characterized in subcortical structures such as the superior colliculus, subsequent work has examined multiple cortical areas to assay the multisensory properties of their neuronal populations (Driver & Noesselt, 2008; Stein & Stanford, 2008). This line of research has proceeded along two complementary paths: studies

of association cortices and, perhaps counterintuitively, investigations of primary sensory cortices (figure 1.1).

1.2.1 Association Cortices

Findings gathered from anesthetized cats provided a useful point of departure for probing the cross-modal response profile of neurons lying on the cortical mantle. In alert cats, neuronal patches in the anterior ectosylvian sulcus (AES) were shown to be sensitive to spatial tuning of inter-sensory stimuli, much as superior colliculus cells were (Wallace et al., 1998). Given the rostrolateral location of this region and its rich connections with subcortical centers and primary sensory cortices, these observations set the neurophysiological stage for studies in nonhuman primates. The posterior parietal cortex (PPC) of macaques thus became a primary focus, owing to its visual, auditory, and somatosensory afferents. At the functional level, this area is parcelled into lateral, ventral and medial intraparietal sub-regions (LIP, VIP, MIP) encoding spatial features of the environment that inform goal-guided motoric planning underlying gaze-shifting and reaching movements (R. A. Andersen & Buneo, 2002). Both LIP and MIP were proved to integrate auditory and visual cues to flexibly reframe coordinate schemes based on the to be gazed or to be reached item (Batista et al., 1999; Stricanne et al., 1996). In addition, VIP was found to support peripersonal space representation through tri-modal integration of auditory, visual and tactile signals, via spatial tuning of auditory responses to visuo-tactile receptive fields (Schlack et al., 2005).

Similar patterns of cross-modal integration were also documented in the upper bank of the superior temporal sulcus (STS), a cortical locus rich in afferents from auditory and visual cortices and projections to parieto-frontal circuits (Cusick et al., 1995), when video clips of facial movement presented to monkeys were paired with congruent (as opposed to incongruent) sounds (Barraclough et al., 2005). STS sensitivity to the temporal proximity of cross-modal stimuli is likely mediated by feedforward connections to primary auditory cortices, as revealed by visual facial motion modulating auditory cortical responses (Ghazanfar et al., 2008). Beyond PPC sub-regions and STS, the ventrolateral prefrontal cortex (VLPFC) was proved to serve as a multisensory site supporting optimal integration and recognition of face-voice information pivotal to communicative behavior (Averbeck & Romanski, 2006; Sugihara et al., 2006). These observations prompted further investigations aimed at mapping the cortical circuitry that orchestrates cross-modal interactions in the human brain, beginning with the anatomical homologues of macaque association cortices. Using functional magnetic resonance imaging (fMRI) it has been possible to confirm the involvement of STS in perceptual binding heteromodal pairs in participants presented with audiovisual speech epochs. STS

displayed subadditive and superadditive activation in response to semantically congruent and incongruent auditory and visual cues, respectively (Calvert et al., 2000). In this vein, high-resolution fMRI showed how STS is populated by functionally heterogeneous patches of neurons, some of which reflecting inputs from auditory and visual cortices, some other multisensory in nature and responsible for mechanisms of inter-modal binding (Beauchamp et al., 2004). Parametrical manipulation of cross-modal signals strength and speech features further proved that STS indeed appears to perform audiovisual computations compatible with the *inverse effectiveness* principle, coupled with reduced reaction times at the behavioral level (Stevenson & James, 2009). Disruption of STS activity with transcranial magnetic stimulation (TMS) reduced susceptibility to the McGurk effect, which relies on the efficient fusion of speech and lip movements, without affecting single-modality processing of the same stimuli (Beauchamp et al., 2010). This complex set of operations is likely implemented by ongoing, dynamic reconfiguration of STS functional connectivity as a function of the sensory reliability of unimodal signals (Nath & Beauchamp, 2011; H. Park et al., 2018).

Fingerprints of cross-modal processing have also been documented in the intraparietal sulcus (IPS) and the temporo-parietal junction (TPJ), association regions within the PPC that exhibit long-range connectivity with STS and the frontal lobe (Caspers et al., 2011). Positron emission tomography (PET) revealed IPS bimodal encoding of spatio-attentional features for both visual and tactile signals, suggesting that IPS implement a cross-modal priority map coding attended location, regardless of sensory channel (Macaluso et al., 2000b). An fMRI-based follow-up confirmed IPS supra-modal mapping of visuo-tactile spatial coordinates subserving eye and hand movements, dissociable from unimodal and motor-related activations (Macaluso et al., 2003). Spatial tuning of this parietal hub was also examined with tactile, visual, and auditory motion, where IPS showed reliable engagement across modalities (Bremmer et al., 2001). Akin to STS, TMS-based disruption of IPS activity during a tactile localization paradigm abolished the behavioral advantages of multisensory integration (i.e., observing congruent touch video clips) witnessed when TMS was not delivered (Pasalar et al., 2010). Together, these findings implicate IPS in the supramodal encoding of modality-diverse spatial information that supports navigation, posture, and goal-directed behavior.

Cross-modal properties have also been reported in the lateral occipitotemporal cortex (LOTC; also labelled as hMT+/V5), as this site sits at the interface of the dorsal and ventral visual streams, and lies adjacent to STS and lateral temporal cortex (Malikovic et al., 2007). LOTC showed modality-invariant responses to object shape, either when seen or haptically-explored (Amedi et al., 2001), which were absent when object-related auditory information was presented (Amedi et al., 2002). In a similar fashion, both visual motion and vibrotactile stimulation were found to elicit patterns of activation in LOTC (Beauchamp et al., 2007). In blindfolded participants, viewing and haptic exploration of objects

evoked overlapping LOTC activity, and enhanced LOTC responses during subsequent visual recognition of the primed items, arguing for a meaningful role played by LOTC in supramodal shape processing rather than parallel unimodal streams (T. W. James et al., 2002).

1.2.2 Primary Sensory Cortices

Alongside evidence for association hubs supporting multisensory and supramodal processing after early unisensory computations, a complementary view has challenged this sequence. On this account, cross-modal integration occurs not only in established regions such as STS or IPS, but already within primary sensory cortices (Ghazanfar & Schroeder, 2006). Although seminal reports documented paradoxical activations in the primary visual cortex (V1) in response to acoustic stimuli (Fishman & Michael, 1973; Morrell, 1972), it was not until robust ERP evidence reporting early V1 interactions during an audiovisual task was provided (Giard & Peronnet, 1999) that a paradigm shift from a convergence-zone account toward models incorporating multisensory properties of primary cortices gained traction (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006). Initially construed as the by-product of feedback signaling from higher-order areas, the case for a direct involvement of primary sensory cortices in cross-modal integration was further strengthened by anatomical evidence. Retrograde tracers injected into macaques V1 revealed monosynaptic inputs from homologous somatosensory and auditory cortices, consistent with modulatory influences from nonvisual regions onto V1 (Falchier et al., 2002). Similar conclusions emerged from anterograde tracing in the primary auditory and somatosensory cortices (A1, S1), which showed patchy, feedback-like terminations in V1 (Rockland & Ojima, 2003). A subsequent study extended these findings by comprehensively detailing a dense, bidirectional network of incoming and outgoing heteromodal cortico-cortical projections linking primary sensory areas (Cappe & Barone, 2005).

This body of work catalyzed a new wave of experiments probing how primary sensory cortices contribute to multisensory processing. Starting from V1, fMRI-based inquiries on participants engaged in a sound-induced flash task revealed retinotopically-specific, auditory-driven increases in blood-oxygen level dependent (BOLD) signals. This V1 modulation during audiovisual trials was stronger than in unisensory regimes, and more pronounced on illusory-flash reports (Watkins et al., 2006). Remarkably, enhanced V1 BOLD responses to audiovisual streams not only exceed those elicited by auditory-only stimulation, but also track the temporal statistics of multisensory inputs, in line with the *temporal coincidence* principle: audiovisual streams in which auditory tones and visual cues are time-aligned evoke greater V1 activity than non-coincident streams (Noesselt et al., 2007). Feedback projections from non-visual sensory cortices can modulate V1 to the extent that, in blindfolded

participants hearing naturalistic sounds, multi-voxel pattern analysis (MVPA) could decode sound categories and imagery content from early V1 BOLD patterns (Vetter et al., 2014). The causal involvement of V1 in shaping cross-modal perception have also been probed with TMS. In a series of experiments leveraging neurostimulation and electroencephalography (EEG), Romei and colleagues demonstrated how looming sounds increased cortical excitability over the occipital pole (as indexed by the increased amount of TMS-induced phosphene reports), according to chronometric properties consistent with an early and pre-perceptual modulation of visual activity by sounds (Romei et al., 2009). Cross-modal phase alignment prompted by sound-evoked reset of occipital alpha rhythms has been listed among the electrophysiological mechanisms more likely to promote optimal audiovisual interplay, as shown by alpha phase-dependent cyclic fluctuations of TMS-induced phosphene reports following sounds presentation (Romei, Gross, et al., 2012). However, V1 modulation during multisensory processing can arise from somatosensory inputs as well. During the simultaneous visuo-tactile stimulation, event-related BOLD responses showed a retinotopic increase specific to congruent trials (tactile and visual stimuli presented on the same side) relative to incongruent trials, indicating touch-induced V1 activation consistent with spatial attention decoding mechanisms (Macaluso et al., 2000a). Comparable retinotopic, feedback-mediated effects of tactile stimuli on V1 BOLD were observed in blindfolded participants asked to haptically-explore raised-dot patterns (Merabet et al., 2007).

Albeit the aforementioned findings compel us to acknowledge the robust V1 engagement in cross-modal integration, A1 as well harbours synaptic afferents from heteromodal cortical areas, and is likewise liable to feedback-driven modulations (Cappe & Barone, 2005). A noteworthy instance of visually evoked activity in A1 appears in the silent lipreading paradigm, where visual linguistic cues prompt early BOLD increases in the absence of speech (Calvert et al., 1997). The same task was adopted to better detail how A1 modulation depends on visual input, with results showing maximal visually mediated BOLD increases in the Heschl's gyrus extending to primary auditory cortices (Pekkola et al., 2005). Early A1 visually induced responses (120-190 ms) have been also documented in an ERP study adopting an auditory recognition task when the to be recognized syllables were presented bimodally rather than unimodally (Besle et al., 2004), with similar patterns supporting audiovisual speech integration reported using intracranial recordings (Besle et al., 2008). Of note, vibrotactile stimulation can likewise elicit early activity in the human auditory cortex, implying somatosensory input capable of modulating A1 beyond speech (Schürmann et al., 2006).

S1 also shows cross-modal properties. In both participants reporting mirror-touch synaesthesia and neurotypical controls, merely observing touch on a body part evokes somatotopic S1 activations detectable via fMRI (Blakemore et al., 2005). In a visuotactile paradigm where participants' digits

were touched either synchronously or asynchronously with video clips showing digits being touched, S1 displayed dynamics, visually-dependent activation patterns (Schaefer et al., 2006). S1 contributions to the perceptual binding of bimodal stimuli also emerged during ecological visuo-tactile hand stimulation: as compared with unimodal stimulation, the audio-tactile condition produced multisensory enhancement via greater (additive) BOLD shifts, likely subserving a broader body ownership system (Gentile et al., 2011). The pivotal role played by S1 as a hub in the integration of visual and tactile signals was further corroborated by MVPA, which decoded content-specific S1 activity while participants watched a hand exploring different objects, without tactile inputs (Meyer et al., 2011). Importantly, repetitive TMS disrupting ongoing activity over S1 (as compared to S2 or the occipital lobe) during a visual discrimination task with tactile stimuli selectively impaired contact judgments for contralateral stimuli, consistent with the causal involvement of primary somatosensory cortices in the visual perception of touch (Bolognini, Rossetti, Maravita, et al., 2011).

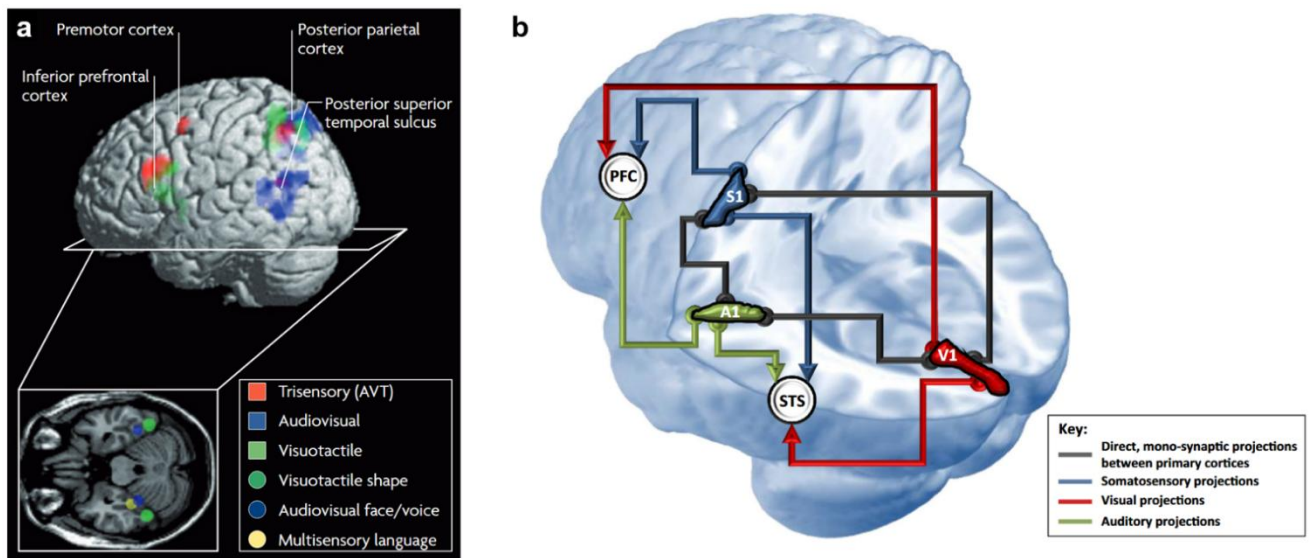


Figure 1.1 Neural systems supporting multisensory integration. **a)** Example cortical regions implicated in multisensory processing, showing partially distinct zones for audiovisual, visuo-tactile, and tri-sensory responses (adapted from Stein & Stanford, 2008). **b)** Schematic pathways linking primary sensory cortices (V1, A1, S1) with higher-order regions (e.g., STS, PFC), illustrating possible routes for cross-modal interactions (adapted from Murray et al, 2016).

1.3 Instances of Multisensory Integration

So far, we have outlined what computational principles govern multisensory processing, and which cortical sites are recruited to instantiate them. Anatomical findings are indeed suggestive of extensive axonal pathways routing feedforward signals to association hubs (e.g., STS or IPS), and feedback projections among primary sensory cortices. Such a complex cytoarchitecture provides a

neurophysiological substrate for many instances of cross-modal functioning that allow the orderly interplay of audition, vision and touch.

1.3.1 Audio-Tactile Interactions

The functional anatomy of audio-tactile integration relies on cortico-cortical feedback terminations landing in A1 from S1 (approximately 10% of all retrogradely labelled A1 neurons), with reciprocal yet sparser axonal projections in the opposite direction, suggesting more frequent tactile-to-auditory modulation than the reverse (Budinger et al., 2006). In right-hemisphere-damaged patients suffering from tactile extinction (failure to report a light touch on the contralesional hand when delivered simultaneously with an ipsilesional touch), this phenomenon was exacerbated when task-irrelevant pure tones or complex sounds were presented near (vs far) and rear (vs front of) the ipsilesional head space, arguing for an auditory peripersonal field interacting with somatic representations to shape perceptual awareness (Farnè & Làdavas, 2002). Intriguingly, the dependence of audio-tactile interactions on sound location was investigated in a later study adopting both a temporal order judgment (TOJ) and a distractor-interference task (Kitagawa et al., 2005). Result showed better performance and shorter reaction times when auditory stimuli were delivered from opposite (vs. same-side) locations behind the head, and when sounds were presented in the near (vs. far) peripersonal space. Consistent with prior work, strict spatial tuning is not required for behavioral facilitation: a significant reaction times reduction was reported in audio-tactile trials, relative to unimodal trials, regardless of whether bimodal pairs occurred in spatial register (Zampini et al., 2007). The impact of sound location was ecologically probed with looming or receding tones presented near vs far from the hand just before tactile stimulation. Again, looming (as opposed to receding) tones delivered near (as opposed to far) the to be stimulated hand shortened reaction times, likely via dynamic interactions with peripersonal space representations in the somatosensory domain (Canzoneri et al., 2012). Separately, the extent to which features of audio-tactile stimuli beyond timing and space putatively affect cross-modal judgments was quantified using a speeded detection task where auditory, somatosensory and simultaneous auditory–somatosensory stimuli were presented. Sound location and spectral content, emerged as the key drivers of behavioral facilitation, as the largest effects were reported with sounds presented near (vs far from) the body, at high (vs low) frequencies (Tajadura-Jiménez et al., 2009). The relevance of sound spectral statistics was further underscored in a study manipulating the spectral frequency of vibrotactile stimuli and auditory distractors: the closer their frequencies, the greater the interference and the worse tactile discrimination performance (Yau et al., 2009). Cross-modal frequency alignment can also benefit performance by shrinking the detection threshold in bimodal (vs

unimodal) trials, as long as audio-tactile stimulation is delivered in-phase (Wilson et al., 2009). Beyond spatial location and temporal alignment, it thus seems audio-tactile integration builds supramodal representations of sensory events based on the spectral features of multisensory signals. All these findings prompted debate on whether heteromodal inputs contribute to audio-tactile integration either by sharpening perceptual sensitivity or shifting response bias. The issue was tested by asking participants to perform a tactile detection task while irrelevant tones were delivered. Tactile sensitivity to near-threshold stimuli, but not response bias, increased with synchronous auditory inputs, especially for same side pairings, underscoring genuine multisensory gain (Ro et al., 2009).

Let it be noted that evidence for tactile-mediated modulatory effects on auditory perception has also been documented. In a series of auditory discrimination paradigms in which task-irrelevant tactile stimulation was provided, multisensory pairings increased detection and intensity ratings for near-threshold sounds (Gillmeister & Eimer, 2007). Perceptual benefits scaled with inverse effectiveness (weaker stimuli produced greater multisensory enhancement), and cross-modal temporal tuning (more synchronous pairings improved performance), but not with spatial congruence. Similar results were gathered through a sophisticated combination of aero-tactile stimulation (i.e., externally delivered air puffs) time-locked to auditory speech perception (i.e., aspirated vs unaspirated consonants), where identification of aspirated vs unaspirated items was significantly increased and decreased, respectively. The largest somatosensory-mediation on auditory responses was found with aero-tactile puffs delivered to participants' cheeks or necks, in temporal alignment with to the presentation of speech tokens (Gick & Derrick, 2009).

1.3.2 Visuo-Tactile Interactions

Retrograde tracer work in non-human primates V1 suggest that visuo-tactile integration engages cortico-cortical pathways operating predominantly in a feedback fashion, with more somatosensory inputs reaching the visual cortex than the reverse (Falchier et al., 2002). A rather seminal instance of how visuo-tactile interactions unfold traces back to the 60': reports about the shape of haptically-explored objects under an optically distorted visual regime were shown to follow vision over touch (Rock & Victor, 1964). From those years on, a great deal of studies investigating visuo-tactile interplay focused on vision-induced peripersonal space recoding. Evidence from right-hemisphere-damaged patients suffering from tactile extinction indicates visually-driven remapping of peripersonal space. Visual stimuli presented near the ipsilesional hand reduced detection of contralesional tactile stimuli, whereas visual stimuli near the contralesional hand improved detection; the same visual stimulation routines, when applied far from the hand, yielded weaker modulatory outcomes instead (Làdavas et

al., 1998). Such peripersonal space is sensitive to visual inputs even when dilated through experimental manipulation. Wielding a stick in each hand remapped the boundaries of visuo-tactile interactions to the extent that, in a patient with tactile extinction, a far-space visual cue paired with touch reinstated the extinction typically seen when visual stimuli occur in perihand space (Maravita et al., 2001). Spatial reframing of visuo-tactile interactions due to tool-driven remapping of peripersonal space has been further detailed in healthy individuals. In a visuo-tactile interference paradigm with participants holding a stick in each hand, incongruent visual distractors presented far from the hands (targets of the tactile stimulation) disrupted tactile discrimination when delivered on the same side as the stimulated hand. Crucially, these side-specific effects reversed when participant performed the very same task holding the tools in crossed positions, with visual bias flexibly tuning to newly defined peripersonal boundaries (Maravita et al., 2002). These cross-modal adjustments can occur on a very short time scale, and do not depend on predictability about which tool will be used (Holmes et al., 2007). The impact of hand posture manipulation on visuo-tactile integration was further assayed in a tactile discrimination task in which participants were asked to cross or uncross their unseen hands while tactile stimulation was delivered either on the thumb or index finger. Tactile judgments performance was better when the stimulated hand lay on the same side as the visual cue, regardless of whether the hand posture was crossed. Similar improvements were observed (no difference between crossed and uncrossed hands) for visual judgments when the visual cue was presented on the same side as the unseen hand undergoing the stimulation, indicative of dynamical audio-tactile remapping of spatial attention (Kennett et al., 2002). In this vein, in participants performing a discrimination response task with either tactile or visual targets, covert attentional reorienting produced faster reaction times even though the target modality was unpredictable. Of note, cross-modal effects were larger when visual and tactile attention were directed to the same rather than different position (Spence, Pavani, et al., 2000). Visually-mediated spatial modulation of touch becomes even clearer when visual distractors are presented during vibrotactile discrimination task: irrelevant visual cues impairs tactile discrimination as long as they are spatially congruent with the tactile target (Spence et al., 2004). Ecological assays of visuo-tactile integration have been also taken conducted using a texture discrimination paradigm (visual and tactile judgments between pairs of fabric stimuli). On each trial, targets in one sensory modality were paired with distractors in the other. Visual judgments proved to be systematically biased by incongruent tactile inputs, whereas no such modulation did occur in the reversed condition (Guest & Spence, 2003).

The role of cross-modal spatial tuning has been further scrutinized in a task probing the temporal properties of visuo-tactile integration. In the visuo-tactile version of the TOJ task, participants' temporal precision improved when cross-modal pairings were delivered from different positions, and

this benefit was abolished with crossed-hands posture (Spence et al., 2003). The contingency of multisensory benefits on spatial and proprioceptive features of was also tested with a simultaneity judgment (SJ) task in which tactile stimulation was delivered to distinct body parts. Intriguingly, reaction times predicted the *point of subjective simultaneity* (PSS): simultaneity was veridically perceived when touches and visual cues occurred on different rather than the same portions of the body. This pattern was construed as a compensation mechanism to ensure “simultaneity constancy” (Harrar & Harris, 2005). Even non-informative visual cues (neither task-relevant nor acting as distractors) can boost sensitivity to touch. In a two-point tactile discrimination task, the spatial resolution of touch improved when the stimulated body part was visible. Remarkably, visual magnification further increased tactile sensitivity, whereas viewing a neutral object did not yield any behavioral change (Kennett et al., 2001). Visual enhancement of touch also encompassed reaction times, such that viewing the to be stimulated arm sped up tactile responses (spatial discrimination) within a somatotopic bodily map, while no benefit was documented either when spatial computations were unnecessary or stimuli were not near-threshold (Press et al., 2004). This tactile facilitation was shown to persist in the absence of visual inputs: in a tactile orientation discrimination paradigm (haptic exploration of oriented gratings with the fingertip), viewing the fingertip, as opposed to a neutral object, improved discrimination, with the effect lingering for around 10 ms after the very view of the fingertip (Taylor-Clarke et al., 2004). The same paradigm revealed feature-selective tactile influence on vision, as haptically-exploring oriented gratings increased the perceptual dominance of a congruent (vs incongruent) visual grating during binocular rivalry (Lunghi et al., 2010)

1.3.3 Audiovisual Interactions

Among the many facets of multisensory processing, audiovisual integration has likely been under scrutiny the longest. The first pioneering inquiries date back the 50' and 60', showing that lipreading improves speech intelligibility in noise (Sumby & Pollack, 1954), and that intersensory pairings, as relative to unimodal stimuli, shorten reaction times (Hershenson, 1962). Following foundational works in the superior colliculus of anesthetized cats (Meredith & Stein, 1983), anatomical evidence for corticocortical feedback projections from the auditory cortex to V1 (Falchier et al., 2002; Rockland & Ojima, 2003) paved the way for several studies in humans. Benefits of audiovisual interplay have been documented in patients with hemianopia (visual field loss due to focal occipital lesions) or neglect (failure to reorient attention toward the left side of space due to right parietal lesions). In a multisensory detection task where unimodal and bimodal (audiovisual) stimuli were presented either on the same or different spatial locations, patients displayed enhanced visual detection in the spatially aligned bimodal

condition, provided that they suffered either from hemianopia or neglect, but not both (Frassinetti et al., 2005). Further, cross-modal stimulation has been proved to produce long-term improvement in individuals with visual deficits. Hemianopic patients undergoing a two-weeks long neurorehabilitation program requiring detection of visual targets under both unimodal and bimodal regimes, showed progressive improvement in visual detection and oculomotor exploration, maintained at one month follow-up (Bolognini et al., 2005).

These experimental probes were preceded by evidence gathered from healthy participants. Studies of covert spatial attention showed that orienting attentional resources to one hemifield in response to a cue in a given sensory modality also affected behavioral changes the other modality, as revealed by faster side-specific (but not modality-specific) reaction times, consistent with a supramodal system encoding spatial information across senses (Spence & Driver, 1996). In line with this interpretation, inhibition of return has been documented across auditory, visual, or tactile stimuli appearing at the same location as the preceding cue, regardless of the very cue modality (Spence, Lloyd, et al., 2000). This system, however, handles sensory signals asymmetrically: elevation judgments (no right-left components involved) in both audition and vision were better when an uninformative auditory cue occurred at the same target location (Spence & Driver, 1997). Auditory-driven visual facilitation is remarkably evident under high perceptual loads conditions, with bimodal cues capturing visuo-spatial attention better than unimodal stimuli (Santangelo & Spence, 2007). Behavioral facilitation was also documented during cluttered visual search, where the to be detected object is tracked faster when it co-occurs with task-irrelevant auditory pips (Van der Burg et al., 2008). This effect is reliant on temporal coincidence between heteromodal sensory cues, which predicts more efficient pop-out search, as shown in a later follow-up where transient auditory cues, temporally aligned with visual stimuli, decreased reaction times (Burg et al., 2010). Building on these findings, uninformative sounds that co-occurred with visual targets did shorten reaction times in a contrast detection task, whereas informative cues also increased detection rates, as reflected by significant shifts in the psychometric detection curve (Lippert et al., 2007). The spatiotemporal profile of this modulation was probed with basic stimuli embedded in dynamic 2D noise that participants were asked to detect under unimodal and audiovisual conditions. Results are suggestive of non-linear cross-modal interactions suppressing pre-target sensory activity, thereby sharpening perceptual sensitivity (i.e., signal-to-noise gains) through reduced temporal uncertainty (Pascucci et al., 2011).

Of note, audition and vision share a common frequency-based code that cross-modal processes exploit to facilitate behavior. Participants completing an audiovisual task (i.e., Gabor patches of varying spatial frequency co-occurring with tones of different temporal frequency) displayed better performance when frequency rates across sensory modalities matched, likely due frequency-

modulated sounds biasing awareness toward specific visuo-spatial frequencies (Guzman-Martinez et al., 2012). Such cross-frequency coupling in the perceptual domain subserves visual search: auditory cues spectrally attuned to the spatial frequency of a subset of Gabor patches among distractors improved search efficiency relative to uninformative (untuned) cues (Orchard-Mills et al., 2013). Auditory dynamics also shape visual operations when it comes to cross-modal motion processing, with near-threshold bimodal cues moving congruently along the horizontal plane prompting shorter reaction times compared with unimodal cues (Harrison et al., 2010). Moreover, this auditory bias impact visual motion perception even when uninformative acoustic cues are delivered. Using apparent-motion stimuli matched with alternating sound sources (left-to-right vs right-to-left, or up-to-down vs down-to-up), which provided task-irrelevant spatial information (visual motion was always orthogonal to the sound alternation), it was highlighted that visual direction responses systematically deviated toward the sound-defined axis (Teramoto et al., 2012).

Beyond compelling evidence that audition can bias vision, several findings support the reverse. Following up on classic demonstrations that lipreading improves speech intelligibility in noise (Sumby & Pollack, 1954), later work underscored the resulting cross-modal gains to be around 11 dB, and depended on visual-only proficiency, with wide differences across participants and sentences (Macleod & Summerfield, 1987). Lipreading influences auditory perception occurs at the earliest stages of cross-modal integration, as shown in a speech detection (rather than recognition) task where the average threshold improved by 1.6 dB when bimodal stimuli were congruent (acoustic traces matched the lip-read sentence). The threshold gain scaled with the degree of audiovisual temporal coincidence between the lip-opening area and the envelope of mid-high frequency energy derived from the acoustic signal (K. W. Grant & Seitz, 2000). Visually-enhanced speech detectability was also scrutinized in a later study using multiple control conditions to address whether this effect was speech-specific or driven by non-speech visual properties of co-occurring stimuli; improved speech detectability relied on speech-specific visual dynamics that provided a reliable temporal scaffold for the detection of acoustic signals (Bernstein et al., 2004). Consistently, older adults compensate for hearing loss with disproportionately larger gains from visual lipreading signals across a wide range of ecologically valid speech stimuli such as consonants, words and sentences (Tye-Murray et al., 2007). Finally, audiovisual integration has often been probed by manipulating temporal asynchrony within the same cross-modal pair. Among the first instances of this approach was the quantification of human tolerance to timing asymmetries instantiated by desynchronizing motion pictures from their soundtracks, in which a lesser temporal sensitivity was reported during vision-led trials relative to audition-led trials (Dixon & Spitz, 1980). However, these seminal findings overlooked spatial factors, later addressed in a TOJ task where sounds and lights were presented from the same or different sides.

Block-wise, participants were asked to report either which modality occurred first (modality-specific judgment), or which side occurred first (side-specific judgment). The authors found smaller *just noticeable differences* (JNDs) for modality-specific judgments in which stimuli were delivered from different sides, with no such effect for side-specific judgments, implicating both modality and space in sensitivity to temporal asynchronies (Zampini et al., 2003). The mechanisms shaping temporal sensitivity also appear plastic and amenable to changes. In a SJ task with consistent audiovisual asynchronies (sound-leading vs sound-lagging), the perceived PSS shifted toward the adapted lag, a phenomenon known as temporal recalibration (Fujisaki et al., 2004). Notably, a direct comparison of these audiovisual paradigms showed that, albeit related, their fitted parameters carry complementary information. PSS estimates in SJ tasks better reflect perceived synchrony, whereas TOJ parameters better index order sensitivity (van Eijk et al., 2008).

1.4 Instances of Multisensory Illusions

In the previous sections, we broadly outlined the computational principles governing multisensory integration, and their reliance on a neurophysiological substrate spanning from associative cortical areas to primary sensory cortices. We also concisely reviewed key instances of cross-modal interactions across touch, audition and vision, emphasizing the nuances of experimental paradigms and behavioral outcomes used to test them. However, a rather relevant family of multisensory phenomena was deliberately left aside. It is the case of cross-modal illusions, which arise when specific sensory parameters and stimuli properties are tuned in ways that bias conscious perception. The study of perceptual illusions has a long history that goes way back to von Helmholtz notion of perception as resulting from an *unconscious inference* process (Gregory, 1997). From this perspective, perception is not merely a passive recipient of external inputs, but it proactively operates on a moment-to-moment basis, by deploying prior knowledge and efficient heuristics, to resolve ambiguities inherent to sensory signals. Whether sensory information is degraded due to low signal-to-noise ratio, or by the physiological constraints of a single sense to access all relevant features of an object under scrutiny, perception would act as a compensatory mechanism: much like in hypothesis testing, perceptual routines operate in an inductive fashion to infer, rather than record, items and events in the external world (Gregory, 1997). An appealing implication of such a way of reasoning is that perception is fundamentally a generative (as opposed to a receptive) process, with conscious percepts representing best estimates of our surroundings given the subset of both sensory and prior information available (figure 1.2). Accordingly, perceptual representations are better construed as externally-referenced psychological projections, and not mere internal impressions of the outside world (Gregory, 1997). It

follows that illusory phenomena are not to be regarded as error or flaws, but as informative probes about the rules and priors driving our perceptual machinery, thereby bringing us closer to the foundational syntax which brain “language” is built upon (Gregory, 1997).

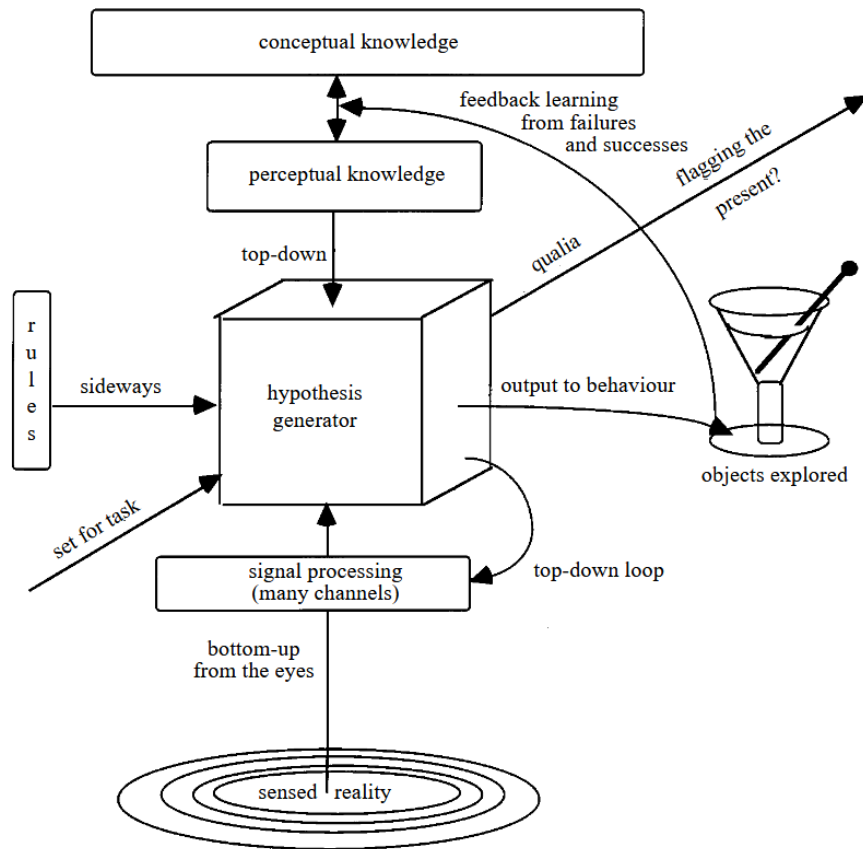


Figure 1.2 Perception as hypothesis testing: sensory input is combined with prior knowledge and rules within a “hypothesis generator,” and perceptual interpretations are updated via top-down feedback and learning from outcomes (adapted from Gregory, 1997).

The visual system has traditionally been the testbed to gain a better understanding of perceptual illusions (for a review and a tentative classification, see Gregory, 1997). However, this approach has progressively been challenged by accruing evidence suggestive of sensory modalities operating jointly, rather independently, at the earliest stages of perception when dealing with multisensory signals (Kujala et al., 1997; Sadato et al., 1996; von Melchner et al., 2000). Beyond conventional modular accounts that casted each sense as a separate module performing basic univariate operations, a new complementary framework posited the opposite: multisensory cues are combined or integrated within primary sensory cortices through synergistic, often non-linear, interactions (Ghazanfar & Schroeder, 2006; Shimojo & Shams, 2001). Cross-modal illusions have drawn increasing attention ever since, providing neuroscientists and psychophysicists with an additional tool to probe the neural and computational mechanisms of perception. Temporal synchrony, spatial alignment, and semantic

coherence are among the most diagnostic experimental factors for the perceptual dynamics underlying multisensory illusions (Shimojo & Shams, 2001). Notably, this paradigm shift helped push the main focus beyond vision, placing the spotlight on other senses (audition, touch) with the capacity to influence, under certain circumstances, vision itself (Shams & Kim, 2010; Shimojo & Shams, 2001). From a computational standpoint, multisensory illusions have served as valuable benchmark to compare and validate the model and algorithms through which cross-modal operations are instantiated. On the one hand, vigorous emphasis has centered on what could be broadly defined as *reliability weighting* strategies, in which an ideal observer integrates heteromodal signals in proportion to their sensory reliability (i.e., level of noise, as indexed by their inverse variance) to attain the most unbiased cross-modal estimate, and minimize as much as possible the variance inherent to each unisensory signal (Ernst & Bühlhoff, 2004). These normative models have been further refined to include multiple priors (e.g., causal, feature-based) to better capture the behavior of an ideal “Bayesian” observer (Shams & Beierholm, 2010; Shams & Kim, 2010), and account fairly well for phenomena such as modality-appropriateness shifts, and even the emergence of multisensory illusions (Alais & Burr, 2004; Körding et al., 2007; Noel et al., 2018). On the other hand, a more parsimonious, yet effective description of cross-modal interplay has been developed by borrowing psychometric modelling from psychophysics. Here, either a Gaussian or sigmoid curve is fit to the empirical data, and the resulting parameters such as the JND and PSS (i.e., gaussian function), or the inflection point and the slope (i.e., sigmoid function) are indicative of an observer’s perceptual precision and response bias (Vroomen & Keetels, 2010; Wallace et al., 2020). These psychometric accounts hold fine when spatial or temporal features of multisensory integration are the main variables of interest, with sensitivity to spatial disparities or temporal asynchronies (i.e., temporal binding window, TBW) serving as reliable indices of performance and proneness to cross-modal illusions (Bishop & Miller, 2011; Ferri et al., 2018; Stevenson et al., 2012). Taken together, all these pieces of knowledge position multisensory illusions as a convenient entry point for probing both neurotypical and abnormal dynamics of perception.

1.4.1 Audio-Tactile Illusions

Albeit audio-tactile interactions are perhaps among the less studied instances of cross-modal integration, some intriguing audio-tactile illusions have nevertheless been reported, many of which revolved around the influence of sound on perceived roughness/texture. The “parchment-skin” illusion belong to this family of phenomena. Participants were asked to rub their hands while receiving online audio feedback via a microphone that could deliver either the veridical sound or a spectrally warped version (high-frequency–boosted or attenuated). When listening to the high-frequency–boosted track,

as opposed to high-frequency-attenuated tracks, subjects rated their skin as rougher and drier (Jousmäki & Hari, 1998). In a similar fashion, it was shown that manipulating the spectral content of contact sounds during haptic exploration of abrasive surfaces biased participants toward reporting rougher or smoother ratings when, respectively, high-frequency spectral amplification or attenuation was attained. Crucially, these effects persisted regardless of participants' awareness of spectral manipulation, but were abolished when the auditory feedback was temporally desynchronized from the ongoing haptic exploration (Guest et al., 2002). Spectral manipulation of sound content also revealed a different yet informative type of audio-tactile illusion, the "light-body" illusion: real time high-frequency boosting of own's own walking sounds induces a lighter body sensation, prompting favourable changes in gait kinematics and enhancing the motivation for physical activity (Tajadura-Jiménez et al., 2015). The same group also reported what was defined as the auditory "Pinocchio" effect. In participant pulling up or down their right index fingertip alongside their left hand (both occluded) while hearing brief pitch-varying tones (e.g., rising, falling, constant), perceived finger length scaled as a function pitch, with rising sounds increasing the length estimates (Tajadura-Jiménez et al., 2017). Auditory-mediated proprioceptive illusions occur even with naturalistic sounds. The "marble hand" illusion arises when participants' occluded hands are gently tapped with a small hammer, while the veridical contact sound is progressively replaced by audio of a hammer striking a piece of marble (delivered via headphones). After approximately five minutes, such experimental manipulation results in participants perceiving the struck hand as unnaturally stiffer and heavier, coupled with enhanced skin-conductance responses, which could not be ascribed to mere audio-tactile synchrony (Senna et al., 2014). Overall, these audio-tactile illusions demonstrate that tuning specific auditory parameters during tactile or proprioceptive tasks may induce not only feature-level misperception, but also bodily misrepresentations.

1.4.2 Visuo-Tactile Illusions

Instances of visuo-tactile illusory-like phenomena often entail visual bias on tactile or proprioceptive judgments, broadly revealing the role played by visual-capture in touch perception or bodily representation. A notable case is mislocalization of touch when visual cues appear near a fake hand. This was shown in an experiment where vibrotactile stimuli were delivered on participants' occluded hands while distractor lights flashed. Under control conditions, mildly slower reaction times were reported when distractor lights were incongruent with the tactile targets. This interference increased, and a significant bias toward tactile mislocalization emerged, when a rubber hand bearing the distractor lights was placed in front of them, provided that it was spatially aligned with participants' own hands.

Notably, under spatial alignment, participants were also more likely to report the illusory sensation of feeling the touch on the fake hands, rather than their own (Pavani et al., 2000). Beyond mislocalization, synchronous visuo-tactile stimulation might elicit what is known as the “enfacement” illusion. Namely, tactile stimulation delivered on the face of participants viewing a morphed face on a screen being touched in the same way, produced a self-other judgment shift, as they appeared more likely to identify the morphed face as their own, demonstrating that multisensory integration can update one’s own bodily representation and sense of ownership (Tsakiris, 2008). Synchronous visuo-tactile stimulation was indeed shown to re-anchor body ownership in virtual reality: when participants received gentle stroke on the back simultaneously with a virtual body placed in front of them, they reported a strong sense embodiment toward of the virtual avatar, and a shift of their bodily representations and selfhood well beyond their physical body (Lenggenhager et al., 2007). Along these lines, a milestone study proved that the sense of ownership can be completely disrupted by manipulating cross-modal inputs. Leveraging an experimental setup similar to the earlier paradigm, participants wearing a head-mounted display viewed their-own body from behind, while their chest and the seen body’s chest were synchronously stroked with a stick. Most of participants reported an out-of-body experience, which was strikingly corroborated by increased skin-conductance responses when a virtual hammer struck the illusory body, provided that multisensory cues were delivered synchronously (Ehrsson, 2007). This methodological approach was widely adopted and extended in subsequent work. For instance, participants viewing a first-person video from a third person viewpoint, while both bodies were synchronously stroked, were shown to embody said virtual person, as indexed by subjective reports and skin-conductance measurements (Petkova & Ehrsson, 2008). Such illusory bodily representations also arise when participants view first-person videos from the perspective of overly tiny or large bodies, as it was documented in participants experiencing the ownership of a doll’s or a giant’s body. Notably, body ownership reports were accompanied by behavioral measures showing that objects size and distance rescaled with the embodied size: objects appeared, respectively, larger and farther away when embodying a doll, or smaller and nearer when embodying a giant (Hoort et al., 2011). The same visuo-tactile manipulation has been also proved to elicit illusory ownership of an extra limb (a third arm), and, quite strikingly, ownership of an “invisible” hand occupying an otherwise empty volume (Guterstam et al., 2011, 2013).

The relevance of the hand within one’s own bodily representation was further illustrated in what perhaps is the best-known visuo-tactile misperception, the “rubber-hand” illusion. This phenomenon was first revealed in seated participants with their left arm resting on a table, occluded from view by a standing screen. When a rubber model of the left hand, placed on the table in front of them, was stroked synchronously with the hidden hand, participants reported, after approximately 10 minutes, to oddly

feel the touch on the rubber hand, rather than on their own occluded hand (Botvinick & Cohen, 1998). An impressive demonstration that manipulating multisensory input can rewire, not only body ownership, but also autonomic responses was provided in later study, in which “injuries” to the embodied rubber arm elicited skin-conductance responses comparable in magnitude to those evoked when the real hand was similarly threatened (Armel & Ramachandran, 2003). Moreover, the strength of rubber-hand embodiment was shown to predict the degree of cortical activation in interoceptive areas: the stronger the illusory sense of hand ownership, the larger the BOLD signal recorded in the insula and the anterior cingulate cortex when the prosthetic hand was threatened (Ehrsson et al., 2007). Physiological changes stemming from rubber-hand-induced reshaping of body schema also include basic homeostatic processes such as skin-temperature regulation. Across six experiments where the rubber-hand illusion was successfully elicited, participants’ hidden arms displayed a significant decrease in skin temperature that could not be ascribed to visual or tactile stimulation alone, nor was reported in the unstimulated hand or the ipsilateral foot (Moseley et al., 2008). Overall, these data indeed suggest that disrupting the complex interplay between visual, tactile and proprioceptive information to the point of rewriting one’s own body awareness might top-down modulate autonomic, cortical, interoceptive and homeostatic activity. The joint integration of interoceptive and proprioceptive signals represents a key basis on which bodily representations are built. This was elegantly demonstrated in a rubber hand illusion paradigm that assessed introspective and physiological indices of interoceptive ability for each participant. Results showed that individuals with lower interoceptive sensitivity (as probed using a heartbeat detection task), and thus poorer internal bodily awareness, were more susceptible to the rubber hand illusion and, more broadly, to exogenously driven changes in body schema (Tsakiris et al., 2011). Interoceptive contributions to the sense of body ownership extend even beyond heartbeat sensitivity, encompassing the affective value of tactile stimulation. When the rubber hand illusion was induced, subjective embodiment of the prosthetic hand appeared stronger with slow (mimicking affective touch) than fast stroking, and the illusory touch was perceived as more pleasant (Crucianelli et al., 2013). Of note, once the illusion of a different body schema is set in motion, sensory properties associated with the replaced body part (i.e., the hidden hand) can transfer to the artificial limb. In a rubber hand illusion paradigm combined with a self-touch attenuation, reduced perception for self-generated touch transferred to the embodied hand, suggesting that reshaping body schema might also disrupt sensorimotor predictions behind self-generated sensation (Kilteni & Ehrsson, 2017).

1.4.3 Audiovisual Illusions

Within the broad family of cross-modal misperceptions, audiovisual illusions are arguably the earliest documented, and remain among those receiving the widest attention. Most audiovisual illusions involve auditory input biasing vision; a relatively recent example is the sound-induced visual motion illusion. This multisensory phenomenon relies on the exposure to a pair of alternating visual cues (flashing circles) set to induce apparent motion, coupled with a pair of alternating tones each one of a distinct frequency, such that a given specific tone within the auditory pairing always co-occurred with the onset of a specific cue within the visual pairing. When a static, blinking circle is later presented in synchrony with the same auditory pairing used during exposure phase, the auditory sequence drives a strong illusory motion percept aligned with the direction of the prior audiovisual pairing (Teramoto, Hidaka, et al., 2010). A follow-up study tested whether this auditory-driven visual motion illusion generalizes to more complex stimuli deploying binaural cues to simulate auditory horizontal motion while static flashes appeared in the peripheral visual field. Participants first displayed a perceptual motion shift toward the auditory direction, which reversed after adaptation (Hidaka et al., 2011). This effect also extended to sound-induced motion along the vertical plane, scaling with the retinal eccentricity of static visual stimuli (Teramoto, Manaka, et al., 2010). Moreover, the same group showed that pairing visual apparent-motion stimuli with alternating sounds delivered from vertically and horizontally aligned loudspeakers elicits illusory motion, with the perceived direction deviating as systematically toward the sound defined axis (Teramoto et al., 2012). All in all, these piece of evidence argue for a common cortical circuitry engaged by audiovisual stimulation, which nurtures illusory perception by overweighting auditory signals, thereby warping visual experience.

Another well-known audiovisual illusory phenomenon involving visual motion is the stream-bounce illusion: two identical discs that slide toward each other from opposite sides of the screen at the same speed, end up coinciding (i.e., overlapping) right at the center, and then slide away symmetrically, are oftentimes perceived as streaming through. However, when a brief non-spatial auditory click is delivered right at the moment the discs coincide, observers are strongly biased toward perceiving them as bouncing rather than streaming. Simultaneity is crucial for this illusion to occur, with temporal delays between discs coincidence and auditory clicks over 150 ms abolishing the bouncing reports, flipping perception back to streaming (Sekuler et al., 1997). The contingency of this illusion on genuine audiovisual integration mechanics has been detailed in subsequent study that parametrically probed the temporal properties of auditory tones driving the bouncing reports. Paramount above all other parameters were timing and duration, with the greatest bounce-inducing effect elicited when both the onset and offset of the acoustic stimulus matched with, respectively, the onset and offset of the spatial

coincidence relative to moving discs (Remijn et al., 2004). This pattern points to audiovisual TBW dynamics, rather than exogenous attentional cueing, being responsible for the emergence of the illusion. Consistent with this view, manipulating some key acoustic features of auditory tones delivered simultaneously with the overlapping of moving discs differentially affected the stream-bounce illusion. By tuning both the amplitude and decay of colliding sounds such that they could be perceived either as impact-similar or impact-dissimilar, it was indeed shown that the latter, although as distracting as the former, did not elicit a perceptual switch from streaming to bouncing reports (Grassi & Casco, 2009). Alongside temporal coincidence, semantic congruence also plays an important role, enhancing the likelihood of perceptual swaps toward “bounce” reports. When disks’ motion was paired either with naturalistic bounce-congruent (i.e., billiard ball impact) or bounce-incongruent (e.g., water drop) sounds, both conditions induced more bounce responses than the silent display, but the former elicited stronger perceptual switches than the latter (Grassi & Casco, 2010). The sound-induced bounce illusion was shown to generalize beyond simple moving disks defined by luminance contrast, to disparity-defined moving objects (Grove, Kawachi, et al., 2012). Sound-driven biases on motion perception were further investigated, first by making moving disks visually distinguishable in the silent display condition, and then by implementing a 2AFC regime. Results argued for coincidental sounds driving the illusion by inflating observers’ criterion bias toward a more liberal (bounce over stream) response style, rather than perceptual sensitivity, with the illusion primarily occurring due to the concurrent reshaping of decisional factors (Grove, Ashton, et al., 2012).

Temporal coincidence and spatial congruence, two of the three pivotal principles of multisensory integration, also underpin what is known as the “ventriloquist” illusion (or “ventriloquist” effect): a salient, but spatially discrepant, visual cue tricks an observer into mislocating the source of a sound closer to said visual event. A phenomenon we experience on a daily-basis (for instance, while watching TV), the psychophysical bases thereof were first described experimentally in the 1940s. Two light were presented at spatially separated position, while a buzzer was sounded from various locations between them, and participants were asked to estimate where did the buzzer come from (left, middle or right). In key conditions (e.g., “in-rhythm”), one of the lights flickered synchronously with a buzzer, although both the lights and buzzers were delivered according to different rhythmic patterns. Remarkably, spatial judgments skewed toward the “in-rhythm” light position in synchronous trials, while no such response distribution occurred in “non-rhythm” trials, with participants denying the use of lights to orient their choice and typically unaware of sound-light congruence (Thomas, 1941). Spatial disparity and cross-modal bias in ventriloquism were further scrutinized in a subsequent study showing that auditory and visual stimuli are perceived as fused or separate events due to perceptual effects rather than alterations in response bias (Bertelson & Radeau, 1981). Visually-induced sound

mislocalization underlying ventriloquisms have indeed been proved to result from recalibration of auditory space via cortical plasticity, which persist for tens of minutes after prolonged exposure to audiovisual spatial disparities (Recanzone, 1998). This effect appears independent of both endogenous and exogenous spatial attention, reflecting genuine pre-attentive inter-sensory dynamics (Bertelson et al., 2000; Vroomen et al., 2001). The perceptual computations subsuming the ventriloquist illusion were identified in a foundational study, in which participants were asked to localize Gabor patches of varying widths and auditory tones, presented unimodally, or bimodally at different spatial disparities. Under optimal visual conditions, spatial judgments in bimodal trials skewed toward the location of visual cues. The reverse occurred under noisy visual conditions, where sound spatially captured vision. Ventriloquisms seemingly emerge from the reliability-weighted combination of perceptual cues performed through maximum-likelihood estimation: the blurrier the visual information (i.e., the higher the uncertainty), the heavier the contribution of auditory signal to spatial localization (Alais & Burr, 2004). Audiovisual illusions might thus be reframed as informative probes of how a Bayesian observer weights priors and sensory likelihood when evidence is conflicting (Ernst & Bühlhoff, 2004).

This consideration leads to perhaps the most widely known misperception within the audiovisual domain: the “McGurk” illusion. First reported in 1976, it occurs when participants hear a speech-related phonetic sound (i.e., /ba/) while lipreading a face articulating a similar, yet incongruent, syllable (e.g., /ga/). When asked which syllable was presented, observers more often report a fused percept (e.g. /da/), rather than either of the veridical stimuli actually presented, although they accurately perceive those same syllables when presented in unimodal sequence (McGurk & Macdonald, 1976). Robustly replicated English-speaking participants, but weaker in non-English speakers (Sekiya & Tohkura, 1991), the McGurk effect, like many multisensory illusions, critically depends on temporal alignment between auditory and visual cues. Strict synchrony is not required for the illusion to emerge, as the binding window within which cross-modal information can be optimally fused appears broad and asymmetrical, with sounds allowed to lag lipread syllables up to approximately 200 ms (Munhall et al., 1996). Coarser sensitivity to timing mismatches predicts the extent to which audiovisual pairings could be fused into a McGurk percept. To isolate the brain circuits underlying fusion (strong McGurk effect) or fission (weak McGurk effect), a subsequent fMRI study compared perceivers and non-perceivers presented with congruent audiovisual syllables, McGurk syllables, and non-McGurk incongruent syllables. Results showed that the greater the activity in STS, a well-known transition hub subserving multisensory integration, the more likely the occurrence of the McGurk effect when McGurk syllables were delivered, with strong perceivers displaying larger STS activity as opposed to non-perceivers (Nath & Beauchamp, 2012). At the computational level, the seamless fusion of incongruent audiovisual phonetic cues into an illusory, McGurk percept follows combination rules

remarkably akin to those responsible for the ventriloquist effect, namely reliability-weighting and causal inference. In brief, observers assign perceptual weights to each phonetic signal in proportion to its precision (i.e., inverse variance, indexing the degree of noise), and estimate their probability of originating from either the same or multiple sources. The illusory outcome is thus construed as the interaction between noisy sensory representations unable to capture subtle incongruencies across cues, and a stronger prior for a common cause that reinforce cross-modal fusion over fission (Magnotti & Beauchamp, 2017).

Chapter 2: What You See Is What You Hear: The Sound-Induced Flash Illusion

The previous chapter concluded with a broad overview of cross-modal illusions, from the rationale for investigating them to a focus on the best-known misperceptions reported in the audiovisual domain. However, one further illusory phenomenon epitomizing the asymmetrical synergy between audition and vision warrants mention: the Sound-Induced Flash Illusion, often referred to as SIFI (Shams et al., 2000). Rather than spatial, temporal, or linguistic judgments, the SIFI revolves around numerosity and the misjudgments thereof. This multisensory illusion was first highlighted in a task where combinations of brief visual (flashing disks) and auditory (pure sinusoidal tones) cues were presented. Audiovisual pairings were arranged in a 4 x 4 factorial design, such that, in each trial, either 1, 2, 3, or 4 interleaved flashes alongside 1, 2, 3 or 4 interleaved tones were delivered in a randomized order, thereby varying visual and auditory numerosity on a per-trial basis. Participants were asked to report how many flashes they saw, irrespective of the number of sounds. Strikingly, in trials in which a single flash was accompanied by multiple tones, observers incorrectly reported that multiple flashes occurred, whereas no such pattern was witnessed in control trials with either one or no tones (Shams et al., 2000). This misperception persisted even in non-naïve participants, remained consistent across many experimental manipulations (e.g., disks eccentricity, contrast, spatial disparity), and survived at inter-stimulus intervals up to 100 ms. The authors construed these effects as a straightforward and robust demonstration of how sound can qualitatively alter vision, likely through polysensory properties of cortical neurons (Shams et al., 2000).

A single flash accompanied by many tones is therefore perceived as multiple, yet multiple flashes are not collapsed into a lone visual transient when paired with a single tone. This asymmetrical tendency toward fission over fusion, along with the temporal profile characterizing the illusion, were further detailed in a follow-up study. Through a two-step experiment, it was first shown that the SIFI was not attributable either to sound-induced attentional arousal (i.e., no illusory flash reports occurred when a single tone was delivered with a single flash, i.e., 1F1S trials), nor was it due to an auditory bias (i.e., perceived flash numerosity, when a single tone occurred alongside multiple flashes, was larger in 1F1S trials). This indeed confirmed fission, rather than fusion, as the SIFI governing mechanism (Shams et al., 2002), which prompted psychophysicist to sometimes rename it double-flash illusion (DFI, figure 2.1). Second, in 1F2S trials (i.e., the minimal tone count for the SIFI to emerge), the illusion appeared reliant on a temporal window of integration spanning 100 ms, peaking at inter-stimulus (i.e., inter-tone) intervals around 50 ms, and a progressively decaying when the second flash fell outside it. Taken

together, these piece of data dismiss an alleged top-down origin of the SIFI, framing the illusion as a the result of genuine bimodal interplay under favourable temporal conditions, consistent with the *discontinuity hypothesis*: during cross-modal processing, the influence of the discontinuous modality on the continuous one is stronger than vice-versa (Shams et al., 2002).

This account was later found to be partly inconclusive given that fusion instances (although weaker than fission) can also occur, and that fine-tuning the sensory parameters of the stimulation can reverse the SIFI into a flash-induced tone illusion (i.e., misjudgment of tone numerosity due to visual cues). The *information reliability hypothesis*, stating that sensory dominance is dictated by the most reliable modality, was thus proposed to better capture SIFI dynamics (T. S. Andersen et al., 2004). Such hypothesis is compatible with a bottom-up account of the illusion, in which early cortical interactions occurring within a 100 ms wide temporal window should elicit two-flash illusory reports, with perceptual sensitivity being the latent variable driving the SIFI. Supportive of this view, it was demonstrated that providing participants with trial-by-trial feedback tied with monetary reward barely reduced the amount of illusory flash perception, the impact of which quickly vanished after feedback was no longer given. Signal-detection theory (SDT) metrics computed on feedback trials revealed that the mild decrease in extra-flash reports reflected changes in response criterion. Namely, feedback likely shifted participants' response style toward a more conservative criterion, while leaving visual sensitivity unaltered, providing an additional argument for the SIFI as being largely independent of decisional factors (Rosenthal et al., 2009).

What was addressed next concerned which facet of visual precision did the SIFI engage: was it driven by purely temporal factors, or did spatial inputs also contribute? Inquiries aimed at clarifying the issue leveraged a standard SIFI paradigm in which auditory and visual cues could either occur in congruent (same side) or incongruent (opposite sides) locations on the screen. However, no change to the illusion rate was reported as a function of spatial mismatch, once more emphasizing the SIFI primarily governed by temporal sensitivity dynamics (Innes-Brown & Crewther, 2009). Spatial congruence was also manipulated in a subsequent study, together with auditory spatial cue composition (tones delivered either in free-field or over headphones; tones endowed with either strong or weak binaurality), and visual spatial cues parameters (either small or large flashes, presented at central or peripheral screen locations). Consistent with previous findings, spatial disparity little affected the occurrence of the SIFI. On the other hand, sensory reliability of acoustic signals and visual cues inflated extra-flash reports: strong binaural cues (large sensory reliability) magnified the illusion when paired with small flashes in the periphery (poor sensory reliability). That is, auditory events drive visual numerosity irrespective of spatial alignment, as long as vision is noisy (e.g., it provides less precise information) in temporal or spatial terms (Kumpik et al., 2014), thereby reconciling what principled by the *information*

reliability hypothesis with earlier stances put forth in the *modality appropriateness hypothesis* (e.g., the modality more appropriate for the task at hand dominates).

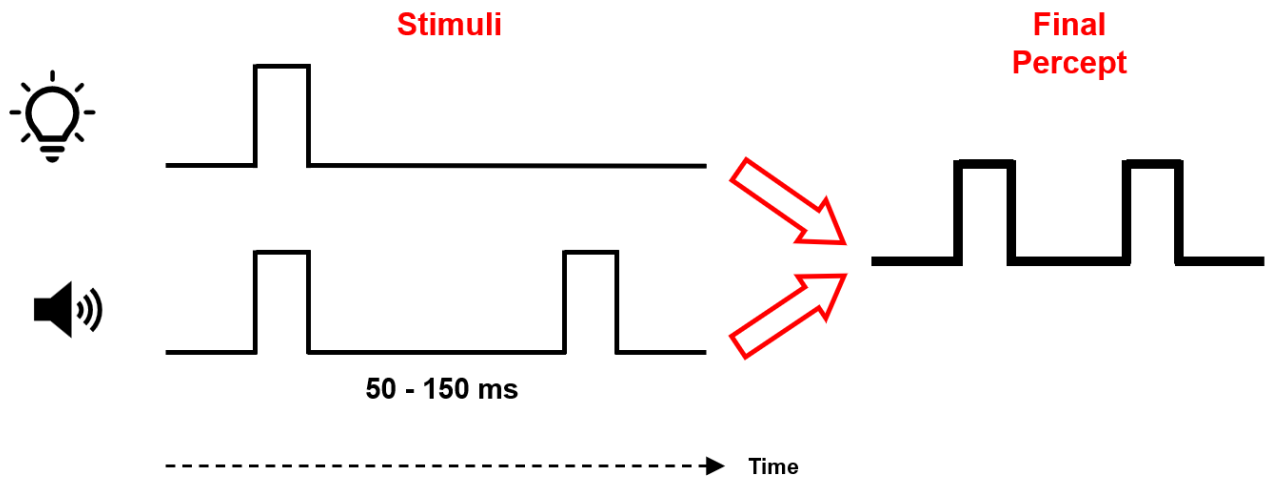


Figure 2.1 Sound-induced flash illusion (double-flash form): In the DFI variant, a single visual flash paired with two brief tones separated by ~50–150 ms can lead observers to report perceiving two flashes, reflecting auditory-driven modulation of visual numerosity.

2.1 Computations and Psychophysics

A seemingly common finding across studies concerns the dependence of the SIFI on poorer visual temporal processing relative to audition. This aligns with behavioral evidence showing that audition encodes fine-grained temporal information more effectively, whereas the visual system is best suited to provide higher-precision spatial estimates (Welch & Warren, 1980). Extra-flash percepts characterizing the SIFI have typically been explained by more reliable auditory signals biasing visual numerosity representations. The mechanisms underlying this cross-modal arbitration have been framed within two complementary accounts of multisensory integration, each with distinct assumptions and practical implications.

2.1.1 Bayesian Causal Inference

As the name itself suggests, Bayesian causal inference (BCI) posits that inter-modal computations are carried out by observers who combine modality-diverse cues via Bayes' rule, not only by weighting their sensory reliabilities, but also by accounting for their causal nature. Developed to refine earlier Bayesian cue-integration models downplaying the putative contribution of inherent causal dynamics (Alais & Burr, 2004; Ernst & Bühlhoff, 2004), the core assumption around which the BCI framework was designed provides that observers confronted with multisensory stimuli are tasked to address the

so-called “binding” problem (Noppeney, 2021): do sensory cues originate either from the same or different events? BCI then models how said “ideal” observers infer the latent causal state of a multisensory observation as a statistical combination of both task-relevant properties characterizing heteromodal inputs, and priors over their causal interactions (Shams & Beierholm, 2022). Importantly, in the context of BCI priors are construed as distinct hypotheses, shaped by learning and experience, about the latent causal profile of a cross-modal observation, which are independent of the sensory evidence. These hypotheses also compete with each other, in the sense that they represent mutually exclusive models concerning the causal structure of co-occurring stimuli. Causal inference instantiated by the BCI model thus arbitrates, in a Bayesian fashion, between prior expectations about either a common cause (e.g., same event) or independent causes (e.g., distinct events) subsuming a given cross-modal stream, and the likelihood that the associated sensory signals indeed derive from a common or independent causal structure (as quantified by the degree of feature-based congruency or similarity across modalities). The resulting posterior probabilities correspond to the optimal estimates regarding the causal profile of said multisensory observation, namely estimates concerning the causal properties of sensory signals under a given prior assumption, weighted by how likely these properties are (Shams & Beierholm, 2022; Zhu et al., 2024a). As such, BCI operates as a normative and generative Bayesian model (figure 2.2), whose posterior probabilities are based on, respectively, how strong the pull for integration or segregation is (common cause vs independent causes), and how reliable sensory likelihoods are (feature-based congruency or similarity). In modelling terms, these posterior probabilities approximate an observer’s latent representation of the causal structure relative to a cross-modal event, which can eventually inform perception once they are fed to the chosen decision-making strategy (Zhu et al., 2024a). Among the most common are *model averaging*, in which optimal estimates relative to each causal structure are merged together in proportion to their probabilities (e.g., resulting in a weighted compromise between integration and segregation); *model selection*, which optimizes causal inference by selecting the causal structure with the highest posterior probability (e.g., resulting in a categorical-like decision between integration or segregation); and *probability matching*, in which on a trial-by-trial basis the causal structure is stochastically selected in proportion to their posterior probabilities (e.g., resulting in trial-by-trial switching between segregation and integration).

Using BCI modelling, it was first demonstrated that the SIFI represents a perceptual epiphenomenon of an otherwise statistically optimal inference strategy (Shams et al., 2005). The authors implemented a wide factorial design (0–4 flashes $\times$ 0–4 beeps) akin to the original one (Shams et al., 2000), with the BCI model set to flexibly allow either fission, fusion, or a mixture of both, depending on the numerical disparity across modalities. Results showed that when a single flash was paired with two tones, the sharper auditory (as opposed to visual) likelihood biased the posterior probability toward a

common cause (i.e., both sensory streams originate from the same event) and the fission illusion. The diametrically opposite combination, two flashes paired with one tone, resulted in the fusion illusion by virtue of the same computational principle: more precise auditory likelihood takes over, and posterior probability is steered toward a common cause structure that collapse two flashes into a lone visual transient entwined with the single tone (Shams et al., 2005). As numerosity mismatches grow, the biasing impact of audition over vision shrinks, posterior probabilities favour independent causes, and the optimal estimates result in a more veridical arbitration between segregation or integration (e.g., fission or fusion illusions vanish). In brief, extra-flash reports occur as monotonic function of the inferred posterior probability of a common cause, weighted by multisensory reliabilities, with stronger illusory percepts emerging under lower visual reliability (Shams et al., 2005). Similar computational evidence was gathered in later studies replicating the above patterns, namely poor visuo-temporal sensitivity fuels the SIFI through a stronger pull toward integration (i.e., common cause) over segregation (i.e., independent causes), provided that numeric disparity is small (Rohe & Noppeney, 2015; Zhu et al., 2024b). This “binding” tendency displays trait-like properties, as shown in participant completing two sessions of a SIFI task one week apart. Results indicated that the propensity to integrate modality-diverse signals, and treat them as originating from a common cause, is strikingly stable over time, yet task-specific (Odegaard & Shams, 2016).

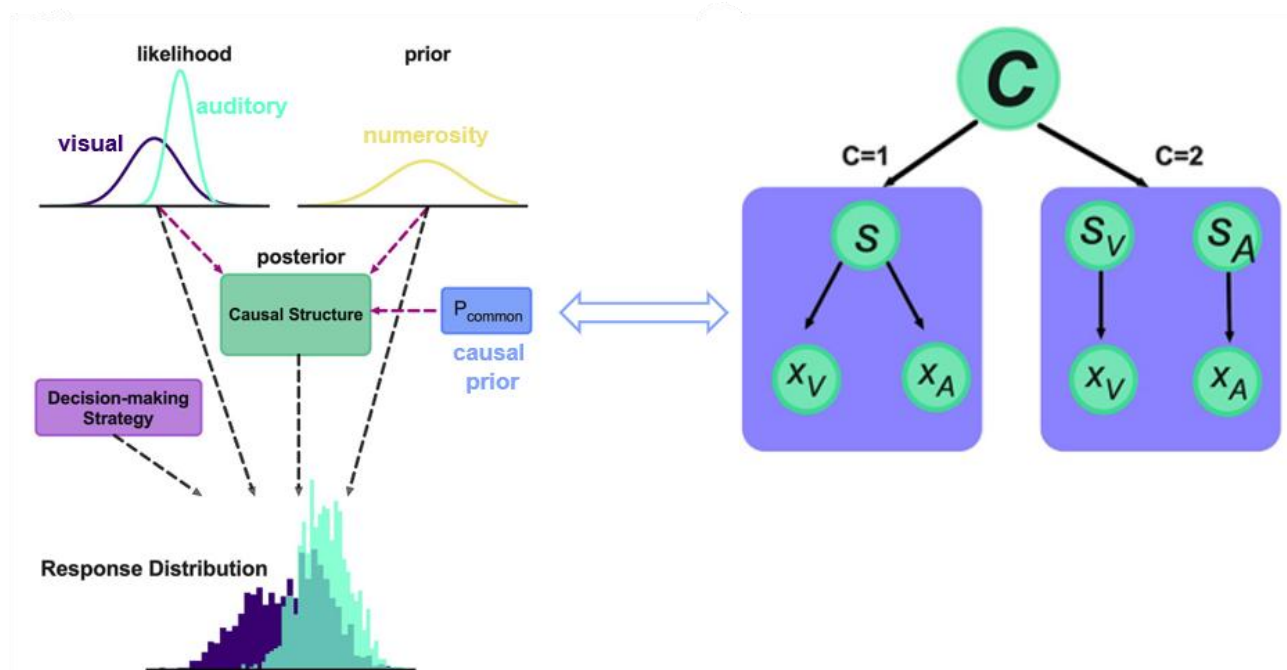


Figure 2.2 Bayesian causal inference framework for audiovisual numerosity. Auditory and visual inputs are represented as noisy likelihoods, and combined with priors (left panel), including a causal prior (P_{common}) over whether signals share a common source ($C = 1$) or arise independently ($C = 2$). Posterior beliefs about causal structure are then mapped onto perceptual estimates via an explicit decision rule, yielding the observed response distribution (adapted from Zhu et al, 2024).

2.1.2 Temporal Windows of Cross-Modal Integration

Alongside BCI, a more conventional yet no less informative approach has been adopted to probe the perceptual dynamics driving illusory reports in the SIFI. This approach, rooted in experimental psychophysics, models observers' performance with psychometric functions that provide meaningful insights into one's own sensitivity to temporal asynchronies between co-occurring heteromodal stimuli (Vroomen & Keetels, 2010). Typically, this is attained by fitting a Gaussian or sigmoid curve to each participant's data, whose parameters are retained for further analyses. Originally developed to capture supramodal properties inherent to temporal coincidence (Vroomen & Keetels, 2010), psychometric assays of multisensory performance mostly focus on the standard deviation of the Gaussian fit, or the inflection point of the sigmoid function. Both parameters are taken as reliable indices of an individual TBW: the temporal span within which cross-modal cues must co-occur to be judged simultaneous (Wallace & Stevenson, 2014). Conceptually akin to the common-cause notion in BCI, simultaneity implies that the cues likely originate from the same event (or same source, hinting to a common cause). Within an observer's TBW, stimuli integration is thus promoted, whereas outside it segregation becomes the most reported scenario (Wallace & Stevenson, 2014). Accordingly, TBWs have been thought to represent the psychometric readout of tolerance to temporal asynchronies, with wider TBWs accommodating the integration over temporally misaligned signals, and therefore enhancing the likelihood of simultaneity judgments (figure 2.3).

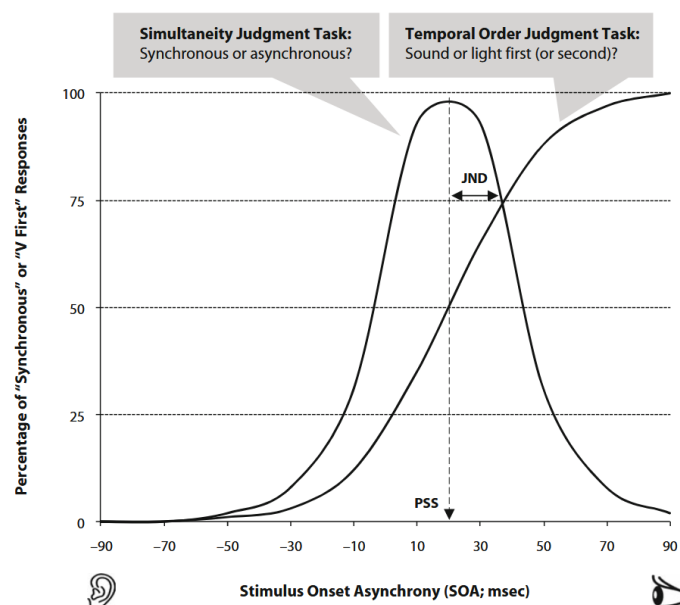


Figure 2.3 Psychometric functions for audiovisual timing judgments. Illustration of typical response curves for SJ tasks (proportion "synchronous") and TOJ tasks (proportion "visual-first") as a function of SOA. PSS and JND are highlighted as standard indices of temporal bias and precision (adapted from Vroomen & Keetels, 2010).

Over time, TBW-informed accounts have progressively surfaced also in the context of the SIFI, consistent with the contingency of extra-flash reports on inter-tones intervals of approximately 100 ms (Shams et al., 2000). Setting the stimulus onset asynchrony (SOA) above this temporal lag deflates the susceptibility to the illusion, which is otherwise preserved when inter-beep delays are kept below it. The mechanistic interpretation of this phenomenon has been borrowed from SJ or TOJ tasks: TBWs are indicative of an individual's visuo-temporal acuity. Along these lines, broad binding windows marks observers who are less sensitive to fine-grained temporal mismatches in numerosity, and more prone to integrate cross-modal events to the point of splitting a lone visual transient into two. Conversely, individuals with sharper visuo-temporal sensitivity display narrower TBWs, and a lower propensity to report extra-flash percepts (Stevenson et al., 2012). The endorsement of a TBW perspective on the SIFI was shown to be fruitful from several angles. First TBWs are rather straightforward to compute given a SIFI dataset spanning multiple SOAs. Second, TBWs exhibit trait-like features (i.e., stability over time) enabling the prediction of putative inter-individual differences in SIFI susceptibility across experimental conditions or groups. Third, and somehow related to the second point, enlarged TBWs have been documented across neurodevelopmental and psychiatric spectra, implying that this psychophysical construct indeed captures latent alterations in low-level cross-modal processing (Wallace & Stevenson, 2014).

A seminal instance of a TBW-based approach for detailing the temporal regimes under which the illusion was most likely to occur, adopted several different stimulus onset asynchronies in a SIFI paradigm where a single flash co-occurred either with the first or last tone within each acoustic pair. Expanding upon previous findings, results showed the illusion peaking at SOAs of approximately 50 ms, persisting up to 100 ms, and rapidly decaying after (Shams et al., 2002). However, the first piece of research to explicitly tie the TBW construct to SIFI proneness appeared some years later. Participants completed three audiovisual tasks: a SJ task with SOAs spanning both audio-lead and audio-lag offsets, a SIFI task in which a single flash was paired with 1-4 near-synchronous beeps, and McGurk task. Results from the SIFI task replicated the monotonic increase in perceived flashes with tone count. Crucially, a composite "SIFI susceptibility" index was found to be positively predicted by the right-side TBW (the TBW for audio-lag offsets) extracted from the SJ task, such that individuals displaying broader right-side TBWs were among those more susceptible to the SIFI. The authors concluded that individual differences in audiovisual temporal processing are large and stable across tasks, underscoring how the TBW construct provides a meaningful parameter linking visuo-temporal sensitivity to distinct integration or segregation outcomes (Stevenson et al., 2012). A recent TBW-based investigation of the SIFI converged with such consideration. Here, professional goalkeepers, outfield players, and age-matched controls performed a SIFI task across various SOA (i.e., from 100

to 500 ms). The authors fit a Gaussian function to the fission rates to estimate each group's TBW width and peak amplitude, showing that goalkeepers displayed narrower TBW and smaller peaks than outfielders and controls. Sharper audiovisual acuity and reduced propensity for extra-flash reports in goalkeepers were interpreted as an adaptive sensory adjustment enabling them to favour segregation over integration when cue timing is near-synchronous (e.g., judging whether a ball was touched, deflected or still in play). Beyond that, this study nicely illustrates a fair example of how a TBW-informed account can capture subtle group differences in SIFI susceptibility and, more broadly, perceptual sensitivity to cross-modal temporal and numeric mismatches (Quinn et al., 2023).

2.2 Cortical Bases

Parallel to research on the mechanistic principles governing the SIFI, a large body of studies has also mapped the cortical loci supporting the perceptual signature of this illusion, namely what brain regions engage the most when illusory extra-flash are reported. Informed by coeval findings concerning multifaceted activations in both associative hubs (i.e., STS) and primary sensory cortices (i.e., V1, A1) during cross-modal processing (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Stein & Stanford, 2008), these pieces of experimental work tested whether, and to what extent, such evidence applied to the SIFI as well. The first attempt of this sort was carried out using fMRI (Watkins et al., 2006) in participants completing a SIFI task in which, respectively, one flash was presented alone (e.g., 1F) or paired either with one or two tones (e.g., 1F1S, 1F2S), and two flashes were presented alone (e.g., 2F) or paired with two sounds (2F2S). At the behavioral level, the SIFI robustly replicated (i.e., large number of extra-flash reports in 1F2S trials), likely due to a substantial drop in perceptual sensitivity (Watkins et al., 2006). At the cortical level, larger BOLD responses in retinotopically defined regions within the primary visual cortex were associated with audiovisual (as opposed to unimodal) trials, consistent with an auditory-mediated feedback facilitation in V1. However, the contrast between trials in which an illusory extra-flash was reported vs not-reported proved to be even more informative. That is, V1 exhibited higher stimulus-evoked BOLD responses in illusory trials as opposed to non-illusory, and similar in magnitude to veridical 2F2S trials. In brief, V1 activation in double-flash reports tracked the subjective (illusory) experience of perceiving an extra-flash, to the point of being, respectively, undistinguishable from trials in which a second flash was actually presented (2F2S trials), and amplified relative to perceptually identical (1F2S) trials (Watkins et al., 2006). Further, illusion-induced effects stretched beyond the primary visual cortex, as significant STS activations were also documented, highlighting how the SIFI reflects cross-modal interactions that reshape visual coding at the earliest stages of perception, rather than postdictive shifts in decision bias

(Watkins et al., 2006). Crucially, these findings were extended in a follow-up study targeting the sound-induced fusion illusion (i.e., one-flash reports in 2F1S trial) to better address whether V1 activity was indeed elicited by subjective percepts rather than sensory stimulation (Watkins et al., 2007). The authors not only replicated the enhanced V1 activity for illusory double-flash reports in 1F2S trials (Watkins et al., 2006), but they additionally showed a robust V1 BOLD suppression associated when 2F1S trials were perceived as one-flash, resembling BOLD response profiles to veridical 1F1S trials. Taken together, these results revealed a profound involvement of the primary visual cortex in shaping SIFI perceptual mechanics, as shown by V1 activity tightly co-varying with perceived flash numerosity, irrespective of whether the pull was strongest for integration or segregation (Watkins et al., 2007). In this vein, a later high-resolution structural MRI study using voxel-based morphometry went into further support of the abovementioned pieces of evidence. In a SIFI task combining five different flash-beep conditions (i.e., 1 or 2 flashes paired with either 0, 1 or 2 beeps), participants' susceptibility to the illusion was regressed onto V1, A1 and STS grey matter volume, while controlling for whole brain grey matter volume, age and sex. Results showed a negative linear relationship between grey matter volume in V1 and proneness to the SIFI, whereas no such trend was found with regard to STS or A1 (figure 2.4 b). In sum, individuals with smaller early visual cortex volume were more likely to experience the illusion, corroborating previous findings that linked SIFI occurrence with visual cortical anatomy (de Haas et al., 2012; figure 2.4 b).

The contribution of parieto-occipital loci to the emergence of the SIFI has been also supported by several EEG-based inquiries mapping the topography of extra-flash-induced cortical responses. A preliminary attempt of this sort revealed an extensive modulation and shorter latencies of visual evoked potentials (i.e., occipital sensors) when flashes were paired with acoustic cues, with electrical activity in illusory trials quantitatively similar to that in veridical two-flash trials (Shams et al., 2001). The temporal cascade of these multisensory interactions was rigorously detailed with source-reconstruction a few years later. The authors adopted high-density EEG recording during the completion of a canonical SIFI task involving 1F2S trials together with unimodal and control audiovisual combinations. The key contrast between evoked activity during 1F2S trials and the algebraic sum of unimodal auditory and visual evoked potentials unveiled a non-linear sequence of electrical activations occurring in 1F2S trials: an early occipital positive waveform (100-130 ms), followed by later temporo-occipital and frontal modulations (figure 2.4 a). Source-modelling confirmed the occipital (i.e., extra-striate visual cortex) and temporal origin of this early component, whose functional dynamics were scrutinized by median-splitting participants into an illusion-immune and illusion-prone group. Unsurprisingly, this occipito-temporal component displayed larger amplitudes in illusion-prone than illusion-immune individuals in both in 1F2S trials and other audiovisual (but not unimodal)

combinations (Mishra et al., 2007). Following-up on these findings, the same group focused on the fusion illusion, documenting an involvement of parietal and polysensory regions at a slightly later time-window (180 ms), whose amplitude was negatively associated with the proneness to collapse two flashes into one in fusion-prone participants (Mishra et al., 2008).

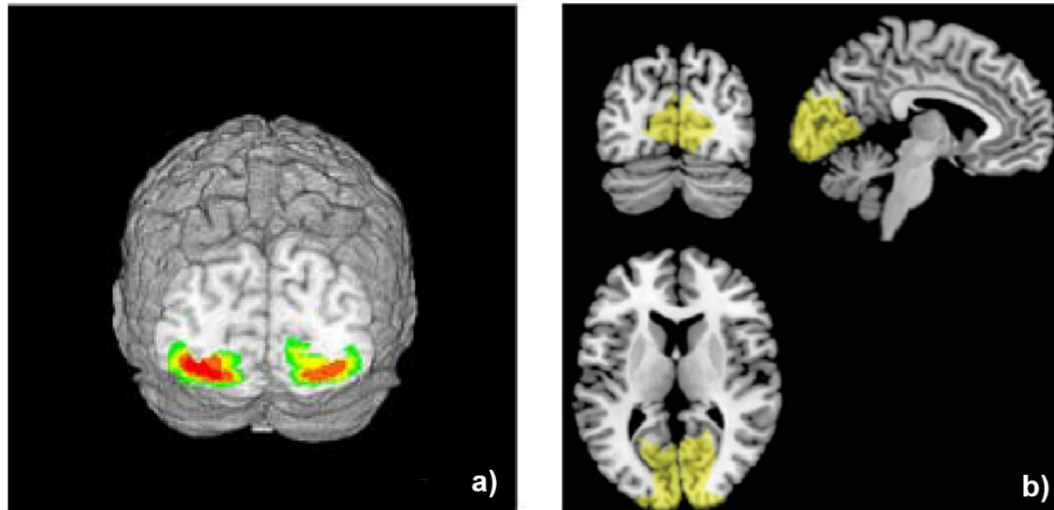


Figure 2.4 Cortical Bases of the SIFI. **a)** source reconstruction of the interaction ERP component from Mishra et al. (2007), showing an early (~120 ms) positive deflection in the audiovisual interaction waveform during the SIFI, with generators localized to bilateral occipital cortex. **b)** Structural MRI results from de Haas et al. (2012)

Building upon this body of work, neurostimulation-based studies provided additional information about the functional anatomy supporting the SIFI. In a within-subjects experimental design where participants completed a SIFI task while cathodal or anodal (i.e., reducing or increasing cortical excitability) transcranial direct-current stimulation (tDCS) was block-wise delivered over the occipital, parietal or temporal cortex, results showed a remarkable functional dissociation across brain regions. On the one hand, fusion reports were unaffected by tDCS polarity or topography. On the other hand, the double-flash illusion proved amenable to changes: anodal and cathodal tDCS over the temporal cortex increased and decreased, respectively, illusion rates, whereas the opposite pattern was reported when tDCS targeted the occipital lobe (Bolognini, Rossetti, Casati, et al., 2011). Beyond auditory and visual cortical loops, neurostimulation showcased the involvement of the parietal cortex. In a series of TMS experiments, offline repetitive rTMS applied to the right angular gyrus disrupted extra-flash reports, while time-locked single pulse stimulation at the same cortical spot shrank the temporal window within which the illusion occurred (Hamilton et al., 2013; Kamke et al., 2012). Together, neurostimulation and event-related findings, converging with functional and structural imaging, locates the cortical foundations of SIFI amidst early parieto-occipital bimodal interactions, once again arguing for a genuinely sensory (rather than a decisional) origin of the illusion.

2.3 Individual Differences, and the Psychosis Continuum

As outlined several times above, the SIFI ranks among the most robust, well-replicated misperceptions within the multisensory realm (Hirst et al., 2020), defies feedback training (Rosenthal et al., 2009), and shows intraindividual stability over time (Odegaard & Shams, 2016). This latter trait-like feature dovetails with neuroimaging evidence linking a stable anatomical biomarker such as V1 grey matter volume to the propensity to experience the SIFI (de Haas et al., 2012), and highlights an often overlooked point: susceptibility to the SIFI, irrespective of whether it is quantified through BCI modelling or TBW accounts, is not uniform across individuals (Hirst et al., 2020). Based on the many pieces of data reviewed so far, this should come as no surprise. The core mechanics around which revolves the illusion entail push-pull dynamics between auditory and visual precision, such that poorer visuo-temporal sensitivity to numeric disparities tilts cross-modal processing toward leaning on auditory signals, favouring extra-flash reports via integration, over veridical single-flash percepts (segregation). It follows that the intraindividual stability and interindividual variability of the SIFI can ultimately be reframed as by-products of variation (or alteration) in the temporal processing of visual inputs within and across healthy, subclinical and clinical samples (Hirst et al., 2020). Much effort has therefore been aimed at isolating specific conditions in which susceptibility to the SIFI might serve as an additional screening, diagnostic or prognostic behavioral marker to expand clinicians' toolbox. Evidence from research in non-clinical participants suggests that multisensory training or expertise can sharpen cross-modal acuity, which in turn generalizes to the SIFI. To begin with, musicians are less prone to the illusion, and display narrower audiovisual TBW than non-musically trained individuals (Bidelman, 2016). In this vein, prolonged exposure to audiovisual speech signals has proved beneficial to multisensory processing, greatly reducing fission rates in bilinguals compared with monolinguals (Bidelman & Heath, 2019). The same reasoning applies to first-person shooter videogame players, who displayed reduced susceptibility to the SIFI relative to non-players, presumably due to intensive audiovisual experience (Di Luzio et al., 2021), and goalkeepers, who similarly showed narrower TBW relative to outfield players or controls (Quinn et al., 2023). However, many of the most compelling results have been obtained in participants suffering from clinical or subclinical conditions. Individuals with visual or hearing impairments have been among the first targeted by this approach. For instance, amblyopic patients displayed TBWs and fission rates similar to healthy controls (Narinesingh et al., 2017), whereas individuals with monocular enucleation appeared less prone to the SIFI (Moro & Steeves, 2018). An opposite pattern has been found in hearing aid users, namely wider TBWs and larger numbers of extra-flash percepts (Gieseler et al., 2018). Within this line of research fall also studies on people with migraine, who often experience changes in

sensory processing that encompass hypersensitivity to light and sound (photophobia and phonophobia). Contrary to expectation, adults with migraine appeared less susceptible to the SIFI than healthy controls, prompting the authors to hypothesize that this pattern reflected increased cortical excitability characteristic of this disorder (Brighina et al., 2015). Beyond migraine, the SIFI has served as meaningful probe of cognitive and perceptual functioning in older adults. A substantial body of experimental work in this domain focused on fall-prone older adults, given the tight relationship between postural control and the optimal integration of visual, auditory, proprioceptive and vestibular inputs. Compared to age- and visual acuity-matched non-fallers and younger adults, older fallers exhibited similar fission rates at short SOAs, although at longer delays (up to 270 ms) they did not display the progressive decline in illusion reports observed in the control groups (Setti et al., 2011). A follow-up study expanded upon these findings by showing an even greater SIFI susceptibility in older fallers performing a SIFI task while standing, as opposed to sitting, without a concomitant performance decrement in unimodal or non-illusory trials (Stapleton et al., 2014). All in all, increased susceptibility to the SIFI seems to capture subtle liabilities in audiovisual integration that in turn can compromise postural balance, thereby making this illusion a promising tool to early detect older individuals at elevated risk of falling. Within the neuropsychology of ageing, the SIFI have been also used as a proxy for global cognitive status. A large-scale study recruiting a population-representative sample of approximately 4000 participants aged over 50 years showed that proneness to sound-induced extra-flash reports scales with age and, importantly, is inversely related to scores at the Montreal Cognitive Assessment (MoCA): the lower the MoCA score, the larger the SIFI effect at the individual level (Hernández et al., 2019). These data aligns with previous evidence indicating greater susceptibility to the sound-induced fission illusion at longer SOA in people with mild cognitive impairment compared to age-matched controls (Chan et al., 2015). Alongside postural control, cross-modal operations underlying the SIFI can therefore inform us cognitive functioning and, more broadly, an individual's ageing trajectory.

Intriguingly, the adoption of the SIFI has also provided a convenient experimental route to attain a deeper understanding of inter-sensory processing also in patients suffering from psychiatric disorders, with research on autism spectrum disorders (ASD) offering a notable example. Evidence from individuals with ASD, however, appears mixed, if not inconclusive. Children with ASD have been reported to be more prone to the SIFI due to enlarged audiovisual TBWs, in one study, and less prone to the same illusion in a task that did not explicitly manipulated temporal delays in another (Foss-Feig et al., 2010; Stevenson et al., 2014). Further, adults with ASD displayed fission rates similar to those of age-matched controls (Keane et al., 2010), whereas, in healthy individuals, subclinical ASD traits predicted reduced susceptibility to the SIFI (Kawakami et al., 2020). Such intersperse pieces of

evidence have been construed as resulting either from the diverse constellation of clinical profiles ASD encompasses, or from an over-reliance on prediction errors, rather than priors, which may prevent ASD individuals from fully benefitting from learning and experience (Van de Cruys et al., 2014). Lastly, the SIFI has furnished a pretty robust testbed to explore altered audiovisual dynamics in clinical populations known to suffer from illusion-like experiences such hallucinations, and to which will be devoted the next section.

2.3.1 Schizophrenia Spectrum Disorders and Audiovisual Integration: a SIFI-informed Perspective

Schizophrenia (SCZ) is among the most debilitating syndromes within the neuropsychiatric domain, with patients suffering from this condition displaying a rich nosographic profile (McCutcheon et al., 2020). As such, it represents one of the leading causes of disability worldwide, contributing to the disease burden as measured in years lived with disability (Whiteford et al., 2013). The implications are far-reaching: beyond the severe clinical and functional impairments, SCZ is associated with a substantial socioeconomic impact, encompassing stigma, social isolation, occupational difficulties, and both direct (treatments, hospitalizations) and indirect costs (loss of productivity, informal care), which together account for approximately 0.02 - 1.65 % of gross domestic production (Chong et al., 2016). According to DSM-5 diagnostic criteria, a SCZ diagnosis requires the presence of at least two core symptoms for a minimum period of one month (i.e., the active phase of the disorder), and at least one of these must consist of clinical signs known as positive symptoms: delusions, hallucinations, or disorganized speech. Other features may include grossly disorganized or catatonic behavior and negative symptoms, such as blunted affect, alogia, or avolition (reduced motivation and initiative), often accompanied by a progressive deterioration in the cognitive domain (e.g., attention, working memory and executive functions). Further, the disorder must persist for at least six months, including prodromal or residual periods (American Psychiatric Association, 2022). Over the years, the hallmark manifestations epitomizing this disorder have attracted considerable translational interest. On the one hand, delusions are defined as fixed beliefs spanning a variety of themes (e.g., persecutory, referential, religious etc), which are not amenable to change in light of conflicting evidence, and are deemed bizarre or implausible by same-culture peers. On the other hand, hallucinations are vivid, perception-like experiences occurring in the context of a clear sensorium, without any corresponding external stimulus or voluntary control, which may arise in any sensory modality, although auditory hallucinations are the most common (American Psychiatric Association, 2022).

2.3.1.1 Unifying Bottom-up Accounts of Positive Symptoms and Audiovisual Perception

The intrinsically sensory nature of hallucinatory features has increasingly motivated a shift in translational models of SCZ, away from canonical accounts that primarily attributed hallucinations to higher-order cognitive deficits, towards frameworks emphasizing early sensory dysfunctions as the key mechanistic substrate of positive-like symptoms (Javitt, 2009b, 2009a). Such theoretical proposition recasts hallucinations as misperceptual phenomena rooted in bottom-up impairments, whereby defective processing occurring in primary sensory cortices generates noisy perceptual traces that eventually propagates upstream. Complementary to top-down models of psychosis, this novel account places weight on sensory hypofunctional channelling to association and frontal regions of impoverished inputs that cascade into hallucinatory-like experiences (Javitt, 2009b). Accordingly, computational disruptions are assumed to arise early on, before any complex decisional stage, arguing for a genuinely perceptual impairment in which already compromised high-order functions are forced to operate on blurred and imprecise sensory representations. What was once construed mainly as the result of aberrant, prior-conveying feedback projections is now reframed as the elusive interplay of noisy feedforward signalling defying likely sub-optimal top-down compensatory mechanisms (Javitt, 2009b). Within this integrative model, positive symptoms, with hallucinations at the core, result from distributed systems failure, where sensory (un)reliability plays a foundational role, alongside higher-order malfunctioning (Javitt, 2009b, 2009a). Here, a key conceptual addendum pertains to the notion of “panmodal” processing imprecision: the brain encodes signals with decreased fidelity or temporal precision, not only within, but also across senses. This implies that the bottom-up disruption extends beyond isolated auditory and visual systems to the very cross-modal dynamics binding them (Javitt et al., 1999). Such consideration resonates with what mentioned above concerning the computational roots of audiovisual perception. Both BCI and TBW accounts provide theoretical and empirical evidence that coarser visual precision, relative to auditory, is the main driver of the cross-modal misperceptions (Shams et al., 2005; Stevenson et al., 2012), with the involvement of low-level sensory mechanics at the earliest stages of multisensory processing further bolstered by neuroimaging studies (Mishra et al., 2007, 2008; Watkins et al., 2006, 2007). When properly couched into a translational framework hinging on psychosis, these findings raise compelling questions as to whether multisensory paradigms such as the SIFI might lend additional insights into the physiological and computational building blocks which positive-like symptoms are made of. Firstly because we inhabit an inherently multisensory world that constantly saturates our sensorium with streams of data, and this line of research stands as a well-suited and ecological probe of how this information is gracefully pooled across sensory channels (Noppeney, 2021). Moreover, accommodating modality-diverse signals into

a unified representation poses our nervous system a far greater computational challenge than solely unimodal perception (Stein & Stanford, 2008), thereby foregrounding latent liabilities otherwise overlooked by unisensory assays (Wallace et al., 2020; Wallace & Stevenson, 2014).

In this regard, some attempts to address the issue have been carried out focusing on the audiovisual domain. Evidence is suggestive of impaired visuo-acoustic abilities in patients diagnosed with SCZ spectrum disorders (de Gelder et al., 2005; Ross et al., 2007). These results have been shown to depend on the degree of perceptual sensitivity to stimuli asynchronies, where coarser cross-modal acuity predicts a higher likelihood of integrating temporally misaligned signals in patients, as compared to controls (Borgolte et al., 2024; Foucher et al., 2007; Stevenson et al., 2017; H. Zhou et al., 2022). Of note, the severity of psychotic symptoms emerged as a key determinant of perceptual tolerance to large SOA: the greater the severity, the longer the SOAs required to match controls-level binding performance (Amadeo et al., 2024; Borgolte et al., 2024; Stevenson et al., 2017). Even more informative, though, were findings gathered using illusion-inducing audiovisual regimes, such as the McGurk effect (McGurk & Macdonald, 1976), the bounce-stream illusion (Sekuler et al., 1997), or the ventriloquist task (Thurlow & Jack, 1973), each showing defective integration mechanisms along the SCZ spectrum (de Gelder et al., 2003; Szyck et al., 2009; Pearl et al., 2009; Tschacher & Bergomi, 2011; H. Lee & Kim, 2021; Zvyagintsev et al., 2017).

2.3.1.2 Psychosis and the SIFI

Among the family audiovisual illusions, the SIFI provided a remarkable testing ground wherein it was possible to probe the extent to which bottom-up sensory impairments drive hallucinatory reports (Javitt, 2009b). This was attained in a multi-modal fashion through different studies, each one approaching the issue from a distinct computational angle. Starting from a BCI perspective, bottom-up signatures of increased SIFI susceptibility (i.e., stronger pull toward audiovisual integration over segregation) expected in psychosis-prone patients should primarily translate into poorer visual precision (tilting reliability weighting toward audition), rather than abnormally high priors for a common audiovisual cause. To test this proposition, post-acute SCZ patients and age-matched healthy controls were asked to report the number of perceived flashes and tones in a SIFI paradigm using a factorial design (1-4 flashes combined with 1-4 beeps) that involved both congruent trials and graded numeric mismatches (Rohe et al., 2024). At the behavioral level, each group displayed classic SIFI-like patterns, namely visual reports pulled toward tone numerosity at low numeric discrepancies (e.g., illusory extra-flash reports in 1F2S trials, or two-flash fusion in 2F1S trials), with negligible differences in accuracy rates and cross-modal bias between patients and controls (Rohe et al., 2024).

BCI modelling was then adopted to compare ten different computational accounts combining five distinct decision-making strategies with either constant or scalar sensory variance. Results showed that in both groups model-averaging with scalar sensory noise provided the best fit to the data. That is, SCZ patients and healthy controls alike issued their responses based on a combination of common-cause and independent-causes estimates, weighted by their posterior probability given graded levels of noise embedded in each flash-beep combination. Importantly, the fitted parameters (sensory variance, causal and numeric priors) resulting from this model did not differ significantly across groups, with several implications from a translational standpoint. First, SCZ patients followed the same computational and decisional heuristics as healthy controls. Second, performance accuracy defied the straightforward prediction that hallucination-prone patients should be more susceptible to the SIFI. Third, but foremost, the fitted parameters argue against a bottom-up account of positive symptoms, given that patients did not display poorer sensory precision than healthy controls (Rohe et al., 2024). Bottom-up accounts of disrupted cognition in SCZ (Javitt, 2009b), have been also examined through the lens of Signal Detection Theory (SDT; D. M. Green & Swets, 1966). In psychophysics, SDT formalizes an observer's response as a decisional process in which he/she is tasked to disambiguate whether a given sensory input correspond to a target signal or not (figure 2.5). Such operation is nothing but trivial, since both signals-present (target) and signal-absent (catch) trials give rise to internal representations corrupted by noise, which typically follows as Gaussian distribution with equal variance across conditions. Under these assumptions, the observer's decisions are sampled from two overlapping internal response distributions (target signal and noise) and compared against a decision criterion: the farther apart these distributions lie, the higher the probability of correctly disentangling signal from noise. The distance between distributions is taken as the index of an observer's perceptual sensitivity (d'), such that the larger, the better the decision-maker is at dissociating signal from noise. Orthogonal to sensitivity, SDT also quantifies an observer's decision criterion: the internal threshold separating "signal-present" from "signal-absent" responses. Shifts in criterion capture response bias (c : a liberal vs. conservative tendency to report a signal) without altering d' (D. M. Green & Swets, 1966). Borrowing this framework, bottom-up operations subsuming increased susceptibility to the SIFI in psychosis-prone patients should map onto lower d' levels in illusion-inducing conditions as compared to controls, rather than a shift in response criterion. This was investigated in a cohort of SCZ patients and healthy controls viewing fission (1F2S) and fusion (2F1S) variants of the SIFI, along with unimodal visual (1F and 2F) and congruent audiovisual (1F1B, 2F2B) trials (Vanes et al., 2016). All participants, irrespective of group, showed a clear modulation of visual reports by tones numerosity. However, when comparing fusion and fission versions of the SIFI across groups, patients displayed weaker fusion tendency than controls, whereas no significant difference was observed for fission rates.

The different combinations of unimodal and congruent trials were then leveraged to compute SDT metrics by modelling 2-flash fission responses in 1F2S trials and 1-flash fusion responses in 2F1S trials as false alarms, with 2F2S trials and 1F1S trials providing hits/misses, respectively, for the fission and fusion subsets. Counterintuitively, controls showed stronger changes in perceptual sensitivity (more negative d' shifts) and response criterion than patients when comparing d' and c levels in illusory conditions (1FS2 and 2F1S) with the corresponding unimodal baselines (1F and 2F) effects that could not be attributed to temporal deficits or poor attentional allocation (unimodal performance discrimination was adequate). Against prediction, psychosis-prone patients displayed weaker multisensory capture than healthy controls, which translated into a reduced susceptibility to auditory-driven modulations of visual percepts, and, ultimately, fewer sound-induced illusory flash reports (Vanes et al., 2016). In sum, patients did experience fission and fusion percepts to some extent, yet appeared less able or inclined to let auditory reliabilities optimize visual judgments under a plausible common cause structure in which sensory modalities conflict. These pieces of evidence only partly accommodate bottom-up accounts of perceptual deficits in SCZ, and did so from a diametrically opposite angle than anticipated: patients are less prone to the SIFI not because of better visual sensitivity, but due to pathologically reduced auditory capture of vision (Vanes et al., 2016).

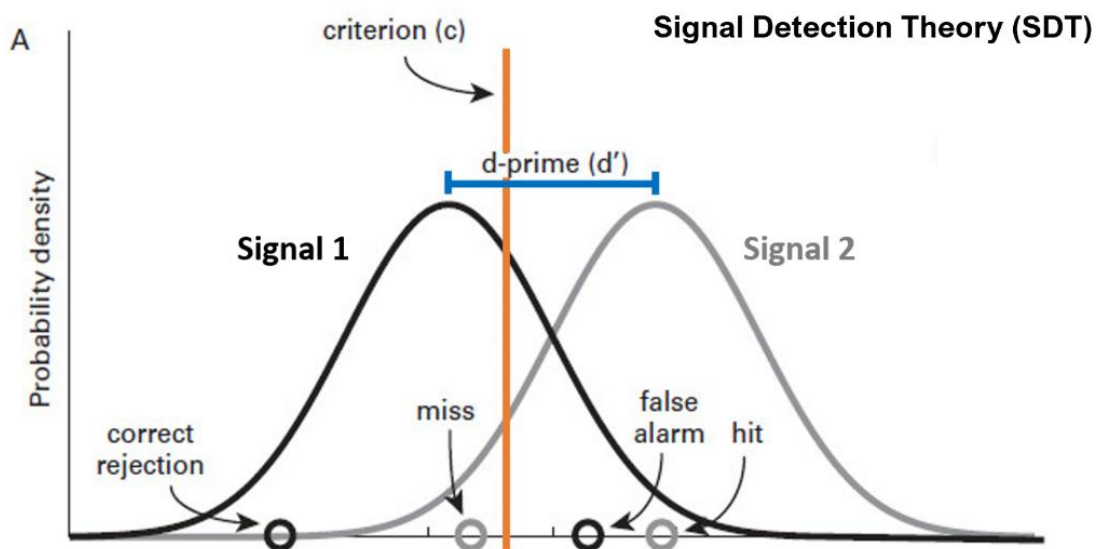


Figure 2.5. Schematic illustration of SDT modelling: an observer's decision is sampled from two overlapping probability distributions representing internal responses to noise (Signal 1) and signal-plus-noise (Signal 2). Perceptual sensitivity is indexed by d' , reflecting the separation between the distributions, while the decision criterion (c) determines response bias, partitioning outcomes into hits, misses, false alarms, and correct rejections.

The temporal extent to which this interpretation held was subsequently detailed in a study probing whether audiovisual alterations observed in psychotic patients applied to the SIFI within a TBW-informed framework. As previously mentioned, TBWs offer a privileged perspective on the temporal constraints that govern multisensory integration. Provided that audiovisual processing in SCZ results

from low-level sensory impairments sharing the same computational roots as hallucinations (Javitt, 2009b; Stevenson et al., 2017), this should be reflected in wider cross-modal binding windows. That is, patients characterized by a prominently positive-symptom profile should display poorer visuo-temporal sensitivity to large stimuli asynchronies, which in turn inflates illusory extra-flash reports through an increased tendency to inappropriately integrate heteromodal signals. To test this hypothesis, a sample of SCZ patients and healthy controls were asked to judge whether they saw one or two flashes presented in either 1F2S or 1F1S trials at several SOAs (from 25 to 300 ms) in double-flash illusion task (Haß et al., 2017). Here, the SIFI effect was documented in both groups at short SOAs (75-100 ms), although with some important caveats. While in healthy controls the proportion of extra-flash reports rapidly decayed for SOA larger than 100 ms, this was not observed in SCZ patients, who showed persistently elevated illusion rates at larger SOA (from 150 to 300 ms). The authors interpreted these findings as robust evidence that this disorder is characterized by abnormally enlarged windows for multisensory binding, consistent with the notion that degraded sensory (visual) precision in the temporal domain (Javitt, 2009b) promotes the dysfunctional integration of temporally misaligned signals.

Together, these studies tackled bottom-up accounts of psychotic hallucinations from a SIFI perspective, under three distinct computational regimes, each one returning conflicting evidence about alteration in visual sensitivity being the key driver of positive symptoms in this psychiatric population.

2.3.2 Schizotypal Traits and the Psychotic Continuum in Audiovisual Integration

More than decade has passed since the first call for a paradigm shift from symptoms-based to pathophysiology-informed diagnoses and interventions in the field of psychiatry (Insel et al., 2010). A key recommendation for this transition to occur was to accommodate insights from genomics, neuroimaging, and cognitive sciences, within a mechanistic framework expanding upon descriptive symptomatology into a pathogenetic account of psychiatric illness (Cuthbert, 2014; Insel et al., 2010). Such translational heuristics compel a departure from conventional nosology toward diagnostic models recasting symptoms as dimensionally-arrayed across the population (Cuthbert, 2014), and mental disorders as poles along a seamless continuum ranging from adaptive to dysfunctional behavior (Krueger & Eaton, 2010). The tenability of this proposition has gained growing support within the domain of psychosis-like syndromes and, more broadly, SCZ spectrum disorders (Allardyce et al., 2007; Johns & Van Os, 2001). While SCZ biosignatures remain elusive, clinical phenomenology is suggestive of many dimensional continua across the psychotic spectrum (Ettinger et al., 2014): from temporal (subtle psychotic-like phenomena in childhood to full-blown psychosis in adult age), to

functional (symptoms vary dimensionally rather than being clearly present or absent), and, importantly, at the population level (psychotic features distributed in the general population). This latter observation fuelled many lines of research reframing SCZ as dimensional phenotype, of which schizotypy represent the milder and often prodromal manifestation (Nelson et al., 2013).

The concept of schizotypy originates in early work on the genetic predisposition to SCZ (Meehl, 1962), where a dominant “schizogene” was posited to underlie a neurobiological dysfunction termed *hypokrisia*, referring to a disruption in the synaptic integration of information. This condition, labelled *schizotaxia*, was conceived as a latent vulnerability which, interacting with environmental and psychological factors, may evolve into schizotypal traits and, in a subset of cases, into SCZ. The taxonic model was progressively replaced by a full-dimensional account where variance across the schizotypy-SCZ axis is assumed to be continuous (Claridge et al., 1996; Nelson et al., 2013), consistent with clinical and biological measures showing heavy overlap and graded distributions (Ettinger et al., 2014; Johns & Van Os, 2001), and the absence of any robust biomarker that cleanly separates SCZ patients from healthy controls. For instance, the case for SCZ as a fully dimensional phenotype encompassing schizotypal traits has been buttressed by genetic studies, showing heritability of 66–83% for SCZ and 30–50% for schizotypy (Cardno & Gottesman, 2000; Linney et al., 2003), with overlapping risk architectures spanning similar polymorphisms and polygenic profiles in both SCZ and schizotypy, such as associations between core SCZ risk genes and schizotypal traits in non-clinical samples, supporting shared liabilities (Fanous et al., 2007; Stefanis et al., 2007). Further, high schizotypy individuals display subtle but reliable deficits resembling SCZ at the perceptual, cognitive and motor level (Ettinger et al., 2014; Johns & Van Os, 2001; Nelson et al., 2013). For example, intermediate impairments in working memory, executive control, antisaccade performance and prepulse inhibition that scale monotonically with schizotypy and recapitulate patients endophenotypes (Cochrane et al., 2012; Ettinger et al., 2014; Giakoumaki, 2012). Finally, shared neuroanatomical alterations including reduced volumes in mediodorsal and pulvinar thalamic nuclei and overlapping frontal–temporal cortical thinning patterns in SCZ and schizotypal disorder further reinforced a common neurodevelopmental substrate (Byne et al., 2001, 2002; Takayanagi et al., 2020).

Crucially, these similarities also extend to the clinimetric profile: schizotypy is currently regarded as a multidimensional construct clustered in a trichotomic structure that maps onto SCZ core symptoms (Raine, 2006). Blunted socio-affective functioning (negative symptoms), along with eccentric behavior and disorganized speech (Raine, 1991), indeed mirrors with high fidelity many of SCZ core diagnostic criteria, although the sharpest resemblance has been reported in the cognitive and perceptual domains (Johns & Van Os, 2001). Odd beliefs and anomalous perceptual experiences (positive symptoms) are arguably hallmark features of schizotypal personality, which in turn can be traced to

SCZ first-rank symptoms such as delusions and hallucinations (Soares-Weiser et al., 2015). To summarize, rather than a strictly binary construct, SCZ would thus display trait-like features, graded across the general population: absent (or nearly-absent) in healthy individuals, and markedly expressed in patients suffering from this disorder (Cochrane et al., 2012). In between, neurocognitive patterns consistent with a schizotypal portend a greater risk of psychosis onset (Cochrane et al., 2012; P. Grant et al., 2018). From this perspective, schizotypy should represent a milder or perhaps alternative developmental trajectory relative to overt SCZ, with clear implications for early detection and prevention, supporting the notion of a continuity between these two conditions that spans both clinical and neuropsychological factors (Cochrane et al., 2012; Ettinger et al., 2014; Nelson et al., 2013). Intriguingly, albeit the long-standing recognition of schizotypal personality as psychiatric disorder (American Psychiatric Association, 2022), broad consensus holds that subclinical schizotypal traits can be also witnessed in the healthy population, from which came important contributions to our understanding of this condition. That is because the study of schizotypal traits in healthy sample enables the investigation of SCZ vulnerability mechanisms without contamination from factors related to chronic illness or long-term medication (Lenzenweger, 2010). Moreover, this approach aligns with the view that schizotypy is not inherently pathological but represents a liability dimension whose clinical expression likely depends on the balance between risk and protective factors. Accordingly, healthy individuals high in schizotypy may show subtle ‘intermediate’ perceptual or neurocognitive signatures without marked functional impairment, offering a uniquely clean window onto early mechanisms of psychosis proneness (Claridge, 1997; Mohr & Claridge, 2015). As a dimensionally distributed trait in the general population, non-clinical schizotypy thus offered a valuable opportunity to investigate risk and resilience factors associated with SCZ outside the clinical setting, and test whether graded vulnerability translates into measurable alterations in cross-modal temporal tuning in SIFI-like paradigms.

2.3.2.1 Schizotypy and the SIFI

Audiovisual integration has recently surfaced as a topic of interest in the exploration of the psychosis continuum, given the additional insights into aberrant perceptual mechanics it may furnish as compared to unimodal tasks (Stein & Stanford, 2008; Wallace et al., 2020). To some extent, it can be argued that investigating multisensory processing in high schizotypals might not only be informative about what underlies hallucinatory phenomena, but can also provide clinicians with a stable and reliable marker to early detect individuals at heightened risk of developing psychosis (Stevenson et al., 2017; Wallace et al., 2020). This was pursued mainly within a bottom-up framework of positive

symptoms, in line with the idea that disruption at the earliest stages of sensory encoding cascade into fully fledged psychotic-like manifestation (Javitt, 2009b). In the context of the continuum hypothesis (Cochrane et al., 2012), low-level alterations idiosyncratic to SCZ patients should as well be observed, albeit in a milder and more subtle form, in individuals with high levels of schizotypy and, as such, at greater liability for SCZ onset.

Consistent with this view, the most sought after strategy to quantify audiovisual disruptions in high schizotypals involved the well-known psychometric construct of TBWs, assessed during simultaneity or temporal order judgments. For instance, individuals with high schizotypal traits have been shown to display laxer cross-modal temporal tuning, as revealed by greater audiovisual synchrony perception than controls at longer SOA in a SJ task (Fenner et al., 2020). These results were replicated in a later study using a similar task design (Marsicano et al., 2022), with the key addendum of a positive linear association between temporal acuity (i.e., TBWs width) and scores on cognitive-perceptual scale of the Schizotypal Personality Questionnaire (SPQ, Raine, 1991), whose items track the severity of positive-like schizotypal sub-traits. Moreover, the perceptual-cognitive schizotypal axis was found to be tethered to audiovisual precision in a TOJ performed by healthy participants screened with SPQ, such that the more prominent was the “positive-like” subclinical profile, the wider the TBW (Dalal et al., 2021). This pattern of results partially extends to audiovisual speech perception as assayed using a McGurk task (Muller et al., 2021): odd-speech and disorganized features appeared the main driver, rather than cognitive-perceptual sub-symptoms, although the same authors did not observed this effect in an earlier work (Muller et al., 2020). In and of themselves, these studies highlighted how altered cross-modal integration might be subsumed into a broader perceptual-temporal phenotype driving psychosis-proneness.

Germane to this consideration, illusion-inducing paradigms like the SIFI can further illuminate the translation implications this relationship may have for healthy individuals lying along the psychosis continuum. This was achieved by recruiting healthy participants from the general population based on their schizotypal traits, as assessed through the SPQ. The sample was stratified by SPQ scores distribution, yielding low- and high-schizotypy groups whose scores fell, respectively, within the lowest and highest quintiles of the scores distribution (Ferri et al., 2018). Each group was asked to report how many flashes (1 vs 2) they perceived during a DFI task where, unbeknownst to participants, one (and always one) flash was presented with two (and always two) acoustic tones, interleaved by a varying number of SOAs (from 36 to 204 in steps of 12 ms). For each participant, the proportion of two-flash reports across SOAs was fitted with a sigmoid function, from which individual inflection points (i.e., the psychometric proxy for TBW width) were derived. Results showcased greater overall proneness to the illusion (higher proportion of two-flash reports across all trials) in high-schizotypy

individuals, which was accounted for by interpersonal and perceptual-cognitive factors of the SPQ. Moreover, the high-schizotypy group displayed later inflection points than low-schizotypy individuals, a pattern indicative of broader TBWs and reduced visuo-temporal precision, with this index positively predicting the overall proneness to the illusion (Ferri et al., 2018). To rule out the hypothesis that greater overall SIFI susceptibility in the high-schizotypy group merely reflected the by-product of a generic “illusion bias” masked by larger TBWs, this index was normalized by TBWs (i.e., weighted proneness to the illusion, computed on a per-individual basis solely from the three SOAs preceding the inflection point). As expected, this analyses returned no significant difference across groups, arguing for a tight link between temporally imprecise cross-modal encoding and psychosis-related schizotypal sub-traits, rather than a nonspecific tendency of high schizotypy individuals to perceive two flashes irrespective of timing (Ferri et al., 2018). This dataset was also explored in a follow-up study adopting a computational perspective on the issue (Paredes et al., 2025). The authors built a recurrent neural network implementing multisensory BCI that modelled the probability of a common cause vs independent causes, and was tuned to reproduce DFI data from low schizotypy individuals (i.e., capturing audiovisual Bayesian inference dynamics in a “healthy” regime). Systematic manipulation of parameters indexing recurrent excitatory connectivity, cross-modal weights, feedback gains, and synaptic density uncovered a central finding: increasing or decreasing recurrent excitation, respectively, enlarged or shrunk TBW width and illusion rates, mirroring the empirical patterns observed in the high schizotypy group (Paredes et al., 2025). Under heightened excitation, the network degraded in temporal precision, and was therefore tilted toward assigning a common-cause structure to multisensory events, boosting integration over segregation even when auditory and visual stimuli displayed large temporal offsets (Paredes et al., 2025). Expanding on prior behavioral analyses (Ferri et al., 2018), this study provided additional support for the idea that bottom-up alterations at the earliest stages of the sensory chain dictate greater SIFI susceptibility in individuals with high schizotypal traits, aligned with the notion of a common dimensional endophenotype contributing to both clinical and perceptual signatures witnessed along the psychosis continuum (Ferri et al., 2018; Javitt, 2009b).

Chapter 3: Individual Alpha Frequency and the SIFI

In the previous sections, we reviewed the most plausible accounts regarding the computational and psychophysical fingerprints of the SIFI, as well as their cortical sources. We also foregrounded the extent to which disruptions to such dynamics subsume an increased susceptibility to this illusion in clinical and subclinical samples, placing a strong emphasis on hallucination-prone individuals along the psychosis continuum. A recurring question running alongside these piece of evidence therefore concerned the neurophysiological mechanisms governing adaptive versus disrupted modes of cross-modal integration on which the SIFI relied. The departure point of several inquiries on the matter pivoted around the temporal regime under which this phenomenon most likely occurs. Whether probed at a single, near-threshold SOA (Shams et al., 2000), or across a wide range of inter-stimulus delays (Shams et al., 2002), the illusory extra-flash reports declined at inter-beep intervals exceeding 100 ms. This sub-second timescale fuelled a progressive interest in cortical electrophysiology, with a focus on pre- and peri-stimulus brain oscillations.

At the macroscopic level, EEG rhythms primarily reflect integrated postsynaptic (excitatory/inhibitory) currents in aligned cortical pyramidal cells, shaped by their interplay with inhibitory interneurons within thalamo-cortical and cortico-cortical circuits, which generate large-scale dipoles whose cycles of depolarization and rebound excitability manifest as synchronous oscillatory fluctuations (Jackson & Bolger, 2014). First documented almost a hundred years ago (Berger, 1929), and for a long time regarded as a cortical “idling” phenomenon (Pfurtscheller et al., 1996), they have progressively been put under the spotlight by clinical and cognitive electrophysiologists due to their topographical pervasiveness and massive involvement in several psychological domains: unisensory and multisensory perception, overt and covert attention, long- and short-term memory, motor planning and movement execution, as well as higher-order cognitive functions (Hari & Puce, 2023). These observations, together with accumulating evidence on the functional organization of such phenomena around specific frequency clusters, prompted researchers to develop a taxonomy of brain rhythms, stratified into five well-known frequency bands based on functional, topographical and morphological features. In this framework, low- and high-frequency oscillations include, respectively, delta (1-3 Hz) and theta (3-7 Hz), along with beta (15-35 Hz) and gamma (> 35 Hz) activity (Hari & Puce, 2023; Jackson & Bolger, 2014). However, within this rich taxonomy, the brain oscillations that have drawn most attention are those roughly between 7 and 14 Hz (70 – 130 ms per cycle), known as alpha rhythms (Klimesch, 2012).

3.1 The Many Facets of Alpha Rhythms

Predominantly occipito-parietal in their scalp distribution, alpha oscillations appear in EEG recordings as sinusoidal voltage fluctuations that become particularly prominent when participants close their eyes, and as a characteristic “knee-like” deviation from the $1/f$ aperiodic decay in the power spectrum (Klimesch, 2012). Closely tied to the visual system, these rhythms have been linked to a myriad of functions broadly clustered into five operational domains. (Clayton et al., 2018).

First, posterior alpha oscillations provide an electrophysiological architecture that selectively suppress task-irrelevant sensory inputs via “gating-by-inhibition” mechanisms (Jensen & Mazaheri, 2010). In this context, each peak within an alpha cycle is thought to act as an inhibitory pulse, shielding a given cortical region from incoming information. Here, oscillatory amplitude is key: the higher, the greater the inhibitory peaks, and the more effective the suppression, making alpha power fluctuations a pivotal lever through which sensory gatekeeping is instantiated. Consistent with this hypothesis, increased prestimulus alpha power in parieto-occipital areas has been associated with reduced detection of near-threshold stimuli (Van Dijk et al., 2008), spatially specific suppression of stimuli presented at unattended locations (Worden et al., 2000), and enhanced resistance to distractors (Kelly et al., 2006). Moment-to-moment phase dynamics play a central role for this “pulsed” inhibition to occur, with greater inhibition (reduced detection of near-threshold stimuli) observed when prestimulus alpha power was higher, and targets presented at specific oscillatory alpha phases, indexing cyclic changes in cortical excitability that gate near-threshold perception on a 100 ms timescale (Mathewson et al., 2011). This body of knowledge was further bolstered in a causal manner via alpha-tuned rhythmic TMS paired with online EEG (Romei et al., 2010), where detection of near-threshold targets presented at TMS-train offset was modulated by the TMS protocol, producing spatially lateralized effects (impaired vs enhanced detection contralateral vs ipsilateral to stimulation). Overall, these findings highlight that rhythmic fluctuations within the alpha band govern cortical excitability, which in turn can gate visual input via pulsed inhibition (figure 3.1).

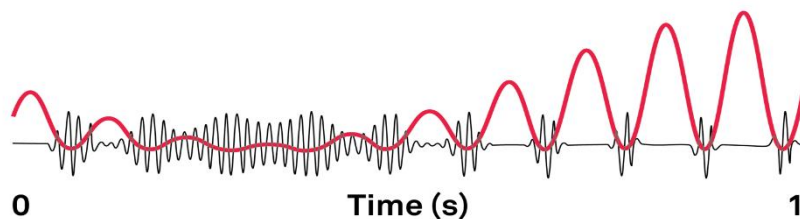


Figure 3.1 Schematic illustration of the “pulsed inhibition” mechanism as outlined in Jensen & Mazaheri (2010). The red trace represents fast-changing alpha activity, whereas the black concurrent high-frequency activity. As alpha rhythms increase their amplitude, faster oscillations reduce their “duty-cycle” and, consequently, the information they are carrying is suppressed.

Second, alpha oscillations have been shown to deploy top-down control, such that anticipatory modulations of alpha power track attentional priors and predictive cues. Complementary to the “gating-by-inhibition” hypothesis, this account shifts the emphasis from the mechanics to the functional role of alpha rhythms, and how they prioritize relevant information that biases sensory processing before stimulus onset (Foxe & Snyder, 2011). For instance, attentional bias induced by predictive cues has been proven to modulate prestimulus posterior alpha power and perceptual performance such that lower alpha contralateral to the attended side facilitates targets detection (Thut et al., 2006). The magnitude of this oscillatory modulation is, in turn, parametrically shaped by the strength of spatial prioritization and probabilistic value of cues (Gould et al., 2011). Importantly, these dynamics extend beyond space to feature-based expectation: feature-predictive cues elicit a comparable increase vs decrease in alpha power over cortical regions processing, respectively, task-irrelevant vs task-relevant feature dimensions (Snyder & Foxe, 2010). This relationship holds even in trial-by-trial analyses, in line with the assumption that anticipatory alpha dynamics encode priors and expectations about upcoming stimuli, thereby shaping discriminability and reaction times (Kelly et al., 2009).

Third, alpha rhythms can also act as a carrier signal for inter-areal communication, coordinating long-range cross-talk. As posited by the “communication-through-coherence” theory (figure 3.2), optimal inter-areal phase alignment between alpha oscillations across cortical nodes should dictate whether, and the extent to which, high-frequency bursts can be transmitted across a given network (Fries, 2005). This model dovetails with top-down views of alpha amplitude modulation (see previous point) by explicitly framing an upstream mechanism routing priors and expectations from anterior to posterior sites. A striking instance thereof comes from a spatial working memory task, in which stronger posterior alpha power suppression and alpha phase-coupling within the frontoparietal network were observed contralateral to the to be attended hemifield, suggesting an alpha-mediated top-down control over posterior excitability (Sauseng et al., 2005). In a similar vein, the interplay between alpha power suppression and phase synchronization was confirmed in a cued-spatial attention task, showing that local desynchronization (reduced alpha amplitude) paired with inter-regional coupling (increased alpha phase synchronization) contralateral to the to be attended location supported better top-down-guided attentional performance (Doesburg et al., 2009). These co-occurring dynamics have been further refined in a subsequent spatial attention study: stronger long-range high-alpha phase synchronization predicted a larger contralateral–ipsilateral asymmetry in low-alpha suppression and greater behavioral benefit (i.e., faster reaction times), suggesting that network-level alpha coupling can accompany local alpha desynchronization in sensory cortex (Lobier et al., 2018). Of note, thalamic nuclei such as the pulvinar have been implicated in channelling top-down attentional signals, as shown

by increased pulvino-cortical coupling and inter-areal coherence between visual sites during cue-target delay (i.e., prior to stimulus onset) within the broad alpha range (Saalmann et al., 2012).

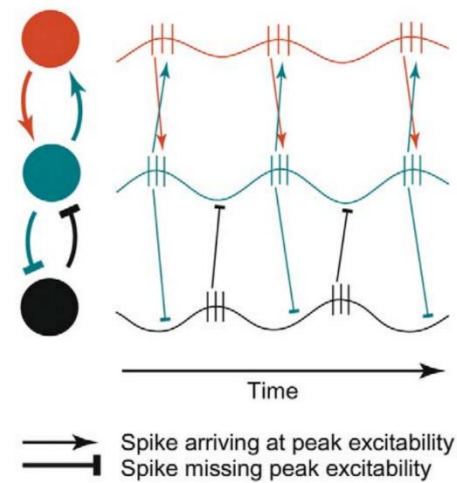


Figure 3.2 Communication-Through-Coherence (Fries, 2005): oscillatory synchronization between neuronal populations aligns phases of high excitability, thereby increasing the probability that incoming signals arrive at optimal phases and are effectively transmitted, whereas signals arriving out of phase are attenuated.

Fourth, alpha oscillations exhibit stabilizing properties that support the maintenance of ongoing perceptual and attentional states. From this perspective, increases in alpha power may preserve the internal representational states by decreasing cortical excitability, and therefore brain's responsiveness to external inputs (Clayton et al., 2018). Building on the “gating-by-inhibition” hypothesis (Jensen & Mazaheri, 2010), and compatible with top-down accounts of alpha oscillations (Foxe & Snyder, 2011; Fries, 2005), empirical evidence for a stabilizing function of alpha rhythms has been primarily drawn from working memory paradigms. Among the earliest examples, during the retention interval of a modified Sternberg task, it was shown that alpha peak power over parieto-occipital sites increased monotonically with memory load, persisted through most of the delay, and collapsed rapidly after the probe. The authors interpreted these oscillatory patterns as resulting from load-dependent, temporally specific alpha enhancement supporting short-term retention (Jensen et al., 2002). Similar results emerged in a working memory paradigm in which predictable distractors were presented during the retention interval: alpha power increased in anticipation of the distractor, and this enhancement scaled with the need to suppress interfering stimuli (Bonnefond & Jensen, 2012). The involvement of alpha rhythms in the online maintenance of perceptual representations was also causally probed using alpha-tuned TMS. In a visual short-term memory task, parietal alpha power suppression tracked participants' capacity to inhibit contralateral irrelevant information, and this effect was further boosted by TMS trains delivered during the retention interval (Sauseng et al., 2009). Taken together, these experimental works highlight how alpha rhythms can also promote persistence of internal states, reducing spontaneous switching and enhancing continuity.

3.2 Alpha Oscillations: a Sampling Rhythm for Conscious Perception

The last, yet no less compelling account concerning the role played by alpha oscillations is grounded in a long-standing debate over the supposedly cyclic nature of perception. The appealing notion of conscious experience as a granular phenomenon has deep philosophical roots in the concept of *specious present* (W. James, 1886), later formalized as *psychological moment* (Stroud, 1956). According to this view, perception is not continuously updated, but arranged into discrete temporal epochs providing the minimal units for perceptual experience. Within these building blocks, incoming information is integrated, while finer-grained temporal order remains largely unavailable. Framed in computational terms, perception would operate as a system that periodically samples external information at a sufficiently high temporal resolution to yield apparent continuity from a succession of discrete moments (Stroud, 1956). Later refined into an explicit psychophysical model providing the best fit to previous empirical observation regarding loudness/brightness thresholds paradigms (Shallice, 1964), the assumptions thereof were formally assayed through a synchrony judgment task (Efron, 1970a). On each trial, participants were presented with a time-varying test stimulus, and a fixed-duration probe, with stimuli within each pair that could be either modality congruent or not (i.e., transient flashes or tones). Upon stimuli presentation, they were asked to adjust the timing of the probe such that either its onset or offset felt simultaneous with, respectively, the onset or the offset of the test stimulus. By computing the difference between onset and offset timing, the author was able to quantify the perceived duration of the test stimulus, showing that offset latency was increasingly delayed when the stimulus was shorter than a critical duration of approximately 130 ms (Efron, 1970a). In short, perceptual operations displayed intrinsic temporal properties that implied discrete windows of integration, compatible with sampling hypotheses of perception (Stroud, 1956).

Evidence for perception as a mechanism parsing an ever-flowing sensory stream into discrete samples of information, readily available to our conscious experience, invited perhaps an even more provocative question: how does our nervous system achieve such a feat? Early attempts to address this issue were pioneered using a successiveness discrimination paradigm (i.e., judging whether two brief events are simultaneous vs successive), from which a psychophysical time “quantum” (i.e., the minimal duration perceived) was derived on a per-individual basis (Kristofferson, 1967). Strikingly, the average span of psychophysical “quanta” closely matched minimum perceptual durations reported by Stroud (1970), to which the author added a physiological lever: across individuals, estimated time quanta correlated with the cycling frequency of resting-state alpha rhythms. Such results represented the very first piece of evidence arguing for a tie between individual differences in temporal resolution and the periodic nature of brain oscillations (Kristofferson, 1967). In a similar fashion, the perceptual

pace-making properties of alpha rhythms were subsequently probed via both a two-flash discrimination task and a duration estimation task (Coffin & Ganz, 1977). Here, faster alpha peak frequency over occipital sensors was associated with trials in which, respectively, two flashes were reported, or duration estimates were closer to objective stimuli durations, and interpreted as the results of differences in cortical excitability cycles shaping temporal discrimination and perceptual sampling rate (Coffin & Ganz, 1977).

This body of knowledge paved the way to what is arguably the first experimental effort to explicitly formalize the relationship between phenomenology (i.e., perception is discrete) to physiology (alpha rhythms as an internal clock). The conceptual target revolved around *perceptual framing*, namely the idea that the visual system periodically samples external inputs through temporal windows, within and outside which stimuli are more likely to be, respectively, integrated or segregated. In this context, ongoing cortical alpha oscillations have been proposed as the candidate neurophysiological mechanism that provides a temporal scaffold for perception, parsing incoming information over time (Varela et al., 1981). Methodologically, the authors backed these hypotheses up using an apparent motion task with stimuli presented phased-lock to observers' posterior alpha cycle, showing that perceived simultaneity was maximal at the positive phase of occipital alpha oscillations. This phase dependence was construed as the empirical evidence for a periodic integration window, a perceptual frame parsing information one alpha cycle at a time (Varela et al., 1981). Over the years, this framework has been refined to accommodate new findings, and recently undergone a lively resurgence due to a renewed interest in the interplay between brain oscillations and visual perception. The emphasis is currently placed on the notion of *perceptual cycles* (figure 3.3), with brain rhythms seen as a temporal organizing principle by virtue of their periodic fluctuations that index waxing and waning neural excitability states (VanRullen, 2016). Perpetual changes from one state to another provide a succession of cyclic windows, snapshots of the external world, in which inputs are preferentially processed. A relevant addendum to the *perceptual framing* model here pertains to the mechanistic implications of a discrete account (experience parcelled into frames), as opposed to a weaker claim of rhythmic modulation (experience is continuous with fluctuations in gain): event between frames do not merely vanish, rather, they are deferred to the next cycle, much like in a system with a finite sampling rate (VanRullen, 2016). Although the author advocates against the concept of a single sampling rhythm, favouring multiple perceptual oscillators depending on stimulus properties, task demand or cortical regions engaged, evidence is consistent with low-frequency waves (i.e., from 6 to 15 Hz) playing a pivotal role in sensory-attentional sampling, and temporal parsing as a constitutive mechanism of perception (VanRullen, 2016).

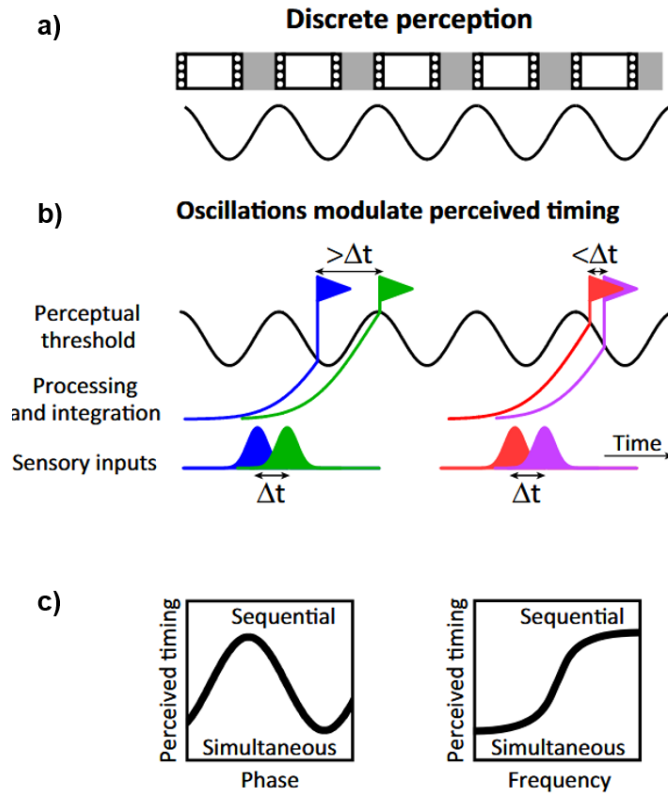


Figure 3.3 Oscillatory models of discrete perception (VanRullen, 2016). **a)** Ongoing oscillatory cycles segment incoming information into successive perceptual “snapshots,” such that events missed in one epoch are deferred to the next. **b)** Oscillations can also modulate perceived timing: two stimulus pairs separated by the same physical interval (Δt) can reach perceptual threshold with an expanded ($>\Delta t$) or compressed ($<\Delta t$) effective interval depending on oscillatory phase, yielding phase-dependent temporal parsing. **c)** From the aforementioned principles, it follows that timing judgments can be either phase-dependent (perceived simultaneity vs sequentiality varies cyclically with oscillatory phase) or frequency-dependent (perceived simultaneity vs sequentiality co-varies negatively vs positively with oscillatory frequency)

Several experimental works lend weight to the aforementioned assumptions. Among the earliest of which, trial-by-trial analyses in a near-threshold visual detection task revealed that prestimulus oscillatory phase clustering was predictive of performance in a probabilistic fashion, such that, depending on the phase of ongoing brain rhythms within the broad alpha range (6-12 Hz), observers were more likely to detect or miss the target (Busch et al., 2009). In this vein, a coeval study using a metacontrast masking paradigm proved how awareness of a target (i.e., seen vs unseen) is defined by the phase of posterior alpha waves, supporting a “pulsed inhibition” mechanism whereby excitability cycles regulate perceptual access (Mathewson et al., 2009). Oscillations in perceptual performance are therefore not to be seen as stationary noise around a mean, but as the behavioral by-product of rhythmic sampling. Akin to these findings, it was later shown that moment-to-moment alpha phase fluctuations govern the temporal resolution of perception by dictating windows of cortical excitability (Dugué et al., 2011). This was achieved by combining online EEG recording with single-pulse TMS to induce phosphene perception (i.e., a proxy for neural excitability), whose variability causally relied on

prestimulus alpha phase: post-hoc analyses demonstrated that TMS pulses delivered at opposite phases yielded a difference in phosphene reports of approximately 15% (Dugué et al., 2011).

Beyond phase-dependent effects, discrete-sampling accounts make a stronger, foundational claim: perception can be treated as a periodic sampling system, whereby temporal parsing is also set by how fast the cycles run (i.e., how dense are cyclic fluctuations per unit of time). In this view, the peak/individual alpha frequency (i.e., IAF) provides a natural index of sampling rate: faster alpha implies shorter sampling intervals and thus higher temporal resolution, whereas slower alpha implies longer windows that favour integration over segregation. Seminal evidence compatible with this proposition has been gathered using the flickering wheel illusion (Sokoliuk & VanRullen, 2013). This misperception surfaces when a static, high-spatial-frequency wheel is viewed in the periphery, prompting the observer to experience a regular flicker at its center. The authors quantified this phenomenon with a psychophysical matching task, showing that participants matched the illusory flicker with a probe flicker around 9 Hz. Moreover, EEG analyses revealed how occipital alpha dynamics tracked the illusion, with higher alpha power resulting in an increased susceptibility to the illusion, and the peak modulation frequency during illusory episodes correlating across individuals with the IAF, pointing to an endogenous alpha-timed perceptual phenomenon (Sokoliuk & VanRullen, 2013). IAF involvement in perceptual sampling was further detailed through a modified Eriksen flanker task in which targets and distractors flickered either at 7.5, 10 or 15 Hz (Gulbinaite, Viegen, et al., 2017). When attentional control demands were high (i.e., incongruent trials) 10 Hz flicker selectively impaired performance as a function of how closely on-task IAFs matched it: the closer the match, the larger the impairment, once again suggesting attentional sampling may be framed by endogenous alpha timing (Gulbinaite, Viegen, et al., 2017).

Given the aforementioned results from flicker paradigms, an intuitive next step was to ask whether IAF also constrains “how wide” a system’s sampling window is. This question is well captured by the psychophysical construct of TBWs: the range of stimulus asynchronies over which inputs are likely to be bound rather than segregated (Vroomen & Keetels, 2010; Wallace & Stevenson, 2014). Here, the IAF becomes a candidate rate parameter for temporal integration. Faster individual alpha would imply shorter cycles and tighter binding windows, favouring segregation of closely timed events, whereas slower alpha would imply longer cycles and broader windows that promote integration. An elegant proof-of principle of such a brain-behavior relationship was furnished in a cornerstone study leveraging EEG recordings during a two flash-fusion task (Samaha & Postle, 2015). On each trial, participants were presented either with two flashes (40 ms each) interleaved by varying SOAs (10-50 ms in steps of 10 ms), or with one flash whose duration varied to match the first-disk onset to second-disk offset at each SOA (e.g. 90-130 ms), such that the total stimulus duration was not informative of

the number of flashes. Upon stimuli offset, participants had to report whether they saw one or two flashes. Accuracy rates at each SOA were fitted to a psychometric function in order to extract on a per-individuals basis the fusion threshold (i.e., inflection point of the sigmoidal curve), a proxy for visual discrimination abilities. Resting-state data were also collected, alongside online EEG recordings. Results showed that eyes-closed resting-state IAF (as computed via spectral decomposition), as well instantaneous frequency estimates relative to on-task prestimulus alpha activity, predicted temporal resolution across individuals: the faster these indices proved to be, the lower the fusion thresholds (Samaha & Postle, 2015). Crucially, the authors also performed within-subject analyses by binning trials according to whether discrimination was correct or not, and found that moment-to-moment fluctuations in prestimulus alpha frequency were faster preceding correct responses. To summarize, this work provided the first piece of evidence that IAF covaries with the temporal granularity of visual perception (figure 3.4), shaping the size of an observer’s discrete sampling window (Samaha & Postle, 2015).

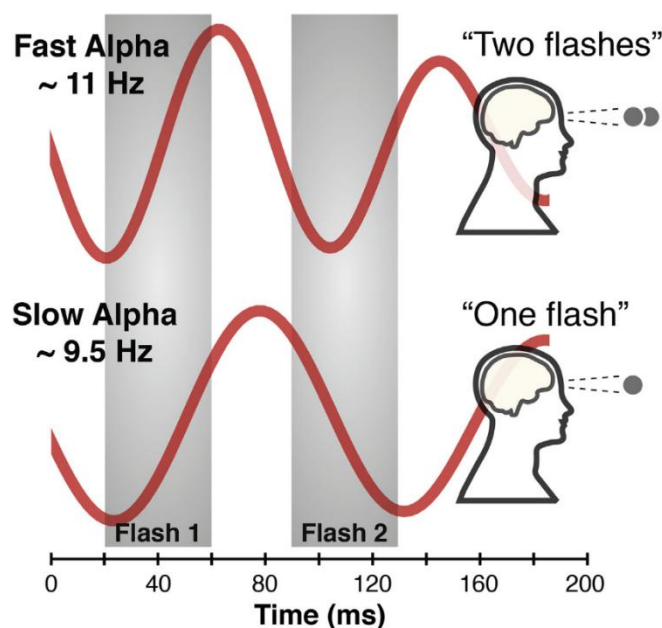


Figure 3.4 Conceptual model linking IAF to temporal parsing of visual events (adapted from Samaha & Postle, 2016). Alpha oscillations define discrete windows of heightened excitability that segment incoming sensory information over time. Faster alpha rhythms (higher IAF) yield shorter integration windows, promoting the segregation of closely spaced visual events and increasing the likelihood of perceiving two flashes, whereas slower alpha rhythms extend the integration window, favouring temporal fusion and the perception of a single flash for the same physical stimulus interval.

Beyond these findings, it was later probed whether alpha frequency could be viewed merely as a marker of temporal resolution or fully-fledged control parameter that could be tuned in a top-down fashion (Wutz et al., 2018). In participants presented with identical sequences of two displays (interleaved by an individually-titrated interstimulus interval) under different instructions that could emphasized either temporal integration (i.e., missing element task) or segregation (odd-element task),

occipito-temporal peristimulus alpha frequency slowed when integration, as opposed to segregation, was required. Crucially, these effects were frequency-specific, and further established that longer alpha cycles accommodate larger temporal windows for sensory binding (Wutz et al., 2018). The very same paradigm was adopted in a coeval study that leveraged IAF-tuned multisensory entrainment deployed during the prestimulus time window (Ronconi et al., 2018). Resting-state EEG was recorded prior to the beginning of the task to estimate each participant's IAF, which was later used to fine-tune the audiovisual entrainment protocol, set to engage either lower frequency (IAF-2 Hz) or upper alpha frequency (IAF+2 Hz). By densely sampling performance at multiple delays after entrainment, the authors found accuracy rates oscillating either at a faster or slower pace when audiovisual stimulation was delivered at, respectively, IAF+2 Hz or IAF-2Hz. Entrainment therefore impacted perceptual sampling in opposite directions: the faster protocol improved segregation by shrinking the individual binding window, whereas the slower protocol improved integration by enlarging it (Ronconi et al., 2018). Lastly, alpha pace-making properties have been tested in a two-flash fusion paradigm that participants performed across several SOAs (33, 67, 100 and 400 ms) under both near-threshold or full-contrast perceptual regimes (Drewes et al., 2022), while EEG was recorded at rest and during task completion. The authors reported that faster resting-state IAF predicted sharper temporal sensitivity at shorter SOAs (33, 67 ms), while the opposite held for longer SOAs (slower IAF predicted better performance). Moreover, within-subject analyses using instantaneous frequency estimates within the prestimulus alpha band predicted individual performance: higher and lower alpha frequency were associated with, respectively, two-flash and one-flash reports, indicative of trait- and state-dependent alpha frequency fluctuations tracking trial-to-trial temporal resolution.

Together, these converging findings establish alpha peak frequency as a flexible yet individually anchored electrophysiological “metronome” for perceptual parsing. Moreover, they motivate its use as a principled neural index of TBWs, setting the stage to further test whether shifts in alpha cycling pace represent a plausible phenotype driving pathological misperceptions and positive symptoms across unisensory or multisensory regimes.

3.2.1 IAF as a Stable and Trait-Like EEG Feature Across the Psychosis Continuum

To evaluate the reliability of IAF as a candidate neurophysiological phenotype that may predict perceptual alterations in clinical and subclinical populations such as those lying along the psychosis continuum, it is necessary to address a basic, preliminary question: does IAF show trait-like features? More plainly, does this EEG index display within-subject stability over time? Empirical answers to such questions began to emerge as early as the 1980s, with what was, to date, the earliest work on the

topic (Gasser et al., 1985). The authors recruited healthy individuals to record resting-state EEG activity across temporally interleaved sessions (i.e., approximately 10 months), and focused on test-retest reliability of several EEG spectral parameters (rhythmic components and broadband activity). Of note, alpha-band metrics such as peak location (i.e., IAF) and power were among those displaying the higher degree of stability using both long and short recordings segments, providing the very first principled evidence that these metrics correspond to a reliable resting-state EEG feature (Gasser et al., 1985). A later study probed the same hypothesis in 19 healthy adults from which EEG activity was serially recorded at 5 minutes, and after approximately 14 weeks (Salinsky et al., 1991). Irrespective of EEG segment length and the retest interval (5 minutes vs 14 weeks), the authors reported that peak alpha frequency and mean alpha frequency (i.e., distinct proxies for estimating IAF) ranked among the most reliable EEG measures (Salinsky et al., 1991). More recently, resting-state IAF has been shown to exhibit very high rank-order stability across sessions separated by approximately 6.6 months in both younger ($r = .89$) and older adults ($r = .82$). Such stability was not altered by extensive cognitive training performed between recording sessions, supporting the view that IAF is a genuinely trait-like marker rather than a state-dependent artifact (Grandy et al., 2013). To a similar end, scalp- and source-level EEG metrics were computed in samples of younger and older adults, with EEG recorded one week apart (Popov et al., 2023). The authors extracted several resting-state EEG metrics spanning peak frequency within different oscillatory bands, to time-reversed Granger causality, and probed test-retest reliability using intra-class correlation (i.e., ICC). Results showed that power spectra and IAF-like metrics were among the most robust and reliable, with good-to-excellent ICCs across age groups, outperforming peak frequency within other oscillatory bands, as well as connectivity measures (Popov et al., 2023). All in all, these findings suggest that IAF is sufficiently reproducible to support brain-behavior and clinical biomarker claims, reinforcing the broader view that this EEG index may exhibit trait-like properties. The biological plausibility of this account is further buttressed by heritability estimates from twin studies. For instance, in a sample of 688 participants drawn from 288 twin families, IAF showed high heritability, with much of its interindividual variability attributable to additive genetic effects rather than shared or unique environmental influences (Posthuma et al., 2001). In this vein, a subsequent study on a large sample of monozygotic and dizygotic twin pairs confirmed a strong additive genetic influence on IAF, as well as the high heritability and good reliability of this index at a 3 months retest session (Smit et al., 2006). In plain terms, the IAF of individuals who share a larger proportion of their genetic makeup (e.g., monozygotic twins) is more similar than the IAF of individuals who share fewer genes (e.g., dizygotic twins or siblings), lending further support to the view that IAF behaves as a stable, trait-like characteristic.

How do these findings fit within broader models of SCZ, and the notion of dimensionally-arrayed biobehavioral markers along the psychosis continuum? Psychosis-prone patients and high-schizotypy individuals share graded alterations in low-level sensory processing (Javitt, 2009b), which dovetails with the assumption of a coarser perceptual sampling rate, perhaps mediated by slower IAF (Samaha & Postle, 2015; VanRullen, 2016). This claim is compatible with frameworks casting SCZ as a disorder of impaired temporal coordination, in which brain oscillations provide the machinery that regulates cortical excitability, gates sensory inputs, and enables effective communication across distributed circuits (Uhlhaas & Singer, 2010). Abnormalities in the timing and cross-talk of intrinsic rhythms may thus represent a plausible endophenotype, rooted in a disrupted excitation–inhibition (E/I) balance (e.g., impaired inhibitory interneuron/NMDA-mediated regulation that destabilizes rhythmic gain), which bridges circuit dysfunction and graded perceptual or cognitive alterations (Uhlhaas & Singer, 2010). Accordingly, IAF might offer a physiological readout of this E/I imbalance, capturing shifts in the intrinsic alpha pace that cascade into bottom-up perturbations of the temporal constraints under which sensory evidence is sampled. Early evidence for such a relationship has been provided by recording resting-state EEG activity from a large sample of first-episode SCZ patients, first-episode bipolar psychosis patients, and healthy controls, as well as their relatives: each proband group was matched with an associated group of relatives (Clementz et al., 1994). EEG spectral analyses returned several alterations encompassing all low-frequency bands, although a significant reduction in alpha peak frequency (as computed from central electrodes) was reported in both bipolar psychosis patients and female relatives of SCZ patients, with a good stability of alpha peak frequencies in a retest sub-group 9 months later (Clementz et al., 1994). These findings have been partly corroborated later on. Relative to healthy controls, slower resting-state IAFs have been reported in SCZ patients with a predominantly negative symptom profile, whereas patients with more prominent positive-like symptoms displayed faster resting-state IAF, suggesting that alpha timing may index nuanced neurophysiological differences between positive- and negative-dominant presentations (Garakh et al., 2012). Moreover, slower alpha peaks in psychosis-prone patients were found to correlate with illness duration, such that longer, the slower the IAF (Goldstein et al., 2015). In recent years, however, these seminal conclusions have been followed-up by a more thorough exploration of alpha band spectral dynamics (Yeum & Kang, 2018). EEG resting-state activity was recorded from a sample of SCZ patients, alongside an age- and sex-matched control group, with peak frequency, power and coherence within the alpha band computed across the full sensors array. Beyond a pervasive reduction in inter-hemispheric connectivity, the patient cohort displayed significantly slower occipital IAF as compared to healthy controls, whereas no difference in alpha power was reported (Yeum & Kang, 2018). Using an high-density EEG montage, these patterns of activity were replicated in first-episodes psychosis

patient (M. Murphy & Öngür, 2019). Here, EEG was recorded at rest and during rhythmic photic stimulation eliciting steady-state visual evoked potentials at different frequencies (1, 4, 10, 20, and 40 Hz). Results again showed reduced peak alpha frequency over centro-parietal/posterior regions in the patient sample, alongside predominantly antero-posterior wave propagation and attenuated steady-state responses, supportive of broader impairments in resonant networks relying on alpha oscillatory substrates, with IAF slowing sitting at their dysfunctional core (M. Murphy & Öngür, 2019). Along this line of reasoning, slower resting-state IAF in SCZ has been observed across several subsequent works, although much of them has focused on related spectral metrics rather than IAF per se (Freche et al., 2020; Koshiyama et al., 2021; Nakhnikian et al., 2024). These findings laid the foundations for a cornerstone study that explicitly tied resting-state IAF to behavioral performance (Ramsay et al., 2021). Eyes-closed resting-state EEG was recorded from over one hundred outpatients with SCZ or schizoaffective disorder, and age- and sex-matched controls. A large subset of participants also completed the Degraded-Stimulus Continuous Performance Test (DS-CPT; indexing visual attentional abilities) and several WAIS-III subtests to estimate global cognition. Consistent with the hypotheses, the patient cohort showed slower resting-state IAF, whereas performance on both the DS-CPT and WAIS-III was predicted by faster IAF. Moreover, visual attentional ability fully mediated the association between IAF and global cognition, suggesting that alpha oscillatory pace may be a plausible driver of perceptual discrimination, with downstream consequences for cognitive functioning (Ramsay et al., 2021).

Importantly, this brain-to-trait approach has also been extended to subclinical individuals with high schizotypal traits, to test whether IAF acts as a reliable electrophysiological marker across the whole psychosis continuum (Trajkovic et al., 2021). To this aim, a sample of healthy individuals (over 300) was screened using the SPQ, and those whose scores fell within the lowest and highest quintiles of the distribution were assigned to the Low and High schizotypy groups, respectively (24 participants each). High-density EEG was recorded at rest (eyes-closed). Using independent component analysis, the authors extracted several topographically-specific components, through which they computed IAF, alpha amplitude and connectivity metrics. Individuals with high-schizotypy displayed slower right posterior alpha frequency, a tendency toward reduced right hemisphere alpha amplitude and fronto-parietal connectivity. These alpha features were then fed into a machine-learning pipeline, in which a classifier distinguished groups with approximately 74% balanced accuracy (Trajkovic et al., 2021). Similarly, in a large cohort of healthy individuals ($n = 318$) screened with the SPQ, IAF extracted from each sensor during eyes-closed resting-state EEG recording were regressed over scores on the “Magical Thinking” subscale, indexing proneness to positive-like schizotypal traits. Results revealed a negative linear relationship between the two measures, such that higher “Magical Thinking” scores

were associated with lower fronto-parietal IAF, a pattern further supported by a small but reliable IAF reduction following a median split (Tarasi et al., 2025). Together, these findings anchor resting-state IAF to the psychosis continuum not only as a putative biomarker of sensory impairments that may contribute to positive-like phenomena and pathological misperceptions via coarser temporal sampling (Javitt, 2009b; VanRullen, 2016), but also as a potential early electrophysiological proxy for identifying individuals at prodromal stages of these disorders (Cochrane et al., 2012; Ettinger et al., 2014; Nelson et al., 2013).

3.2.2 From Trait to State: Entrainment-Based Modulation of IAF

If IAF can be best understood as a trait-like feature of human electrocortical activity whose alterations may underlie the symptomatic profile of psychosis (or the prodromal stages thereof), a key translational question concerns whether, and how, this index may be amenable to change. In other words, can this trait-like feature be up- or down-shifted in a state-dependent manner? A fairly sizeable body of evidence is indeed suggestive that such an oscillatory manipulation can be achieved, through a mechanisms known as “entrainment” (Thut, Schyns, et al., 2011). First shown as the result of photic stimulation using flickering lights (Adrian & Matthews, 1934), with an instance of which already mentioned in a previous section (Ronconi et al., 2018), entrainment can be defined as the synchronization of endogenous brain oscillations to a rhythmic stream (or train) of external events (Thut, Schyns, et al., 2011). Entrainment induction can be instantiated either through sensory drive, or via non-invasive brain stimulation protocols that periodically interact with ongoing brain activity, thereby aligning the phase of a targeted rhythm to the frequency output of an external oscillator (Thut, Schyns, et al., 2011). At the neural level, clear-cut entrainment effects can be claimed only insofar as rhythmic stimulation generates oscillatory-like patterns that are distinguishable from what might otherwise be construed as a train of evoked responses (Thut, Schyns, et al., 2011). Among the core criteria is frequency specificity, namely phase alignment and amplitude increase (i.e., the canonical signatures of oscillatory entrainment) should peak around the frequency output of the external oscillator, indicating a genuine interplay that engaged resonant mechanisms intrinsic to the stimulated regions or rhythms. In addition, rhythmic reverberation (i.e., oscillatory “echoes” outlasting the stimulation train by 2-4 cycles) represents a further hallmark of reliable entrainment-based modulation (Thut, Schyns, et al., 2011). To this end, tuning stimulation parameters to the rhythmic and functional properties of the to be targeted brain circuits is crucial for entrainment optimization (Romei, Thut, et al., 2016). Such physiologically-informed modulation approach holds that entrainment is best engendered (both neurally and behaviorally) when rhythmic protocols accommodate state-dependence

and inter-individual variability. That is, when their periodic drive match (or closely track) at a fine-grained frequency level the participant's oscillatory cycling rate, and they are administered in a cortical excitability state that is optimal for engaging the targeted rhythm (Romei, Thut, et al., 2016). As long as the aforementioned pre-conditions are met, it is possible to causally shape ongoing oscillatory activity to assay its contribution to human cognition (figure 3.5).

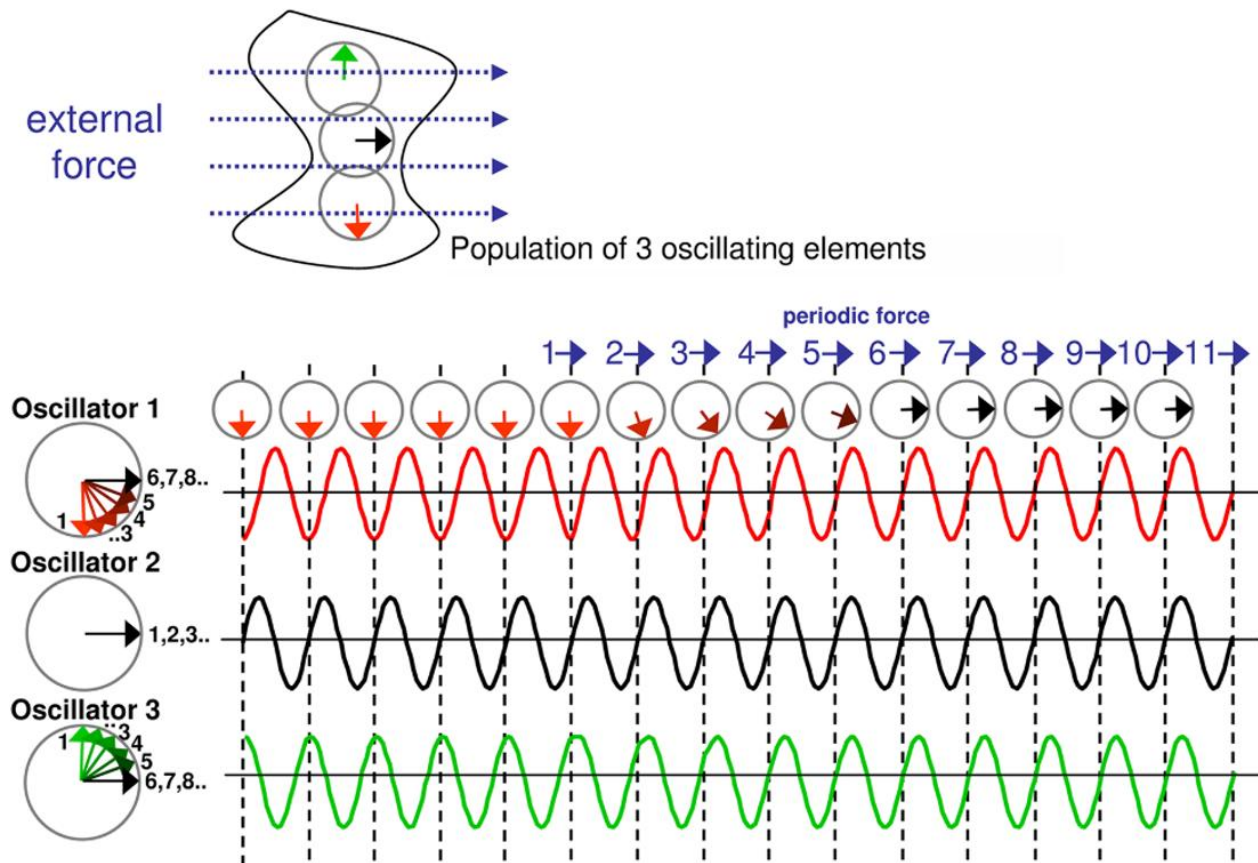


Figure 3.5 Neuronal entrainment by a periodic external force (adapted from Thut, Schyns, et al, 2011): a rhythmic external stream progressively aligns the phase of multiple intrinsic oscillators, reducing phase dispersion across the population and leading to a progressive phase locking of the “driven” oscillators to the “driving” rhythm.

Initially implemented through sensory stimulation (for a review see Schroeder & Lakatos, 2009; or Thut, Schyns, et al., 2011), over the last two decades a growing body of experimental studies leveraged non-invasive brain stimulation techniques such as transcranial alternating current simulation (tACS) or TMS, to entrain spontaneous brain rhythms (Thut, Schyns, et al., 2011; Trajkovic & Sack, 2025). The former delivers weak sinusoidal (i.e., alternating) currents through scalp electrodes, which interact with ongoing cortical rhythms at the applied frequency rate by modulating membrane potentials (Antal et al., 2011). A remarkable instance of tACS-induced entrainment was reported in an oddball task in which participants received parieto-occipital 10 Hz stimulation while EEG was simultaneously recorded. Spectral analyses of denoised EEG data revealed a tACS-mediated frequency-specific

increase in alpha power over the stimulated regions, along with robust moment-to-moment phase alignment to the tACS drive that was paired with co-occurring periodic fluctuations in visual detection performance (Helfrich, Schneider, et al., 2014). Additional evidence for tACS-mediated oscillatory entrainment has been reported across perceptual domains (Battaglini et al., 2020; Helfrich, Knepper, et al., 2014), working memory (Alekseichuk et al., 2016; Polanía et al., 2012) and motor functions (Feurra et al., 2013; Wach et al., 2013). Notably, behavioral outcomes supporting the feasibility of entrainment-based frequency-pulling (i.e., up- or down-shift of endogenous oscillatory peak), beyond simple amplitude increase or phase-locking (Wolinski et al., 2018). However, tACS poses a major challenge for co-registration of EEG activity, as it is still a matter of lively debate whether genuine electrophysiological signals can be reliably recovered amidst the large tACS-related artefacts (Noury & Siegel, 2018), an issue than can be circumvented through rhythmic TMS (i.e., rhTMS).

TMS-based protocols entail the release of transient, non-invasive magnetic bursts perturbing the electric homeostasis of the underneath cortical mantle (Rossi et al., 2021). Here, oscillatory entrainment can be instantiated insofar as these modulatory bursts are delivered in frequency-tuned trains that periodically phase-reset the targeted rhythm (Romei, Thut, et al., 2016; Trajkovic & Sack, 2025). Unlike tACS, TMS-related artefacts in EEG recordings are short-lived (typically less than 10 ms) and well-localized at the topographic level, thereby making denoising pipelines more straightforward and reliable in recovering faithful neural information, and rhTMS-EEG co-registration a principled tool to assay the causal involvement of brain rhythms in cognition (Thut & Miniussi, 2009). A seminal proof-of-concept in this regard was provided by applying alpha-tuned rhTMS over the parietal cortex (i.e., electrode CP4) in resting participants while EEG was simultaneously recorded (Thut, Veniero, et al., 2011). The stimulation site was selected based on prior evidence that this parietal spot exhibited the strongest intrinsic alpha activity, at the group level, during an attentional task. Further, rhTMS was set to deliver trains of five interleaved magnetic pulses at 10 Hz frequency, under different stimulation protocols and control conditions. Spectral analyses focused on denoised electrophysiological activity immediately following stimulation bursts, to verify whether rhTMS was able to entrain a natural cortical oscillator such as the parietal alpha rhythm. Importantly, when TMS bursts matched the resonating frequency (e.g., 10 Hz) of the targeted parietal spot, EEG displayed a clear alpha-band entrainment response: a frequency- and topographically-specific amplitude increase, narrowband phase alignment across trials, and oscillatory “echoes” reverberating right after the stimulation stopped (Thut, Veniero, et al., 2011). The authors additionally showed that such entrainment fingerprints were not uniform, but progressively grew across the pulse train, consistent with increasing phase alignment of the underlying oscillator to the stimulation rhythm and a cumulative profile that spoke against a sum of identical, independent evoked potentials. Germane to

this conclusion, entrainment response magnitude exhibited state-dependent properties. Namely, rhTMS effects appeared contingent on prestimulus alpha phase (i.e., periodic window of cortical excitability). When the first pulse in each train landed at a favourable (vs non-favourable) phase (i.e., neurons closer to a high- rather than low-excitability state), reset of the ongoing oscillation was more effective, yielding stronger phase locking and more pronounced alpha-tuned rhythmic reverberation following subsequent pulses (Thut, Veniero, et al., 2011). This body knowledge ushered in a whole new line of research that leveraged entrainment-inducing rhTMS protocol and concurrent EEG recordings to causally reshape ongoing brain oscillation, and quantify the extent to which they may contribute to many aspects of human perception (Jaegle & Ro, 2014; Y.-J. Lin et al., 2021; Stengel et al., 2021; Vernet et al., 2019), attention (Lu et al., 2025), working memory (Albouy et al., 2017; Riddle et al., 2024), and motor behavior (Uehara et al., 2023).

Together, these TMS-based entrainment studies place functional emphasis on rhythmic synchronization (i.e., phase-alignment and amplitude increase) as the lever to frequency-specific causal control. A natural extension, however, is that, under specific conditions, an endogenous oscillator can also be pulled in frequency, such that its intrinsic pace is deliberately sped up or slowed down to test whether shifting the operating rate may prompt predictable changes in behavior. This brings us back to the central question which this section began with: is IAF sensitive to entrainment, and amenable to state-dependent change? A preliminary answer is to be found in the aforementioned notions of “information-based neuromodulation” and fine-tuning of stimulation parameters (Romei, Thut, et al., 2016). In this vein, frequency pulling can be attained insofar as entrainment is tailored to engage the natural rhythmic fingerprints of a targeted region, which in turn implies that a thorough understanding of state-dependent brain circuit properties is crucial to successfully bias its oscillatory activity toward a faster or slower cycling rate. A recent study combining rhTMS and online EEG has shed further light on the physiological variables to account for in order to maximize entrainment-based frequency pulling (Trajkovic, Sack, et al., 2024). Specifically, the authors delivered rhTMS over the occipital cortex to modulate IAF speed in an individualized manner, by setting the machine frequency output based on each participant's resting-state IAF, rather than adopting an a priori 10 Hz protocol. They then performed spectral decomposition of resting-state alpha activity and fitted a Gaussian function to derive, on an individual basis, key oscillometric features, namely peak “height” (i.e., alpha-peak prominence) and peak “width” (i.e., the breadth of the alpha bump). These metrics were used to anticipate the effects of three rhTMS protocols: two off-peak conditions ($\text{IAF} \pm 1 \text{ Hz}$, designed to induce frequency pulling) and one on-peak condition (tuned to each participant's IAF, to maximize canonical entrainment and amplitude boosting). Results highlight the primary role of individual resonance properties, as framed within an “Arnold tongue” account, in shaping the magnitude of alpha-

tuned rhTMS. On the one hand, alpha peak “height” determined the on-peak outcome: the lower, the greater the amplitude enhancement and vice-versa. On the other hand, alpha peak “width” was predictive of how strongly IAF could be shifted under off-peak stimulation, with broader peaks more sensitive to frequency modulation (toward either faster or slower rates) and vice-versa (Trajkovic, Sack, et al., 2024). Entrainment and, more stringently, frequency pulling can be therefore achieved, but only as far as rhTMS is treated as a resonance-based, biomarker-aware manipulation. Stimulation should thus be tuned to each individual’s intrinsic alpha dynamics (peak frequency and spectral profile) to place the protocol within a regime where the targeted oscillator can be reliably shifted.

Bearing this in mind, we can now turn to a piece of literature that seamlessly translated these methodological recommendations into a rigorous testing ground to assay the causal properties of IAF in shaping visual performance (Di Gregorio, Trajkovic, et al., 2022). Building on the discrete sampling theory of perception (VanRullen, 2016), this study moved one step further and explicitly asked whether exogenously changing ongoing prestimulus alpha frequency would result in finer vs coarser perceptual sampling, as indexed by visual sensitivity metrics (i.e., d'). To do so, participants were asked to complete a near-threshold visual detection task while EEG was recorded, and rhTMS was delivered to the occipital pole prior to stimulus onset (i.e., the final burst within each five-pulse train co-occurred with stimulus onset) at IAF-1 Hz, IAF, or IAF+1 Hz (alongside frequency-matched Sham controls), with IAF extracted from resting-state EEG data on a per-participant basis. The authors reported a clean double dissociation where faster (IAF+1 Hz) versus slower (IAF-1 Hz) rhTMS elicited, respectively, an upward versus downward shift of the alpha peak, accompanied by an increase versus decrease in visual sensitivity. By contrast, on-peak rhTMS (IAF) primarily ignited an amplitude increase coupled with reduced metacognitive performance (Di Gregorio, Trajkovic, et al., 2022). The same group conducted a follow-up study in which rhTMS after-effects were examined alongside prestimulus alpha changes, to assess whether these mapped onto post-stimulus ERP dynamics. Beyond shifting prestimulus alpha frequency, off-peak stimulation tilted P100 waveforms (an early posterior ERP component whose latency is associated with sensory processing) such that faster versus slower rhTMS-driven IAF yielded earlier versus later P100 latencies. Conversely, the prestimulus amplitude increase following on-peak rhTMS was mainly associated with reduced P300 amplitude (Trajkovic, Di Gregorio, et al., 2024). Overall, these studies lend substantial weight to the discrete sampling hypothesis of visual perception, and the notion of a latent electrocortical mechanism that governs observers’ temporal resolution. Moreover, they neatly foreground how rhTMS–EEG co-registration, when deployed under a properly physiologically-informed parameter regime, can be harnessed to causally entrain (and map) the oscillatory signatures subsuming visual perception.

3.3 Rhythmic Windows into Audiovisual (Mis)Perception: Evidence and Controversies

After this long detour across the functional facets of alpha oscillations, their putative contribution to perceptual sampling, psychosis-like symptomatology, and the extent to which they may be reshaped through principled, information-based entrainment protocols, we are now compelled to bring these threads together and return to the overarching question motivating this project. If an observer's visual sampling rate relies on a temporal frame supplied by the cycling pace of posterior alpha rhythms, and if such pace is slower in individuals lying along the upper end of the psychosis continuum, who in turn display coarser cross-modal precision, does this oscillatory index sit among the causal biomarkers that drive audiovisual sensitivity and, more specifically, susceptibility to the SIFI? This intriguing proposition is grounded in well-established theories of discrete perception (VanRullen, 2016; Varela et al., 1981), and resonates with the psychophysical construct of TBWs within the multisensory domain (Vroomen & Keetels, 2010; Wallace & Stevenson, 2014). Moreover, it accommodates bottom-up accounts of SCZ (Javitt, 2009b) by situating the latent sources of positive-like symptoms and psychotic misperceptions at the earliest stages of the perceptual hierarchy, foregrounding a mechanistically- and physiologically-plausible endophenotype that may underlie impaired low-level encoding of sensory inputs (Uhlhaas & Singer, 2010).

A recent meta-analysis on the topic (Samaha & Romei, 2024) tentatively tackled the issue by aggregating a large body of studies in which the speed of posterior alpha rhythms, as measured either at rest or on-task, was correlated with behavioral performance (operationalized in heterogeneous ways from one study to another) at audiovisual paradigms, including the SIFI. The take-home message is clear: despite dispersion in reported correlations and occasional nulls at the study level, evidence converges on a reliable medium-to-large population effect and a robust brain-behavior association, while underscoring how sampling and methodological choices can modulate its detectability (Samaha & Romei, 2024). The studies under meta-analytic scrutiny that were performed on adult participants can be broadly pooled into three families based on the experimental paradigm adopted: SJ, TOJ, and, most notably, SIFI-like tasks.

Regarding SJ tasks and related paradigms, the earliest attempt to link cross-modal temporal abilities to alpha oscillatory speed can be traced back to a milestone study already mentioned above (Kristofferson, 1967). The author employed what he termed a “successiveness discrimination task”, in which participants judged whether co-occurring auditory and visual stimuli were simultaneous. This enabled him to derive individual time “quanta” (i.e., the minimal temporal mismatch reliably perceived). He then reported that the average span of these psychophysical “quanta” correlated with modal zero-crossing interval of resting-state alpha rhythms (i.e., a methodological forerunner of

contemporary IAF estimates), thereby furnishing a mechanistic prelude to later alpha-based electrophysiological models of granular perception (Kristofferson, 1967). More than 50 years later, these findings were replicated using a more conventional audiovisual SJ task sampled across several SOAs (0-360 ms in steps of 40 ms, plus finer sampling of 20 ms around the putative PSS). The authors retained only participants exhibiting a roughly balanced proportion of “simultaneous” versus “not simultaneous” responses, and focused their spectral analyses on EEG segments recorded at each participant’s most ambiguous SOA (i.e., near the individual PSS). In line with Kristofferson (1967), IAF estimated over occipito-parietal electrodes displayed a robust correlation with the steepness parameter of the logistic function fit to each participant’s audiovisual performance, a pattern indicating that faster IAF tracked sharper cross-modal synchrony discrimination and, by extension, narrower TBWs (Bastiaansen et al., 2020).

Beyond SJ, TOJ tasks have provided additional insights into fine-grained temporal mechanics that orchestrate perception across senses. Here, however, evidence for a causal role played by alpha rhythmic pace in audiovisual perception remains inconclusive. In the first experimental work of this kind (Grabot et al., 2017), electrophysiological data were recorded from participants performing an individually-titrated TOJ task (i.e., SOAs within the JND, roughly centered around the PSS), and prestimulus alpha-band activity was decomposed into power, phase and frequency peak (i.e., IAF) measures. While a significant difference in alpha power fluctuations was uncovered as a function of response type (correct vs incorrect), the authors reported null results for the relationship between IAF and both JND and PSS estimates (Grabot et al., 2017). In a subsequent study, each participant’s JND was derived from TOJ performance across SOAs ranging from -350 ms and +350 ms (London et al., 2022). Trial-by-trial fluctuations in alpha power and frequency were linked to trial-by-trial psychometric performance using a jackknife-based statistical procedure. Result showed a robust correlation between prestimulus posterior alpha power and JND (i.e., the lower, the narrower the JND), whereas associations between JND both alpha peak and instantaneous frequency (i.e., two distinct indices of on-task IAF) did not survive cluster-based correction (London et al., 2022).

Where, then, does the SIFI stand in this wider evidential milieu? Are extra-flash illusory misperceptions the phenomenal endpoint of an electrocortical parsing mechanism that tunes observers’ visuo-temporal sensitivity to alpha-paced windows of excitability? This hypothesis was first tested in what arguably is a foundational paper in the field, which harnessed a two-fold experimental design (Cecere et al., 2015). In the first, correlational study, healthy participants were asked to report how many flashes they perceived (i.e., one vs two) at a SIFI task under a DFI regime where (unbeknownst to them) two tones always co-occurred with one (and only one) flash at SOAs ranging from 36 to 204 ms (in steps of 12 ms), while EEG was recorded throughout. Each participant’s behavioral

performance, quantified as extra-flash illusion rates across inter-tone delays, was fit to a sigmoid function to derive the associated inflection point (i.e., taken as a compact proxy for the individual's TBW). Spectral decomposition of alpha-band EEG activity was then implemented to extract IAF estimates across the entire electrode array. Critically, brain and behavior (i.e., IAF and TBWs) showed a robust correlation that peaked over occipital electrodes, consistent with the notion that alpha rhythms pace sets windows of cortical excitability within which cross-modal signals are more likely to be integrated, to the point of “parsing” a single visual transient into multiple percepts as a function of tone numerosity (Cecere et al., 2015). To better detail this assumption, the second study introduced a causal lever. A subset of participants returned to perform the same SIFI-DFI paradigm under three stimulation conditions in which occipital tACS was delivered during task completion. Leveraging each participant's IAF estimates computed in the previous experimental routine, the authors administered individually-tailored entrainment protocols at IAF-2 Hz, IAF, and IAF+2 Hz in a within-subject design. Results strikingly confirmed the working hypotheses: pulling IAF upward or downward engendered corresponding shifts in the psychometric inflection points: faster and slower IAF, respectively, shrank and dilated the individual's TBW (Cecere et al., 2015). In brief, not only visual perception (Samaha & Postle, 2015; VanRullen, 2016), but also audiovisual integration (and the misperceptions thereof) seemed to unfold within alpha-paced temporal cycles (figure 3.6). The breadth of such conclusions was further assayed in a follow-up study using the very same cross-SOA SIFI paradigm (alongside a tactile analogue of the illusion) combined with EEG recordings, which replicated the aforementioned strong association between occipital IAF and temporal windows of illusion at both sensor and source levels (Cooke et al., 2019). These claims were additionally probed in a coeval work that adopted high-density EEG recordings under a SIFI-DFI regime, albeit with a fixed, non-titrated, 57-ms inter-tone delay (Keil & Senkowski, 2017). The key findings closely echoed Cecere et al. (2015), namely IAF localized to calcarine and occipital regions negatively correlated with illusion rates such that slower alpha pacing over these sites was associated with stronger audiovisual capture (i.e., more extra-flash percepts), and vice versa (Keil & Senkowski, 2017).

Of note, the sampling machinery which IAF should preside over appears specific to temporal acuity within perceptual binding constraints, rather than serving as a general-purpose control knob for timing as a broader cognitive faculty. This was shown in later paper where EEG was recorded while participant completed the cross-SOA SIFI paradigm from Cecere et al. (2015), alongside a filled duration illusion task. Here, parieto-occipital IAF reliably predicted the size of the illusory TBWs but not individual differences in time perception (Venskuskus & Hughes, 2021). Along this line of reasoning, different flavours of sound-induced visual misperceptions seem constrained by distinct oscillatory cycles. In this regard, a frequency-specific functional dissociation emerged when the rhythmic

sampling hypothesis was tested using a fully-crossed orthogonal design combining flashes (0-2) and beeps (0-2) at a fixed 50-ms SOA: prestimulus beta speed was associated with the fusion variant of the SIFI (i.e., faster beta rhythms linked to increased “one flash” reports in 2F1S trials), whereas (as anticipated) prestimulus IAF tracked individual’s susceptibility to the illusion (Y. Noguchi, 2022). Together, these findings smoothly converge toward the support of an intrinsic oscillator whose pace dictates the temporal resolution of audiovisual perception through periodic fluctuations in cortical excitability (Cecere et al., 2015; Samaha & Romei, 2024; VanRullen, 2016).

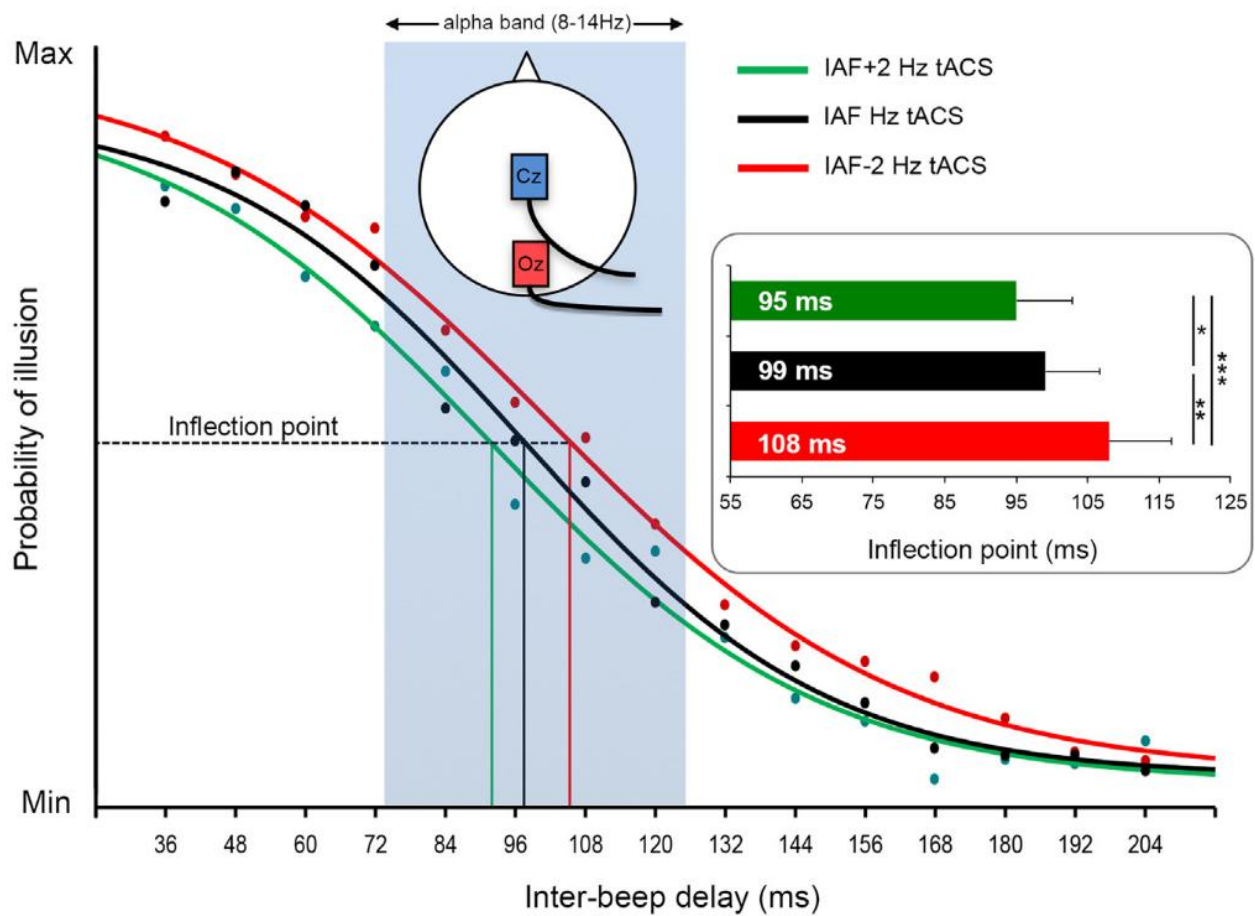


Figure 3.6 Modulation of audiovisual temporal binding by IAF (Cecere et al., 2015). Psychometric functions relating inter-beep delay to illusion probability are shown under transcranial alternating current stimulation (tACS) delivered at IAF, IAF + 2 Hz, and IAF – 2 Hz over occipital cortex. Shifting stimulation frequency systematically displaced the inflection point of the function, such that faster stimulation compressed, and slower stimulation expanded, the temporal window supporting illusory perception.

However, such convergence (though appealing in and all itself) sits uneasily with evidence from unisensory visual tasks under closer scrutiny. How can we reconcile that faster alpha cycles promote finer temporal scanning and more veridical “two-flash” percepts at the two-flash fusion paradigm (Samaha & Postle, 2015), whereas more illusory “two-flash” percepts at the SIFI have been associated with slower alpha rhythms and coarser temporal parsing (Cecere et al., 2015)? This pattern of results

invites a mechanistic dissociation well-framed in causal inference terms: does IAF actually sharpen the temporal precision of sensory representations (i.e., finer bottom-up arbitration between integration and segregation, shifting reliability-weighting toward vision in audiovisual settings), or rather, does alpha speed tune a binding prior (i.e., top-down tendency toward integration)? Mapped onto SDT metrics, a “precision” mechanism should manifest as a change in perceptual sensitivity (i.e., better separation between internal representations evoked by one vs two flashes), whereas a “binding” mechanism as shift in response criterion (greater propensity to report an integrated percept under ambiguous sensory evidence). Of note, much of the evidence reviewed so far has not directly adjudicated between these alternatives, because standard psychometric characterizations of the TBW did not allow to neatly disentangle the respective contributions of perceptual sensitivity and decisional bias to audiovisual performance, nor did they clarify the extent to which IAF may causally shape either component. To resolve these controversies, a multi-day study combining EEG and psychophysics was conducted (Buergers & Noppeney, 2022). Twenty participants were asked to perform three experiments across a five days testing schedule, each presenting 1 or 2 flashes in three distinct sensory contexts (0, 1, or 2 beeps): a two-interval forced choice (2IFC) task to obtain bias-resistant thresholds; a yes–no (2AFC) SOAs task (25–225 ms) whose data were fit to a logistic curve in order to extract the function’s inflection point (i.e., a proxy for the individual TBW); a yes–no (2AFC) individually-titrated threshold task (balanced “1” vs “2” reports per each condition) to extract SDT metrics. EEG was recorded during the 2AFC tasks and at rest (eyes-closed), to compute trial-wise instantaneous alpha frequency (i.e., state-alpha), on-task alpha peaks and power across the prestimulus time window, as well as resting-state alpha frequency peaks (trait-alpha). State-level alpha estimates were binned into terciles (high, medium, low instantaneous alpha frequency and, separately, alpha power), and SDT-derived measures (from either the 2AFC threshold task, and intermediate delays at the 2AFC SOA task) were contrasted across bins using time-resolved cluster-based permutation tests over the prestimulus interval, complemented by time-collapsed analyses to yield a single robust within-subject effect per condition. Trait-level alpha, quantified via peak alpha frequency, was instead related to psychometric TBW and 2IFC estimates using between-subject correlation analyses (Buergers & Noppeney, 2022). Behaviorally, sound-induced fission and fusion variants clearly emerged: the former was accompanied by reduced sensitivity and a more liberal criterion, whereas a shift toward a more conservative bias and little sensitivity changes were observed when the latter occurred. However, the crucial point revolved around electrophysiological data. Across tasks and sensory contexts, prestimulus alpha frequency showed no reliable within-subjects effects neither on sensitivity nor on criterion bias. Similarly, trait-alpha peak frequency did not correlate with individuals TBWs nor with threshold estimates (Buergers & Noppeney, 2022). The authors offered a rather critical

characterization of these results: under a rigorous, fully-crossed psychophysical design, both state- and trait-alpha frequency did not appear among the key determinants of temporal parsing or binding within and across senses. Challenging overly stringent oscillatory interpretations of the discrete sampling hypothesis of perception (Cecere et al., 2015; Samaha & Postle, 2015; VanRullen, 2016), they reframed the mixed findings favouring this account as arising from factors such as task- and context-dependence and heterogeneity in analytical choices, arguing that any fundamental role for alpha frequency should be established using consistent operational definitions and large-scale, multi-lab replications (Buegers & Noppeney, 2022).

Although these conclusions have been partially disputed by subsequent work using an explicit SDT framework (Y. Noguchi, 2023) or a broader meta-analytic approach (Samaha & Romei, 2024), they nonetheless rekindled momentum around a long-standing question: are SIFI-like misperceptions the price of a rhythmic sampling strategy that parcels cross-modal inputs into discrete, alpha-paced temporal windows weaving conscious perception into a unified, seamless stream?

Project Aims

Taken together, the evidence reviewed so far converges on the SIFI as a useful probe of multisensory misperception and a promising model for interrogating low-level perceptual and electrocortical alterations subsuming positive symptoms and hallucinatory-like experiences across the psychosis continuum.

A first unresolved issue, however, concerns the mechanics that this increased tendency to perceive illusory flashes actually reflects: is it best explained by a genuine degradation in visuo-temporal sensitivity that blurs sensory evidence required for segregating flashes from beeps, or by a shift in decisional strategies that favours cross-modal integration under ambiguity (i.e., a more liberal criterion)? Because many studies quantify SIFI susceptibility through psychometric indices alone, these alternatives are often confounded, constraining the interpretability and translational value of SIFI-like behavioral phenotypes across the psychosis continuum.

A second, intertwined question pertains to the neurophysiological operations that may scaffold these psychophysical signatures. Posterior alpha rhythms, most notably their cycling frequency, have been often implicated in perceptual sampling and the temporal parsing of sensory evidence. If alpha speed sets an observer's temporal resolution, then faster versus slower rhythms (i.e., the latter often reported across SCZ-spectrum disorders) should narrow versus widen audiovisual binding windows, by increasing versus decreasing perceptual sensitivity, thereby boosting the balance between segregation or integration of closely timed events. Although recently challenged, this account raises the possibility that individual differences in alpha pace may constitute an endophenotype governing visuo-temporal precision and/or response bias in multisensory contexts, with trait variations in schizotypy putatively modulating how this oscillatory index shapes behavior.

The present thesis tests this mechanistic chain across four studies that combine clinimetrics, psychophysics, electrophysiology, and neurostimulation. First (Chapter 4), we ask whether poorer audiovisual performance (i.e., enlarged TBWs) in individuals high in schizotypy is rooted in diminished perceptual sensitivity rather than a more liberal response bias, and quantify the extent to which positive-like schizotypal sub-traits predict each component. Second (Chapter 5), we critically synthesize the clinical EEG literature to identify which alpha-band alterations are most reliably observed in SCZ-spectrum disorders, motivating posterior IAF slowing as a plausible biomarker target for causal interrogation. Third (Chapter 6), we conduct a feasibility study to establish that alpha-tuned rhTMS (a protocol known to entrain oscillatory activity) does not artifactually influence SIFI occurrence via unavoidable acoustic and somatosensory co-stimulation, ensuring that subsequent effects can be attributed to neural modulation rather than peripheral confounds. Finally (Chapter 7),

we harness rhTMS paired with online EEG recording to causally up- and down-shift the cycling frequency of posterior alpha rhythms in participants screened for schizotypal traits, while they perform a near-threshold modified SIFI task designed to pull apart temporal sensitivity from response bias. This final study directly tests whether manipulating alpha speed engenders predictable changes in perceptual sensitivity and/or decisional bias, and whether schizotypal sub-traits gate these effects. Overall, these studies aim to move toward a mechanistic account of multisensory alterations in individuals at risk of psychosis, clarifying whether alpha speed functions as an oscillatory endophenotype scaffolding the sensitivity–bias trade-offs that shape audiovisual misperceptions and positive-like sub-traits.

Chapter 4: Positive Sub-Traits and Coarser Temporal Sensitivity Dilate Audiovisual Binding Windows along the Schizotypal Continuum

4.1 Introduction

Over a decade has elapsed since the National Institute for Mental Health first call for a paradigm shift toward pathophysiology-informed diagnoses and interventions in the field of psychiatry (Insel et al., 2010). A key recommendation for this transition to occur was to accommodate insights from genomics, neuroimaging, and cognitive sciences, within a mechanistic framework expanding upon descriptive symptomatology into a pathogenetic account of psychiatric illness (Cuthbert, 2014; Insel et al., 2010). Consistently, biobehavioral markers have progressively surfaced as powerful transdiagnostic tools to devise novel classification routines that anchored psychopathology into a wider spectrum of brain functioning variations (Cuthbert, 2014). Such translational heuristics compel a departure from conventional nosology toward diagnostic models recasting symptoms as dimensionally-arrayed across the population (Cuthbert, 2014), and mental disorders as poles along a seamless continuum ranging from adaptive to dysfunctional behavior (Krueger & Eaton, 2010). The tenability of this proposition has gained growing support within the domain of psychosis-like syndromes and, more broadly, schizophrenia (SCZ) spectrum disorders (Allardyce et al., 2007; Johns & Van Os, 2001).

While SCZ biosignatures remain elusive despite extensive research spanning molecular genetics, neurochemical signalling, structural and functional brain anatomy (Ettinger et al., 2014; Nelson et al., 2013), clinical phenomenology is suggestive of temporal, functional and population continua across the psychotic spectrum (Ettinger et al., 2014). The case for SCZ as a fully dimensional phenotype has been further buttressed by heritability studies, as well as perceptual, cognitive and motor tasks (Ettinger et al., 2014; Johns & Van Os, 2001; Nelson et al., 2013). Rather than a strictly binary construct, SCZ would thus display trait-like features, graded across the general population: absent (or nearly-absent) in healthy individuals, and markedly expressed in patients suffering from this disorder (Cochrane et al., 2012). In between, neurocognitive patterns consistent with a schizotypal profile rank among the closest in nosology to SCZ, portending a greater risk of psychosis onset (Cochrane et al., 2012; P. Grant et al., 2018). Albeit the long-standing recognition of schizotypal personality disorder, broad consensus holds that subclinical schizotypal traits can be witnessed in the healthy population (Claridge et al., 1996; Mohr & Claridge, 2015; H. Noguchi et al., 2008), clustered into a trichotomic structure that maps onto SCZ core symptoms (Raine, 2006). Blunted socio-affective functioning, along

with eccentric behavior and disorganized speech (Raine, 1991), indeed mirrors with high fidelity many of SCZ core diagnostic criteria, although the sharpest resemblance has been reported in the cognitive and perceptual domains (Johns & Van Os, 2001). Odd beliefs and anomalous perceptual experiences are arguably hallmark features of schizotypal personality, which in turn can be traced to SCZ first-rank symptoms such as delusions and hallucinations (Soares-Weiser et al., 2015). As for hallucinations and bizarre perceptual experiences, a large body of work locates their computational source early in the perceptual hierarchy, where low-level integration circuitry falters, misweighting noisy sensory inputs (Butler et al., 2008; Fletcher & Frith, 2009; Javitt, 2009a, 2009b; Waters et al., 2012).

In this regard, cross-modal paradigms offer a privileged route into the altered mechanics prompting positive-like phenomena. Firstly because we inhabit an inherently multisensory world that constantly saturates our sensorium with streams of data, and this line of research stands as a well-suited and ecological probe of how this information is gracefully pooled across sensory channels (Noppeney, 2021). Moreover, accommodating modality-diverse signals into a unified representation poses our nervous system a far greater computational challenge than solely unimodal perception (Stein & Stanford, 2008), thereby foregrounding latent liabilities otherwise overlooked by unisensory assays (Wallace et al., 2020; Wallace & Stevenson, 2014). A methodological corridor for cross-modal inquiries into the psychosis spectrum has been successfully carved out through audiovisual tasks. Evidence is suggestive of impaired visuo-acoustic abilities in participants suffering from SCZ (de Gelder et al., 2005; Ross et al., 2007). These results have been shown to depend on the degree of sensitivity to stimuli asynchrony, known as *temporal binding window* (TBW; Vroomen & Keetels, 2010). Coarser cross-modal acuity entails larger TBWs and a higher likelihood of integrating temporally misaligned signals (Wallace & Stevenson, 2014), a pattern frequently reported in both healthy individuals displaying high schizotypal traits (HST) and SCZ patients, as compared to controls (Borgolte et al., 2024; Foucher et al., 2007; S. Lin et al., 2025; Marsicano et al., 2022; Stevenson et al., 2017; H. Zhou et al., 2022). Of note, the severity of psychotic symptoms, or positive schizotypal sub-traits, emerged as key determinants of perceptual tolerance to stimulus onset asynchrony (SOA; the time lag between the onset of visual and acoustic stimuli): the greater, the longer the SOAs required to match controls-level binding performance, and the wider the TBWs (Amadeo et al., 2024; Borgolte et al., 2024; Marsicano et al., 2022; Stevenson et al., 2017). An even more informative strategy to characterize this relationship has been to fine-tune the temporal and sensory properties of audiovisual stimulation in order to instantiate illusion-inducing multisensory regimes (Shams & Kim, 2010). Well-established instances of such an approach involved the McGurk effect (McGurk & Macdonald, 1976), the bounce-stream illusion (Sekuler et al., 1997), and the ventriloquist effect (Thurlow & Jack, 1973), each showing defective integration mechanisms along the SCZ spectrum (de Gelder et al., 2003;

Szycik et al., 2009; Pearl et al., 2009; Tschacher & Bergomi, 2011; Lee & Kim, 2021; Zvyagintsev et al., 2017; although in HST see Muller et al., 2020). Chief among these paradigms is, however, the Sound-Induced Flash Illusion (SIFI; Shams et al., 2000).

In the native version of the SIFI, paired acoustic tones, coupled with a (single) flashing visual stimulus, misled observers into perceiving an additional (illusory) flash (Shams et al., 2000, 2002). Widely replicated across studies (see Hirst et al., 2020 for a review), this phenomenon appears stable across time (Odegaard & Shams, 2016), refractory to feedback training (Rosenthal et al., 2009) and certain neurostimulation protocols (Bertaccini et al., 2023), while also extending to visuo-tactile interactions (Cooke et al., 2019; Violentyev et al., 2005). Beyond providing a further and perhaps elegant illustration of the way audition might bias conscious visual perception, the contingency of the SIFI on SOAs around 100 ms (Cecere et al., 2015; Shams et al., 2000) has invited many experimental questions regarding the putative interindividual factors prompting this cross-modal illusion, some of which addressed to the SCZ domain. Empirical answers to the issue align with prior works on audiovisual integration, insofar as proneness to positive-like symptoms robustly predicted a higher susceptibility to the SIFI and broader TBWs than controls, either in SCZ patients or HST individuals (Haß et al., 2017; Ferri et al., 2018). Under bottom-up computational accounts of perceptual aberrations in psychosis (Butler et al., 2008; Javitt, 2009b), these findings uphold the notion that degraded performance in illusion-prone individuals might result from coarser visual precision, rather than an over-reliance on audition-conveyed sensory priors (Stevenson et al., 2012). Enlarged TBWs should then represent the psychometric readout of temporal sensitivity deficits, driven by a common dimensional endophenotype responsible for some of the clinical and perceptual signatures witnessed within the psychosis continuum (H. Zhou et al., 2018). Concerning the SIFI, broad windows of integration are well compatible with looser decision-making profiles more likely to misbind asynchronous cues, and split a lone visual transient into two stimuli, provided that SOAs range sits inside said profiles' TBWs (Hirst et al., 2020; Stevenson et al., 2012; Cecere et al., 2015).

As far as these pieces of evidence fuel a mechanistic account rooting hallucinatory-like experiences in low-level processing impairments of incoming sensory signals (Javitt, 2009a; Stevenson et al., 2012), some recent findings challenge the stance that SIFI proneness should be due to reduced audiovisual sensitivity. While a study probing the illusion susceptibility in SCZ patients and healthy controls using a fixed-SOA approach yielded inconclusive behavioral results (Balz et al., 2016), inquiries that borrowed bayesian models of perceptual inference either reported no differences in sensory precision between post-acute patients and controls (Rohe et al., 2024), or mixed-evidence suggestive of both increased temporal uncertainty and prior-reliance as pivotal factors underlying higher SIFI rates in HST individuals (Paredes et al., 2025). In this vein, experimental designs leveraging a Signal-

Detection-Theory (i.e., SDT) framework apt to properly disentangle the contribution of audiovisual sensitivity and criterion bias failed as well in replicating patterns of higher proneness to the illusion in outpatients diagnosed with SCZ (Vanes et al., 2018). In the current work, we seek to reconcile these discrepancies by charting the psychophysical fingerprints subsuming increased SIFI susceptibility in individuals falling midway along the SCZ continuum. Can they be retrieved in lower signal-to-noise ratios resulting from poor temporal sensitivity, rather than the adoption of maladaptive response criteria due to an over-reliance on auditory priors? Further, do such alterations scale with the severity of positive symptoms? We addressed these questions by recruiting a sample of healthy participants grouped as a function of their schizotypal traits, and asked to perform a modified version of the SIFI (i.e., mSIFI). SOAs swapping and the number of flashes per trial were manipulated in order to assay the behavioral outcomes of the task through a hybrid approach that merged SDT with psychometric fitting, weaving together conventional sensitivity metrics and temporal windows of audiovisual integration.

4.2 Methods

4.2.1 Participants

892 healthy individuals were screened to assess their schizotypal traits. From this database, a total of 54 participants (37 females, mean age: *24.54 years $\pm$.73 Standard Error of Mean, [S.E.M.]*) were recruited for further testing. All participants reported normal or corrected-to-normal vision, normal hearing, and no history of substance abuse or other (neuro)psychiatric disorders. Each participant provided written informed consent prior to both the personality screening and the experimental session, and all were naïve to the purpose of the study. Sample size estimation was performed via G*Power 3.1 software (alpha level = 0.05, power = 0.80; Faul et al., 2007).

4.2.2 Procedure

Upon schizotypal traits screening, the database sample was sorted into quintiles based on scores at the Schizotypal Personality Questionnaire (SPQ; Raine, 1991). Only survey respondents whose SPQ scores fell within the lowest and highest quintiles of the resulting distribution were classified as, respectively, low- and high-schizotypy traits (i.e., LST and HST), and contacted for further testing (Ferri et al., 2018), which took place at the Center for Studies and Research in Cognitive Neuroscience in Cesena (Italy). LST and HST individuals willing to participate in the experimental session were

then carefully instructed about the task procedure, after which they were asked to perform a modified version of the SIFI paradigm where, besides canonical 1 flash 2 sounds trials (1F2S), 2 flashes 2 sounds trials (2F2S) also occurred. At the end of the session, participants were debriefed about the scope of the study. Of note, audiovisual performances associated with a poor fitting quality (i.e., $R^2 < .5$ in both the psychometric fitting procedures adopted; Quinn et al., 2023) were deemed unreliable (see *Methods* section), and resulted in 2 participants per group being discarded from the analyses, leading to a final sample size of 50 individuals (i.e., 25 per group).

4.2.2.1 Schizotypal Traits Screening and Trait-based Grouping

Schizotypal traits screening was performed via Qualtrics (an online web-based data collection system) using the Italian version of the Schizotypal Personality Questionnaire (Raine, 1991). This instrument comprises 74 items requiring binary responses (e.g., *Yes* vs *No*: all items endorsed *Yes* are scored 1). SPQ items assess behaviors, thoughts, and attitudes typically associated with schizotypal personality. The 74 items are also factored into 9 subscales (e.g., Odd or Eccentric Behavior, Social Anxiety, Ideas of Reference, Suspiciousness, etc.), reflecting behavioral and cognitive–perceptual clusters described in the DSM-5. The broader sample of 892 individuals exhibited a mean SPQ score of $20.80 \pm .43$, the distribution of which was quantile-binned, returning as cut-off parameters for the first and last quintiles of the distribution, respectively, SPQ scores of 10 and 31 (figure 4.1).

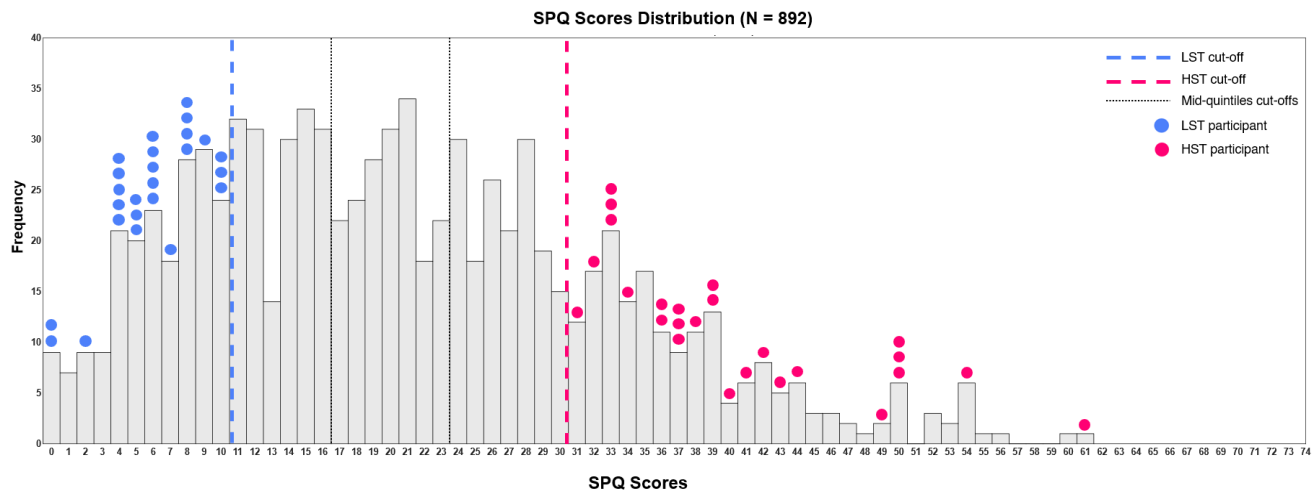


Figure 4.1 Histogram of SPQ total scores from the screening sample (N=892) reached via Qualtrics. The x-axis shows SPQ score bins; the y-axis shows frequency. Vertical dashed lines mark the lower- (blue) and upper-quintile (magenta) cutoffs; dotted lines indicate the intermediate quintiles. Overlaid dots above each bin denote how many participants from that bin entered the final groups (LST, blue; HST, magenta).

As such, subjects displaying SPQ scores ≤ 10 were rated as LST, while those scoring ≥ 31 as HST. The final sample size of 50 participants further recruited for the experimental session, and displaying reliable psychometric fits, was thus arrayed into 2 sub-groups of 25 individuals each, based on whether

they showed low (LST group; median SPQ score: 6) vs high (HST group; median SPQ score: 39) schizotypal traits. Note, however, that as a personality questionnaire, high scores do not indicate a diagnosis of a schizotypal spectrum disorder but rather the presence of schizotypal traits in otherwise healthy individuals.

4.2.2.2 Apparatus and Stimuli

Visual stimuli consisted of solid light-grey [RGB: 136,136,136] disks overlaid on a grey [RGB: 127,127,127] background, subtending 1.5 degrees of visual angle, and displayed at 4.3 degrees of visual angle below a white fixation cross at the center of the screen. Stimuli were presented at 57 cm viewing distance on an 18" CRT monitor (Elo TouchSystems Entuitive, refresh rate 100 Hz, 1024x768 screen resolution) for the brief (flashing) duration of one refresh rate (nominally ~ 10 ms, although way shorter due to CRT phosphor decay rate; Elze, 2010). Auditory stimuli were sinusoidal pure tones (frequency: 5 kHz; sampling rate: 44.1 kHz) lasting 3 ms and delivered via paired stereo speakers located on both sides of the monitor, thus allowing for coincidental spatial perception of visual and auditory stimuli (Ferri et al., 2018). Stimuli presentation and behavioral response recordings were controlled via an automated routine running on a Windows machine equipped with MATLAB 2019b; and the Psychophysics Toolbox (Brainard, 1997).

4.2.2.3 mSIFI Task

To track whether audiovisual performance dynamically changed as a function of the temporal asynchronies between stimuli, we adopted a block-wise task design. Namely, SOAs were held constant within and swapped across all blocks of the mSIFI, meaning that any given block was characterized by unique SOA value, which changed right upon the completion of the block itself. As a result of such fixed-within and swapped-across SOAs manipulation, in every experimental session we employed 23 different SOAs (one per block) spanning from 30 to 250 ms (in steps of 10 ms, one refresh rate) presented in a randomized order across participants (figure 4.2, upper inset), with each block comprising 30 trials for a total of 690 trials per session. Prior to engaging with the block-wise mSIFI, participants performed a brief training session (30 trials) to get acquainted with the experimental protocol. This was followed by a detailed explanation of the task structure, in which it was emphasized that temporal sensitivity recalibration was required after the end of each block, as SOAs (and thus difficulty) randomly changed from one block to another. To that end, self-paced breaks were programmatically inserted at every transition between blocks, to minimize perceptual carryover.

All trials began with a small fixation cross continuously displayed at the center of the screen, which participants were instructed to stare at. After a random temporal lag of 500–1500 ms, a solid-grey disk (i.e., flash) and an acoustic tone (i.e., beep) were simultaneously delivered. While a second auditory tone was always played at a (block-wise) varying SOA from the onset of the first one (1F2S trials), only in half the trials within a given block (i.e., 15 out of 30) a second disk, overlapping with the second auditory stimuli, was presented (2F2S trials). Upon stimuli presentation, participants were asked to promptly report whether they saw 1 vs 2 flashes (i.e. disks), regardless of the number of sounds, by pressing specific key buttons, after which an inter-trial interval of 500 ms followed (figure 4.2, bottom). Overall, including the briefing phase and the training block, each experimental session lasted around 30 minutes. Let it be noted that this task design enabled us to both replicate the perceptual fingerprints of the SIFI (1F2S trials), and compute block-wise SDT metrics via 2F2S trials. Further, we hereby chose to include 2S trials only (rather than 1S or 0S trials) to reduce as much as possible any further sound-induced confound on response criterion.

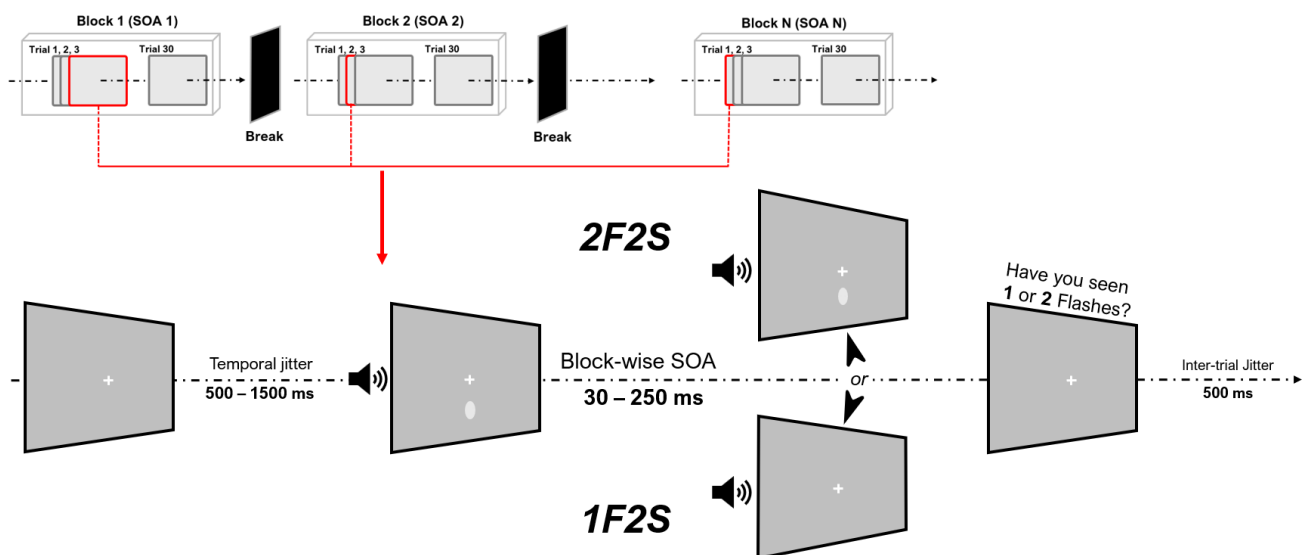


Figure 4.2 mSIFI paradigm. **Top inset)** blockwise task structure: each session comprised 23 blocks (30 trials per block; 15 1F2S, 15 2F2S) with a fixed SOA within a block. Each block ended with a self-paced break to limit perceptual carryover and allow SOAs swapping. **Bottom inset)** Trials structure: a small fixation cross was always displayed at the center of the screen. After a temporal jitter (500–1500 ms), the first audiovisual pair (flash + beep) was presented, followed, after the block-defined SOA (30–250 ms), by either a second beep alone (1F2S) or a second beep paired with a second flash (2F2S). Participants reported how many flashes they perceived, irrespective of the number of beeps. An intertrial interval of 500 ms separated successive trials.

4.2.3 Analyses

4.2.3.1 Behavioral Performance

Perceptual performance was tracked by adopting SDT measurements (Stanislaw & Todorov, 1999). Namely, we classified each individual's response according to an equal variance Gaussian SDT model

where 1-flash trials were treated as noise (catch trials) and 2-flashes trials as signal (target trials). As such, a 2-flashes report was binned, respectively, as a hit in 2F2S trials (i.e., H), and a false alarm in 1F2S trials (i.e., FA). Conversely, a 1-flash report was classified, respectively, as a correct rejection in 1F2S trials, and a miss in 2F2S trials. We performed this classification per each participant, and leveraged these data to evaluate perceptual sensitivity (d'), response bias (c), and error rates (ER) relative to every SOA, as follows:

- *Perceptual Sensitivity (d')* - The difference between z-scored hits and false alarms, according to the formula: $z(H) - z(FA)$, where the former represents the likelihood of reporting 2 flashes in target trials (hits), and the latter the likelihood of reporting 2 flashes in catch trials (false alarms). Larger d' values are indicative of better abilities in disentangling signal from noise, and vice-versa.
- *Response Bias (c)* - The negative half-sum of z-scored hits and false alarms, according to the formula: $-0.5*(z(H) + z(FA))$, where the former represents the likelihood of reporting 2 flashes in target trials (hits), and the latter the likelihood of reporting 2 flashes in catch trials (false alarms). Positive c values are associated with conservative response criteria (less 2-flashes responses as compared to 1-flash responses), while negative c values occur when a liberal response style is adopted (less 1-flash responses as compared to 2-flashes responses).
- *Error Rate (ER)* - The percentage of, respectively, false alarms (2-flashes reports in catch trials, 1F2S) over the total amount of catch trials, and misses (1-flash reports in target trials, 2F2S) over the total amount of target trials.

As a result, every participant was associated with three distinct behavioral indices (d' , c and ER) per each and every SOA of the mSIFI task.

4.2.3.2 Psychometric Fitting

Among our core experimental questions was addressing whether differences in multisensory integration across groups might be attributed to coarser temporal precision in HST individuals, as quantified by both enlarged TBWs and reduced sensitivity in cross-modal signals detection. To this aim, we designed a block-wise task that allowed the implementation of psychometric fitting strategies devised to bridge a long-standing gap between complementary psychophysical approaches to audiovisual integration. Fitting was performed via the Curve Fitting Toolbox in MATLAB 2023b,

using the nonlinear least-squares method leveraging both a robust bisquare function that iteratively down-weights observations with large residuals, and a trust-region optimization algorithm that adapts parameters update step-size based on observed vs. predicted improvement.

We first probed our behavioral data borrowing a TBW perspective on cross-modal integration. Each mSIFI block was partitioned into two equal subset of trials based on the number flashes displayed (15 1F2S trials vs 15 2F2S trials). The resulting 46 SOAs bins (twice the original set) were arbitrarily recoded as signed values (1F2S negative; 2F2S positive), and arrayed from -250 to 250 ms (note that this sign convention does not reflect any physical lead/lag). This procedure was performed on a per-participant basis in order to compute individual *ER* at each SOA bin, and infer the individual TBW width (Stevenson et al., 2012; Vroomen & Keetels, 2010) by modelling this data series via the following gaussian function:

$$f(x) = a \cdot \exp \left(-\frac{1}{2} \left(\frac{x - b}{c + d \cdot (x - b)} \right)^2 \right) + e$$

In which *a* (*ER%*) scales the height (peak amplitude) of the function; *b* (*ms*) centers the peak location with respect to the SOAs axis (*x*-axis); *c* (*ms*) captures the central width (CW) of the gaussian curve (i.e., a standard proxy for the TBW); *d* (*unitless*) models the function skewness (i.e., asymmetry due to the unequal distribution of *ERs* in 1F2S versus 2F2S bins), and *e* (*ER%*) adds a baseline offset.

We next pursued a less conventional, yet informative, routine to relate SDT-derived measurements of temporal precision to psychometric fitting. Namely, the following sigmoid function was fit, on a per-participant basis, to perceptual sensitivity (*d'*) data series (from 30 to 250 ms):

$$f(x) = a + \frac{b}{1 + \exp \left(-\frac{x - c}{d} \right)}$$

Where *a* (*d' units*) identifies the lower asymptote of the function; *b* (*d' units*) sets the inter-asymptotes range (such that *a+b* returns the upper asymptote); *c* (*ms*) captures the inflection point (IP) of the sigmoid curve (i.e., mid-point in between asymptotes, a proxy for the individual temporal sensitivity threshold), and *d* (*ms*) models the slope (i.e., steepness) of the function. As noted above, residuals from each fit were inspected, and participants with poor-quality estimates ($R^2 < .50$) in both psychometric procedures were excluded (Quinn et al., 2023).

In light of the hypotheses the current study was built upon, we primarily focused our analyses on psychometric features bearing information about individuals' audiovisual sensitivity (i.e., CWs of the gaussian curve, and IPs of the sigmoidal function). However, parameters such as skewness, amplitude, and peak location of the gaussian fit, as well as sigmoid slopes, were also examined.

4.2.3.3 Principal Component Analysis and Weighted SPQ Scores

Beyond probing audiovisual temporal precision in LST vs HST participants, we expected that the extent of putative differences across groups could be better accounted for by interindividual variations in positive sub-traits. To test this prediction, we first entered participants' scores on each of the nine SPQ subscales into a Principal Component Analysis (PCA) conducted on the inter-subscale correlation matrix, whose suitability for PCA was assessed via the Kaiser–Meyer–Olkin (KMO) index and Bartlett's test of sphericity. Loadings were orthogonally rotated with Varimax method (Kaiser normalization) to capture latent factors in schizotypal traits. Based on the Kaiser criterion (eigenvalues > 1) and scree plot inspection, orthogonal components accounting for the widest portion of total variance were retained. To compute individual scores weighted according to each retained component, native SPQ subscales scores were then linearly combined with regression-derived component-score weights (CSW) from the rotated solution. Specifically, for each n -th participant and j -th rotated component retained, the weighted SPQ score (wSPQ) was computed as:

$$wSPQ_{n,j} = \sum_{i=1}^I SPQ_{Subscale_{n,i}} \cdot CSW_{i,j}$$

Where I denotes the total number of SPQ subscales, and $CSW_{i,j}$ refers to the signed coefficient representing the contribution of the i -th subscale to the j -th component in the rotated component score matrix. This routine returned, per each individual, as many wSPQ scores as j principal components extracted via PCA (and retained based on scree plot inspection and eigenvalues). Compared with scores on specific SPQ subscales, or trait-based factors (Raine, 1991; Raine et al., 1994), such SPQ composites weight each sub-trait according to how much it contributes to the associated retained component, emphasizing strongly loading features, and down-weighting (rather than not accounting for) weaker ones. Further, this scaling procedure was grounded in a PCA computed on the present sample, and thus more informative of the sub-traits distribution across our experimental cohort.

4.2.4 Statistics

All statistical analyses were conducted using IBM SPSS Statistics 23, Jamovi 2.3.28, RStudio 2024.09.1, and MATLAB 2023b

4.2.4.1 Audiovisual Temporal Sensitivity

Statistical assessment of between-groups differences in temporal sensitivity primarily targeted two psychometric indices: gaussian CWs (*ER* time series; TBW proxy), and the sigmoid IPs (*d'* time series). We used a combination of both frequentist (t-statistics, p-values, and effect sizes reported) and Bayesian (Cauchy prior, $r = .707$; $BF_{10} > 3$ showing evidence for the experimental hypothesis) independent samples t-tests. The same approach was extended to other psychometric parameters such as amplitude, peak location and skewness of the gaussian fits, and slope of the sigmoidal fits.

4.2.4.2 Response Criterion

Along with *ER* and *d'*, SDT computations returned also individual data series relative to response criterion (*c*). However, high interindividual variability made standard psychometric fitting unreliable. To overcome this issue, we applied a null-hypothesis non-parametric cluster-based permutation test, commonly used in electroencephalographic (EEG) analyses (Maris & Oostenveld, 2007), which was implemented as follows. Temporal clusters displaying neighboring significant differences ($p < .05$) were identified via independent samples t-test performed over response bias data (LST vs HST) at each sampling point (SOA). The corresponding *Student's t* were summed and stored as the cluster-level statistic (i.e., cluster mass). Random data permutation was then performed by shuffling participants across groups, to generate surrogate data distributions under the null hypothesis. For each permutation (1000 iterations, $\alpha = .05$, t-threshold = 2.011), the highest cluster-based statistic was retained to derive a reference cluster-level statistic distribution via a Monte Carlo procedure. The proportion of values in this distribution exceeding the empirical (observed) cluster-based statistic served as the cluster-level *p-value* estimate. By means of this permutation procedure, we could circumvent unreliable psychometric fits, while controlling for the family-wise error rate for multiple comparison across SOAs.

4.2.4.3 Receiver-Operating Characteristics (ROC) and Area Under the Curve (AUC)

As a growing body of literature indicates that poorer sensitivity to cross-modal temporal asynchronies may represent a behavioral marker of latent vulnerability across the psychosis continuum, we assessed the ability of each psychophysical index (IP, CW) to discriminate high- vs low-schizotypy group membership (HST = 1, LST = 0) using receiver operating characteristic (ROC) analyses (higher values indicating greater likelihood of HST). For each marker, the area under the ROC curve (AUC) and its 95% confidence interval (C.I.) were estimated using the nonparametric DeLong method (i.e.,

discrimination above chance was tested against $AUC = 0.5$ using two-sided DeLong variance estimates). As a robustness check, AUC C.I. were also obtained via nonparametric bootstrap resampling (5,000 iterations). IP and CW AUCs were then compared using a paired DeLong test. Incremental value was quantified using nested logistic regression models including IP and CW (scaled per 10 ms). Models were compared using likelihood-ratio tests, Akaike's information criterion (AIC), and odds ratios (ORs) with 95% C.I. were reported. Discrimination of the combined model was quantified by computing ROC/AUC on predicted probabilities, and formally contrasted against the best-performing model using paired DeLong tests, as well as bootstrap resampling (5,000 iterations). For an exploratory, decision-oriented interpretation, the Youden J threshold was extracted for each index, and Wilson binomial 95% C.I. associated to sensitivity and specificity were reported. Positive and negative predictive values (PPV/NPV), defined as the probability of belonging to the HST group given a positive test result, and the probability of belonging to the LST group given a negative test result, respectively, were computed at assumed prevalences of 5%, 20%, and 50%.

4.2.4.4 Trait-Behavior Association

To statistically quantify the assumption that cross-modal temporal sensitivity might scale with the severity of positive schizotypal sub-traits at the individual level, we modelled the relationship between audiovisual perceptual metrics and weighted SPQ scores through multivariate multiple linear regression (MMLR). Let Y , X and β_0 be vectors of, respectively, dependent variables, predictors, and intercepts, B the matrix of regression coefficients, and ε be the residual error term, an MMLR models the joint dependence of multiple dependent variables on a common set of predictors as follows:

$$Y = \beta_0 + B \cdot X + \varepsilon$$

Given an N observations (i.e., participants), J predictors, and M dependent variables (DVs), the above equation can be written component-wise as:

$$Y_{m,n} = \beta_{0,m} + \sum_{j=1}^J B_{m,j} \cdot X_{j,n} + \varepsilon_{m,n}$$

Here, $Y_{m,n}$ is the value of the m -th DV for participant n ; $\beta_{0,m}$ is the intercept associated with the m -th DV; $X_{j,n}$ is the value of the j -th predictor for participant n ; $B_{m,j}$ is the regression coefficient linking predictor j to the m -th DV, and $\varepsilon_{m,n}$ is the residual for DV m in participant n , assumed to follow a multivariate normal distribution with unrestricted covariance among DVs. We derived the case-specific form of the above described model by populating the outcome matrix with both our metrics

of temporal sensitivity (i.e., CWs and IP of each participant), as well as including in the predictor matrix as many J vectors as the number of wSPQ scores resulting from PCA decomposition and coefficients scaling, such that:

$$\begin{matrix} CW_n \\ IP_n \end{matrix} = \begin{matrix} \beta_{0,CW} \\ \beta_{0,IP} \end{matrix} + \begin{matrix} \beta_{CW,1} & \dots & \beta_{CW,J} \\ \beta_{IP,1} & \dots & \beta_{IP,J} \end{matrix} \begin{bmatrix} wSPQ_{n,1} \\ \vdots \\ wSPQ_{n,J} \end{bmatrix} + \begin{matrix} \varepsilon_{CW,n} \\ \varepsilon_{IP,n} \end{matrix}$$

This multivariate framework is well suited to simultaneously estimate the unique (i.e., univariate) effects of quasi-orthogonal predictors (here assumed to minimize collinearity due to varimax rotation) on multiple dependent variables, while also capturing their joint influence on the multivariate response space, which accounts for any potential interdependence (i.e., covariance) between DVs. Upon checking model fit (lack-of-fit tests plus *univariate* $R^2 > .13$ for meaningful effect sizes; J. Cohen, 2009), and model diagnostics via studentized residuals to detect per-case misfits ($|t| \geq 3$ for outliers), along with Cook's distance ($D \geq 1$ for problematic observations) to quantify each observation's influence on estimated parameters (R. D. Cook, 1977), we thus tested an additive model (main effect of each wSPQ score resulting from PCA) omitting any interaction between predictors. To ensure robustness against mild deviations from normality, parametric tests were complemented with non-parametric bias-corrected and accelerated (BCa) bootstrap estimates (10000 resamples) to obtain 95% C.I. and two-sides p-values for all parameters.

4.3 Results

Mean and standard error of means are reported via the format *mean* $\pm$ *S.E.M.*, and confidence intervals (*C.I.*) are 95%. When applicable, ranked correlations coefficients (i.e., *Spearman's* ρ) between variables of interest were computed.

4.3.1 Behavioral Metrics

4.3.1.1 Psychometric Fitting

Two participants per group were excluded from further analyses due to $R^2 < 0.5$ across psychometric fits. The remaining 50 participants (25 per group) showed fairly good fits in both the gaussian ($R^2 = 0.78 \pm 0.02$) and sigmoid ($R^2 = 0.73 \pm 0.01$) models, implying reliable parameter estimates.

Led by the assumption that HST individuals should display poorer cross-modal integration abilities than LST controls (Ferri et al., 2018; Marsicano et al., 2022), we first compared CW metrics (i.e., the c parameter of the gaussian fit on ER data, a proxy for TBW) between groups. In line with our predictions, statistics showed higher CWs ($t_{48} = -2.47, p < .05$, *Cohen's d* = $-.699$, $BF_{10} = 3.2$) in HST (51.2 ± 6.46 ms) as compared to LST individuals (34.0 ± 2.65 ms), suggestive of wider TBWs in participants displaying marked schizotypal traits (figure 4.3). Of note, comparisons performed on other gaussian-derived parameters (amplitude, peak location, skewness) did not return any significant difference between groups (all p -values $>.05$) or substantial evidence for group effects (all $BF_{10} < 3$).

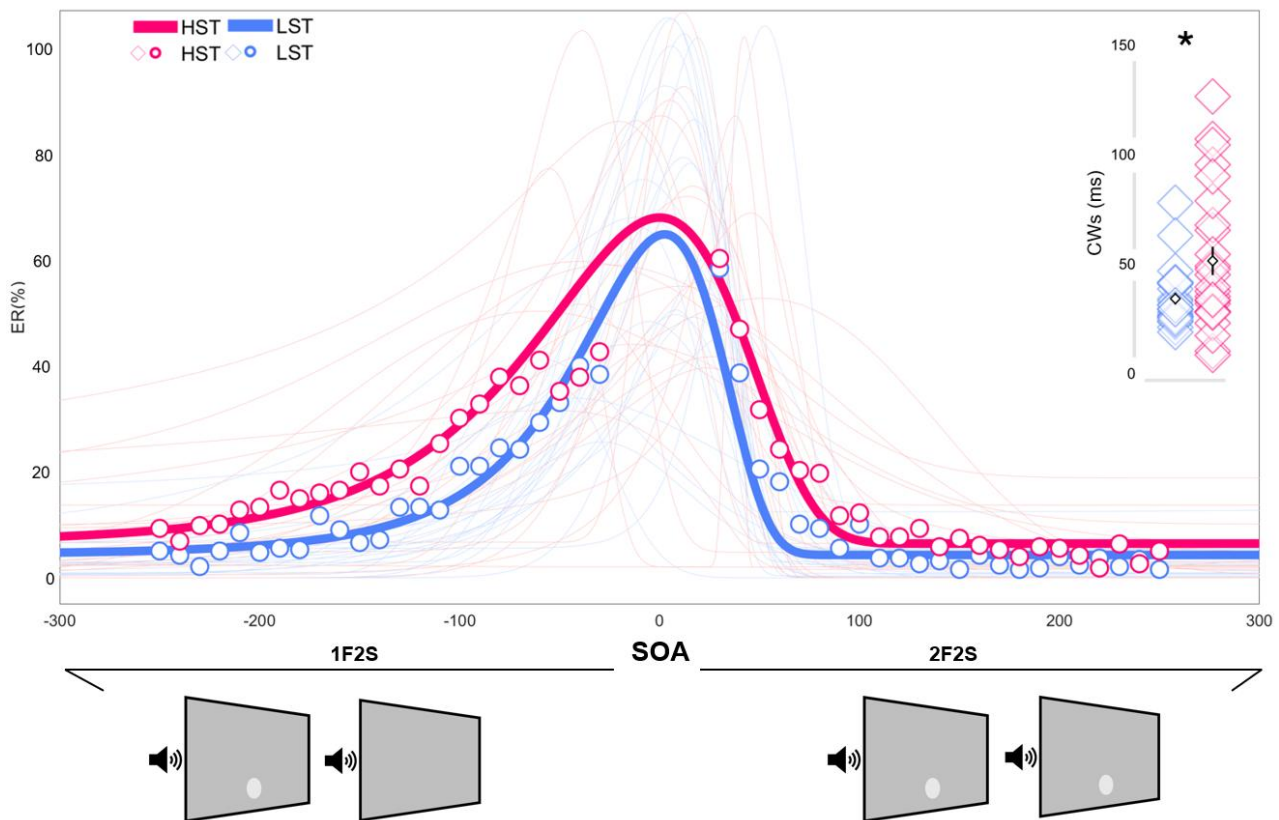


Figure 4.3 Gaussian fits of ER data. SOAs (ms) are displayed on the x-axis, with negative and positive signed values arbitrarily coding 1F2S and 2F2S blocks, respectively. ER (%) is displayed on the y-axis. Color-coded dots show mean ERs for the LST (blue) and HST (magenta) groups at each SOA bin. Color-coded gaussian fits (LST = blue, HST = magenta) are plotted for each participant (faint lines) and for the group average (thick lines). **Top-right inset:** scatterplot showing CW (ms) as a function of group (LST vs HST; y-axis). Black-outlined diamonds and error bars indicate the group mean $\pm$ S.E.M. * $p < .05$.

As altered audiovisual binding in HST participants was hypothesized to result from coarser multisensory precision, we next focused on IPs (i.e., the c parameter of the sigmoid fit on d' data, a proxy for audiovisual sensitivity threshold). Germane to our expectations, the analyses revealed higher IPs ($t_{48} = -3.40, p < .001$, *Cohen's d* = $-.961$, $BF_{10} = 24$) in HST individuals (86.3 ± 6.04 ms) as compared to LST (62.1 ± 3.77), corroborating the assumption of poorer cross-modal signal processing in high schizotypy participants (figure 4.4, a). Conversely, no such difference between groups nor

substantial evidence for group effects were found when comparing slope parameters ($p > .05$; $BF_{10} < 3$) relative to the same sigmoid fitting. To assess the association between parameters that index similar perceptual constructs via different methodological pathways, a cross-metric Spearman correlation between CWs and IPs was performed (figure 4.4, b). Data show a significant and robust positive relationship (Spearman's $\rho = .55$, $p < .001$, $BF_{10} = 2224$), suggesting a high degree of similarity between our two proxies of audiovisual temporal sensitivity (figure 4.4, b). In brief, HST participants display broader TBWs than LST controls, at least partly attributable to reduced temporal sensitivity.

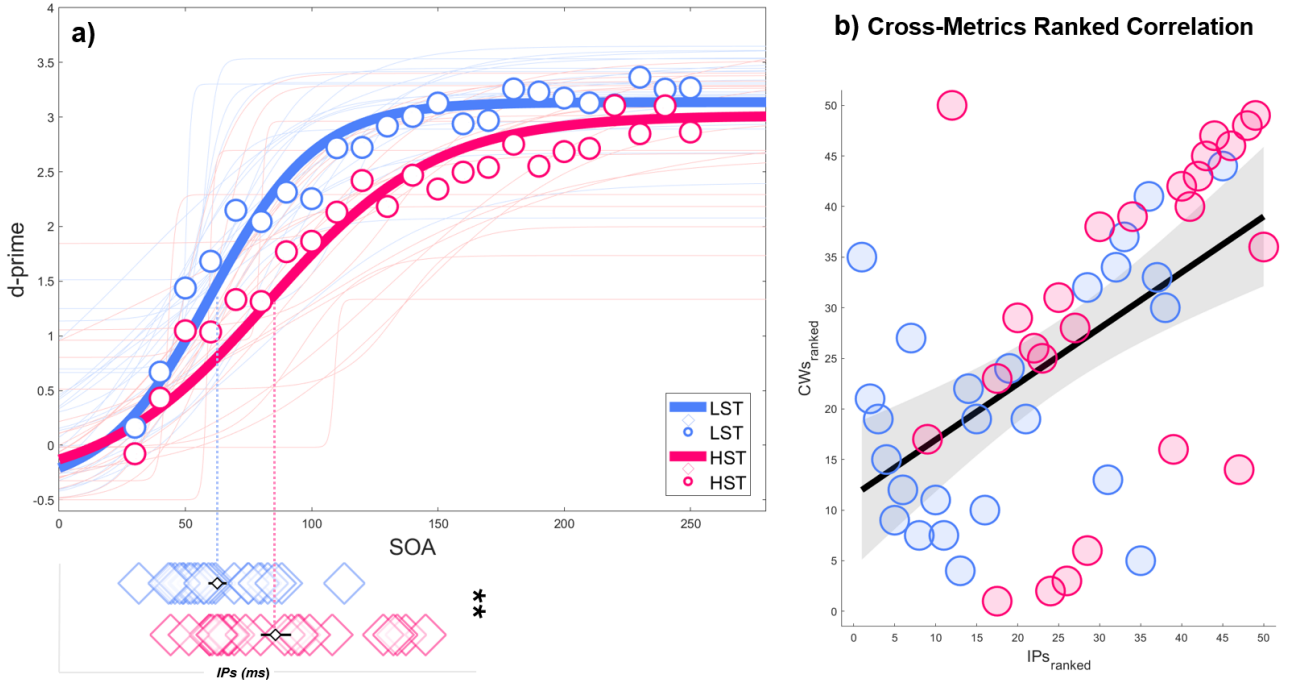


Figure 4.4 a) Sigmoid fits of audiovisual sensitivity data. SOAs (ms) and d' levels are displayed on the x-axis and y-axis, respectively. Color-coded dots show mean d' levels for the LST (blue) and HST (magenta) groups at each SOA bin. Color-coded sigmoid fits (LST = blue, HST = magenta) are plotted for each participant (faint lines) and for the group average (thick lines). **Bottom inset.** Rotated scatterplot showing IP (ms; y-axis) as a function of group (LST vs HST; x-axis). Black-outlined diamonds and error bars indicate the group mean $\pm$ S.E.M. Dotted vertical lines project each group's mean IP onto the midpoint of the corresponding average sigmoid fit. ** $p < .01$. **b)** Scatter plot showing the ranked association between IP (x-axis) and CW (y-axis). The black line and shaded band indicate the fitted trend and its C.I.

4.3.1.2 Response Criterion

Due to high inter-individual variability, we did not endorse a psychometric approach to investigate response criterion patterns. Instead, we performed permutation testing to identify temporal clusters across SOAs differentiating HST from LST individuals. However, no significant cluster detected by this procedure (figure 4.5) survived permutation-based correction (*observed cluster mass* = 2.21; *surrogate threshold* = 4.92). When comparing overall response criteria (averaged across SOAs), no significant difference ($p > .05$; $BF_{10} < 3$) between groups was found either (fig 4.5, right inset). To

summarize, altered multisensory abilities in HST participant do not appear to be steered by the adoption of auditory-driven maladaptive response criteria

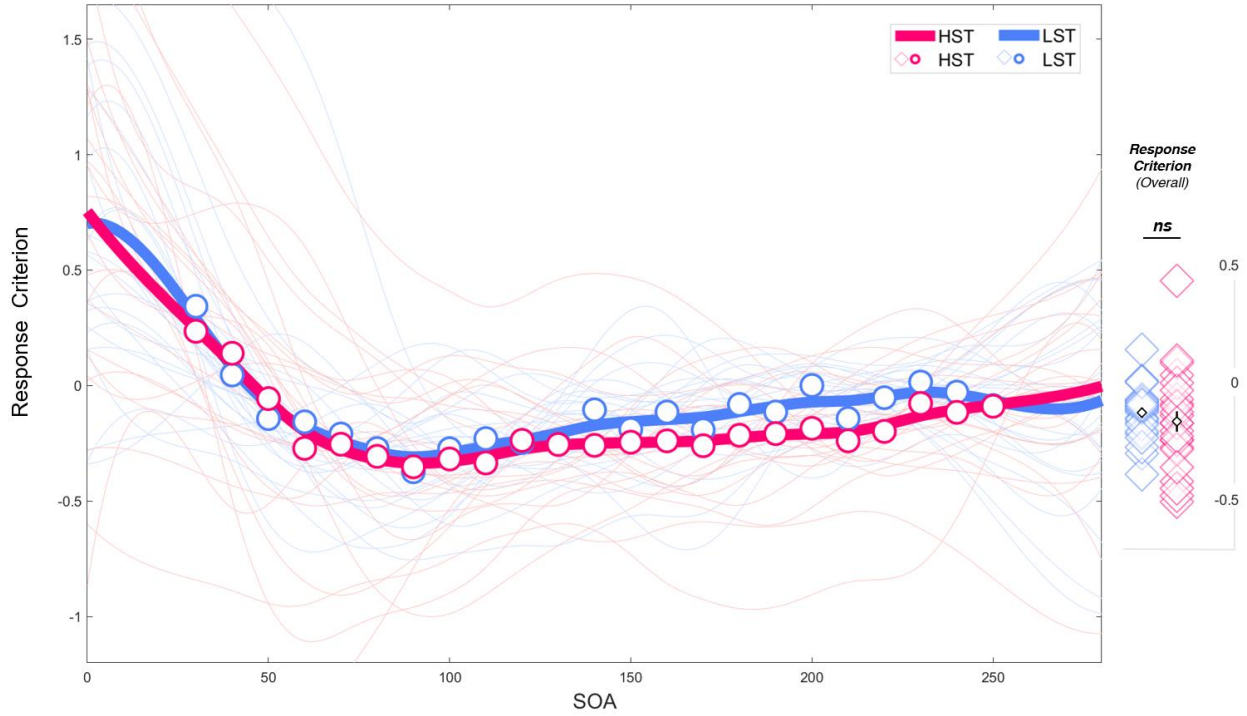


Figure 4.5 Response criterion data. SOAs (ms) and c levels are displayed on the x-axis and y-axis, respectively. Color-coded dots show mean c levels for the LST (blue) and HST (magenta) groups at each SOA bin. Color-coded lines (LST = blue, HST = magenta) are plotted for each participant (faint lines) and for the group average (thick lines). **Right inset.** Scatterplot showing per-participant c levels averaged across SOAs (y-axis) as a function of group (LST vs HST; x-axis). Black-outlined diamonds and error bars indicate the group mean $\pm$ S.E.M. *ns* = no significant group difference.

4.3.1.3 ROC Curves and Discriminative Performance

Across participants, both psychophysical indices showed above-chance discrimination of schizotypy group membership. IP achieved an AUC of .767 ($C.I._{DeLong}$ [.635 .899]), corresponding to discrimination significantly greater than chance ($Z_{DeLong} = 3.97$, $p < .001$). Bootstrap resampling yielded a highly similar AUC interval ($C.I.$ [.626 .885]), supporting the robustness of the estimate. Comparatively, CW yielded a lower AUC of .670 ($C.I._{DeLong}$ [.513 .827]), which remained significantly above chance ($Z_{DeLong} = 2.12$, $p < .05$). Again, bootstrap resampling closely mirrored the DeLong interval ($C.I.$ [.509 .822]). Of note, although IP showed numerically higher discrimination than CW ($\Delta_{AUC} = .097$), the paired DeLong comparison returned no statistically significant difference ($Z_{DeLong} = 1.29$, $p > .05$, $DeLong C.I._{DeLong}$ [-.051 .244]).

Nested logistic regression models tested whether CW provided incremental discriminative information beyond IP. The combined model (i.e., IP+CW) showed above-chance discrimination ($AUC_{COMBINED} = .779$, $Z_{DeLong} = 4.29$, $p < .001$, $C.I._{DeLong}$ [.652 .907], $C.I._{bootstrapped}$ [.640 .893]), although adding CW did not improve model fit relative to IP alone (*likelihood-ratio test*: $\Delta_{DEVIANCE} = .585$, $df = 1$, $p > .05$).

In this combined model, IP remained a significant predictor of group membership ($OR_{10ms} = 1.44$, $p < .05$, $CI [1.06 \ 2.12]$), whereas CW did not ($OR_{10ms} = 1.13$, $p > .05$, $CI [.82 \ 1.61]$). Consistently, discrimination was only marginally higher for the combined model than for IP alone ($\Delta_{AUC} = .012$), and the difference was not significant ($Z_{DeLong} = .55$, $p > .05$, $CI [-.031 \ .055]$). Model parsimony further favoured the IP-only model ($AIC_{IP} = 62.22$, $AIC_{COMBINED} = 63.64$).

As an illustrative, decision-oriented summary of single-marker operating characteristics (rather than a clinic-ready classification rule), Youden's J was used to derive optimal cut-offs for IP and CW (leaving aside the combined model due to its negligible incremental value). For IP estimates, the Youden threshold was 58.75 ms, yielding high sensitivity (.92, *C.I. Wilson* [.75 .98]) but modest specificity (.56, *C.I. Wilson* [.37 .73]). For CW, the Youden threshold was 47.05 ms, showing the opposite profile: lower sensitivity (0.44, *C.I. Wilson* [.27 .63]) but high specificity (.92, *C.I. Wilson* [.75 .98]). Prevalence-dependent predictive values reflected these trade-offs. At a 5% prevalence, PPV remained low for both indices ($IP = .10$, $CW = .22$) while NPV was high ($IP = .99$, $CW = .97$). At 20%, PPV increased ($IP = .34$, $CW = .58$) with NPVs still high ($IP = .97$, $CW = .87$). At 50%, PPV and NPV values corresponded to, respectively, 0.68 and 0.88 for IP, whereas for CW to .85 and .62. Overall, although both IP and CW discriminated HST from LST above chance, IP showed higher discrimination, and their combination added negligible benefit. Notably, IP and CW reflected different error trade-offs: IP favoured sensitivity, whereas CW specificity (figure 4.6).

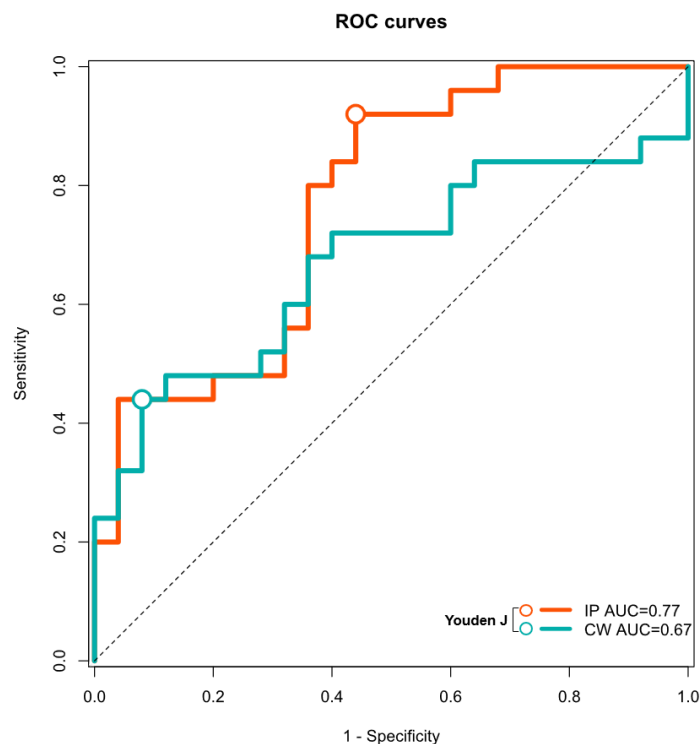


Figure 4.6 ROC curves for IP (orange) and CW (green) discriminating HST vs LST participants. Circles indicate the Youden J operating point for each index. IP showed higher overall discrimination (AUC = 0.77) than CW (AUC = 0.67); the dashed diagonal denotes chance-level discriminative performance.

4.3.2 Trait-Behavior Relationship

4.3.2.1 wSPQ scores

To derive wSPQ scores, a PCA was performed using each participant's SPQ subscale. Sampling adequacy and sphericity assumptions were met ($KMO > .80$; $Bartlett's \chi^2_{36} = 360.13, p < .001$), suggesting adequate common variance and factorability for component extraction. Scree plot inspection and eigenvalues supported retention of a 2-component solution (all *eigenvalues* ≥ 1.195) for the SPQ subscales (figure 4.7, a).

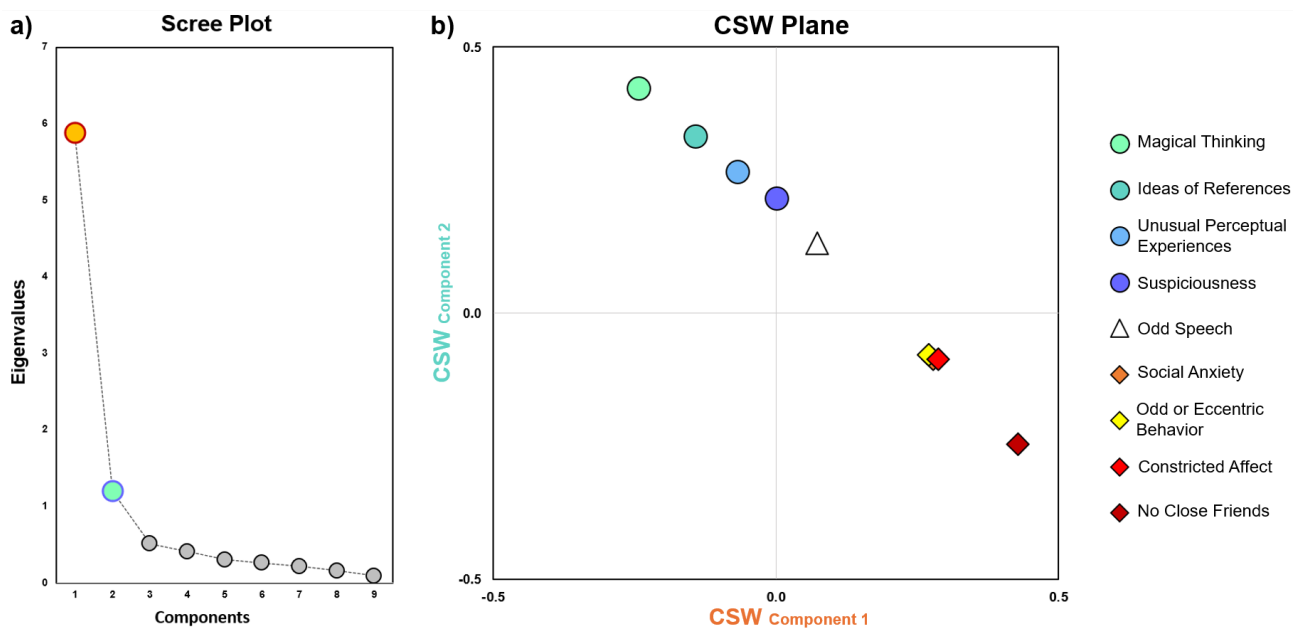


Figure 4.7 PCA results **a)** Scree plot showing the eigenvalues (y-axis) for each extracted component (x-axis). Orange and turquoise markers indicate the two components retained based on the eigenvalue > 1 criterion, and grey markers indicate components discarded (eigenvalues < 1). **b)** CSW plane showing the component score weights assigned to each of the 9 SPQ subscales along the first (x-axis; CSW Component 1) and second (y-axis; CSW Component 2) retained components. Blue-to-turquoise circles and yellow-to-red diamonds correspond to subscales loading on the positive-like and socio-affective dysfunction dimension, respectively.

After Varimax rotation, the two components jointly explained 78.4% of the cumulative variance (39.2% and 39.2%, respectively). The first one assigned positive weights (i.e., CSWs) to subscales tracking poor socio-affective behavior (*No Close Friends* = .429; *Constricted Affect* = .287; *Social Anxiety* = .278; *Eccentric Behavior* = .270), and near-zero or negative weights to subscales indexing positive-like traits (*Magical Thinking* = $-.243$; *Ideas of Reference* = $-.142$). Conversely, the second component showed a complementary pattern: positive weights on subscales assessing positive sub-symptoms (*Magical Thinking* = .423; *Ideas of Reference* = .332; *Unusual Perceptual Experiences* = .265; *Suspiciousness* = .215) and negative weights on social and affective withdrawal (*No Close Friends* = $-.248$; *Social Anxiety* = $-.087$). As such, the components retained after PCA can be roughly

interpreted as carrying information about poor socio-affective functioning (Component 1) and positive-like experiences (Component 2; figure 4.7,b). Linear combination of the associated CSWs with the SPQ subscales produced two wSPQ scores per participant: wSPQ_{SOCIOAFFECTIVE} (overall mean = $2.70 \pm .34$; LST median = 1.15; HST median = 4.21) and wSPQ_{POSITIVE} (overall mean = $1.86 \pm .36$; LST median = -0.08; HST median = 4.52). In short, PCA and coefficient-weighted scores revealed that schizotypy, in our sample, was best captured by two latent dimensions reflecting impaired socio-affective functioning on the one hand, and positive-like subclinical traits on the other. Both the associated weighted SPQ scores were then fed to the MMLR model as predictors.

4.3.2.2 Multivariate Modelling of Trait-Behavior Association

Having established that HST individuals, as compared to LST, exhibit enlarged TBWs due to lesser audiovisual temporal sensitivity, it remained to be detailed whether the severity of positive schizotypal sub-traits might steer or not such differences across groups. To this end, we fit an additive MMLR model on our data to parametrize the extent to which the two main schizotypal dimensions uncovered by PCA (poor socio-affective functioning and positive schizotypal sub-traits) could predict audiovisual performance as assessed through converging metrics such as CW and IP.

Model diagnostics did not flag any problematic cases (all $|t| < 2.86$; all $D < .32$), suggesting all experimental observations could be retained for the main analysis. In this vein, model fit appeared to explain a meaningful share of behavioral variance ($R^2_{CW} = .355$; $R^2_{IP} = .276$), which, coupled with non-significant lack-of-fit tests (all p -values $> .05$), indicated no systematic deviation from a linear additive specification.

Multivariate omnibus tests showed that either wSPQ_{POSITIVE} (Pillai's trace = .367, $F_{2,46} = 13.31$, $p < .001$), and to a lesser extent wSPQ_{SOCIOAFFECTIVE} (Pillai's trace = .157, $F_{2,46} = 4.29$, $p < .05$), affected the joint covariance structure of our audiovisual metrics, implying that both poor socio-affective functioning and positive schizotypal sub-traits predicted a significant portion of shared variance across DVs. Univariate follow-up tests, performed to establish the extent to which any of the predictor(s) shaped each distinct DV, suggested that solely wSPQ_{POSITIVE} reliably predicted both IP ($F_{1,47} = 14.72$, $p < .001$, $\eta^2_p = .239$) and CW ($F_{1,47} = 24.53$, $p < .001$, $\eta^2_p = .343$) patterns, with higher scores on this schizotypy dimension robustly associated with higher IPs ($\beta = 5.15$, BCa C.I. [2.07 8.03], $p_{bootstrapped} < .01$) and broader CWs ($\beta = 5.86$, BCa C.I. [2.47 8.75], $p_{bootstrapped} < .01$), as compared to wSPQ_{SOCIOAFFECTIVE} (all p -values and all $p_{bootstrapped}$ -values $> .05$). To summarize, the additive MMLR model appeared well-suited to adequately parametrize our data, and yielded two key outcomes. First, both positive schizotypal sub-traits and (to a weaker extent) socio-affective dysfunction accounted for

a substantial portion of the variance across CW and IP. Second, only the positive-like schizotypal dimension explained unique variance in each behavioral measure, such that higher positive-like subsymptoms were associated with poorer audiovisual performance (i.e., broader CWs and higher IPs; figure 4.8)

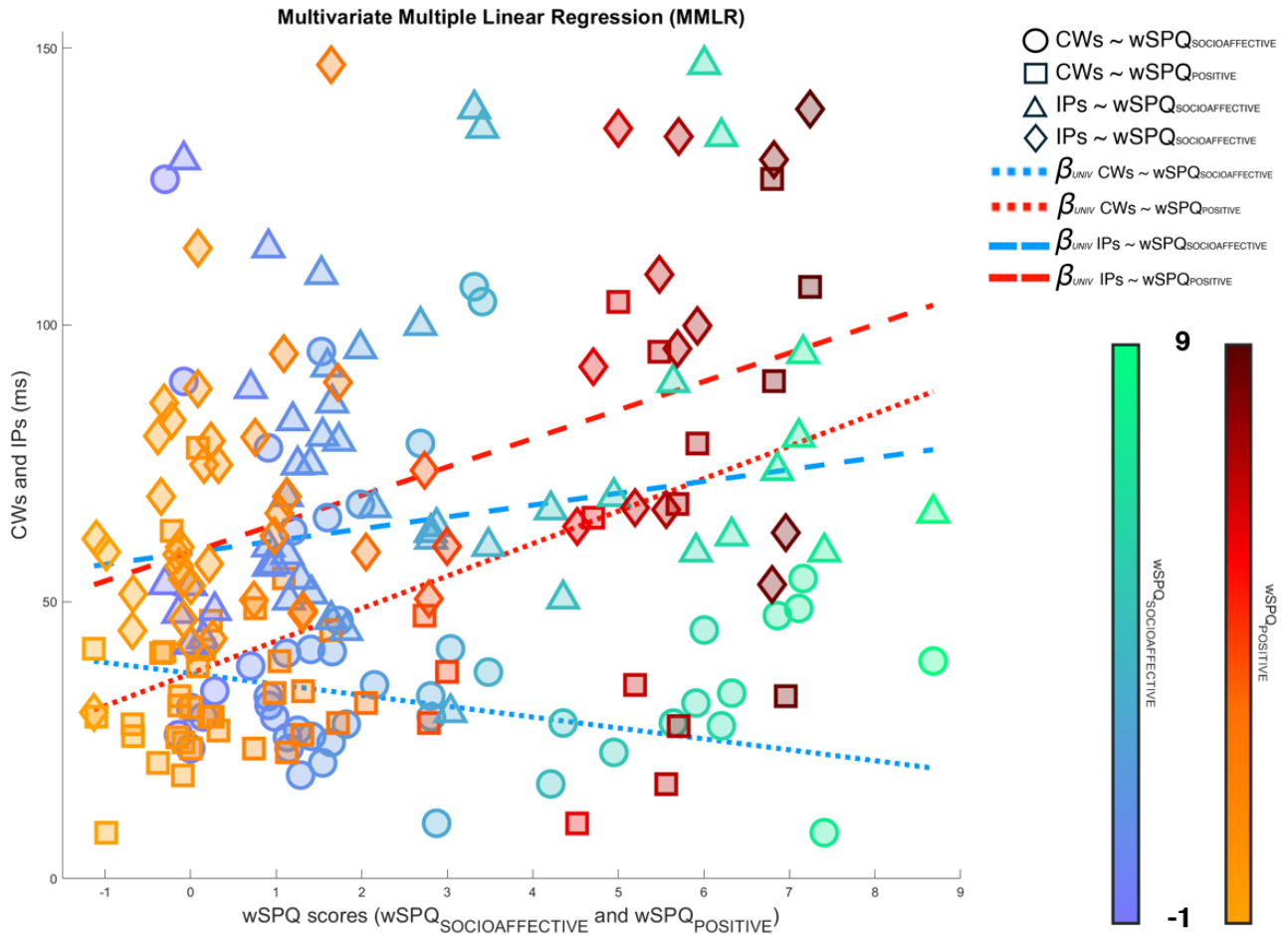


Figure 4.8 MMLR results. The scatterplot shows individual CW and IP values (y-axis, ms) as a function of wSPQ scores indexing socio-affective functioning and positive-like schizotypal traits (x-axis). Circles and squares plot CWs against the socio-affective (wSPQ_{SOCIOAFFECTIVE}) and positive-like (wSPQ_{POSITIVE}) dimensions, respectively. Triangles and diamonds plot IPs against the same two dimensions. Marker color (blue-to-turquoise and orange-to-red) reflects the severity of each dimension from low to high, as indicated by the adjacent color scales. The superimposed regression lines depict the fitted univariate slopes: dotted lines correspond to CWs and dashed lines to IPs; blue lines correspond to the socio-affective dimension and red lines to the positive-like dimension.

4.4 Discussion

Hallucinations sit among the hallmark symptoms in psychosis, the occurrence of which raises clinical concerns for an incipient SCZ presentation. Subclinical precursors of these morbid manifestations, such as unusual perceptual experiences, have been often documented in healthy individuals displaying marked schizotypal traits, consistent with a dimensional account of the SCZ spectrum (Ettinger et al., 2014; Johns & Van Os, 2001; Nelson et al., 2013). Computational models framing these phenomena

as the outcome of early-stage disruptions within the perceptual hierarchy (Butler et al., 2008; Javitt, 2009a) received broad empirical support from studies reporting larger audiovisual TBWs in individuals lying along the upper side of the psychosis continuum (Foucher et al., 2007; Marsicano et al., 2022; H. Zhou et al., 2022). On this line of reasoning, proneness to hallucinations and positive-like schizotypal traits surfaced as the most informative predictors of poorer multisensory abilities (Marsicano et al., 2022; Stevenson et al., 2017). This observation lent momentum to closer scrutiny through experimental analogues of hallucinatory-like experiences, namely illusion-inducing cross-modal paradigms (de Gelder et al., 2003; Pearl et al., 2009; Szycik et al., 2009), of which the SIFI is a flagship example (Shams et al., 2000). As compared to controls, both SCZ patients and HST individuals with a positive symptomatic profile display higher susceptibility to the SIFI and enlarged TBWs (Ferri et al., 2018; Haß et al., 2017), suggestive of a common perceptual liability jointly responsible for hallucination proneness and impaired multisensory processing. This invited a rather mechanistic question: is such liability rooted in coarser temporal precision, or an over-reliance on auditory priors? The current work was set to arbitrate between these accounts. Healthy participants, stratified by schizotypal trait level, completed a SIFI task designed to disentangle the distinct contributions of perceptual sensitivity (d') versus sensory bias (c) to group differences in performance, and parametrize their dependence on positive sub-traits severity.

We first used psychometric modelling to estimate TBW width by fitting to ER data a gaussian function (Stevenson et al., 2012; Wallace et al., 2020) that accommodated the asymmetric error distribution across 1F2S and 2F2S trials. In line with our hypotheses, results showed larger CWs (i.e., our psychometric proxy for TBW) in the HST than LST group (Ferri et al., 2018; Haß et al., 2017; Marsicano et al., 2022; Stevenson et al., 2017). Of note, no other difference across groups was found when comparing parameters assumed to be indexing biased response criteria, such as peak location (Vroomen & Keetels, 2010). In and of itself, this preliminary round of analyses already supports a mechanistic model where impaired cross-modal integration results from defective temporal processing of incoming signals (Ferri et al., 2018; Javitt, 2009a; Stevenson et al., 2012). Wider TBWs imply a lesser precision in detecting stimuli asynchronies, and an increased likelihood of reporting an additional (illusory) flash at larger SOAs (Cecere et al., 2015; Hirst et al., 2020). Here, we replicated previous findings suggestive of schizotypal personality features as among the key drivers in reducing an individual's temporal precision (Ferri et al., 2018; Marsicano et al., 2022).

This led us to SDT-derived metrics of performance computed to directly probe dynamic changes in perceptual sensitivity (d'), and response criterion (c), occurring as a function of experimental group and SOAs. Data distribution across individuals allowed us to fit a sigmoid function to d' temporal series that returned reliable estimates of each individual's IP (i.e., the function's midpoint, serving as

the psychometric proxy for the temporal sensitivity threshold). Crucially, HST participants displayed later IPs as compared with LST, meaning poorer signal-noise segregation at early perceptual stages. Although at odds with some previous studies (Rohe et al., 2024; Vanes et al., 2016), these results trail evidence for disrupted integration of sensory inputs as the mechanistic lever leading to broader TBWs and, ultimately, psychosis-like experiences (Butler & Javitt, 2005; Javitt, 2009b; Stevenson et al., 2017; Wallace & Stevenson, 2014). In HST or SCZ individuals, audiovisual information would thus be routed into perceptual channels idiosyncratically susceptible to noise, leakier in temporal resolution, and more likely to misrepresent the number of flashes occurred, as far as auditory cues fall within a short temporal range (Cecere et al., 2015; Hirst et al., 2020; Javitt, 2009b; Wallace & Stevenson, 2014). The contingency of TBWs on temporal acuity was confirmed by the strong cross-metric association between CWs and IPs, coupled with no substantial group difference in response criterion. The latter null result aligns with the notion that the SIFI, per se, arises from degraded sensory precision rather than an overweight of auditory priors (Mishra et al., 2007; Rohe & Noppeney, 2015; Shams et al., 2002; and see Watkins et al., 2006 for early retinotopic activations in V1), a mechanism abnormally inflated across the SCZ spectrum (Rohe et al., 2024; Stevenson et al., 2017).

Examined through the lens of ROC analysis, these patterns show promising translational implications. Both psychometric indices carried discriminative ability for HST vs LST, consistent with the idea that atypical parsing of audiovisual timing tracks latent vulnerability along the psychosis continuum (S. Lin et al., 2025). The greater AUC for IP than CW supports a larger role for altered temporal sensitivity as a behavioral readout of subtle, low-level disruptions in the sensory machinery presiding over audiovisual integration and, by extension, positive-like symptoms under bottom-up accounts of SCZ (Javitt, 2009b; Javitt et al., 1999). At their respective operating points, our indices showed distinct error profiles: IP favoured sensitivity at the cost of specificity, whereas CW specificity (with more false negatives among HST). This dissociation suggests IP may suit early-stage screening contexts where missed cases are costly, while CW may be more informative in later confirmatory settings that prioritize ruling out false positives. At the same time, the prevalence dependence of PPV/NPV underscores that these preliminary results should be interpreted cautiously, and thoroughly validated in larger, clinically ascertained cohorts.

If temporal sensitivity does underlie cross-modal performance, and by extension SIFI susceptibility, across the psychosis continuum, do then positive schizotypal sub-traits drive its coarsening in HST individuals? This proposition, grounded in recent empirical findings (Ferri et al., 2018; Haß et al., 2017), was tested through a multivariate model that factored in both the variance shared by our psychometric proxies for audiovisual TBWs (CWs) and temporal sensitivity (IPs), together with the latent schizotypy dimensions most informative in our experimental cohort. PCA-derived components

indeed mapped onto the main symptomatic clusters characterizing schizotypal personality, namely poor socio-affective functioning and proneness to positive-like experiences (Raine et al., 1994). As for the former, the resulting weighted scores proved to be mildly predictive of behavior at the multivariate level, yet showed neither coherent nor significant per-outcome impact. This was not the case for the positive schizotypal dimension, which not only strongly predicted the shared variance across psychometric indices, but also exhibited consistent and robust univariate effects. Such tie between positive-like perceptual profiles and looser multisensory integration has been many times highlighted in SCZ (Amadeo et al., 2024; Borgolte et al., 2024; Stevenson et al., 2017) and HST (Marsicano et al., 2022). This association was replicated in experimental set-ups where altered cross-modal binding translated into a higher proneness to illusory reports (Zvyagintsev et al., 2017), with the SIFI serving as a further testbed to probe this relationship (Ferri et al., 2018; Haß et al., 2017).

Our results slot another, perhaps intriguing, piece to the above mentioned mosaic of evidence, as they showcase that the audiovisual windows hosting the illusion hinge on temporal sensitivity mechanics whose integrity scales with the severity of positive symptoms or sub-traits. This echoes what principled in bottom-up models of psychosis: degraded sensory traces propagate upstream, dampen temporal precision, and culminate in hallucinatory-like misperceptions (Butler & Javitt, 2005; Javitt, 2009b). In a multisensory environment, the former steps assume the shape of broader TBWs that increase the likelihood of misbinding asynchronous cues, turning a single flashing stimulus into a double-flash report (Hirst et al., 2020; Shams et al., 2000). From a translational standpoint, our findings provide additional support for a dimensional continuum in which specific personality traits and symptoms share similar computational and pathophysiological principles (Cochrane et al., 2012; Ettinger et al., 2014; Johns & Van Os, 2001; Nelson et al., 2013), with promising, long-term implications for screening and diagnostic pipelines within the clinical setting (S. Lin et al., 2025).

Whereas impoverished temporal sensitivity may alone represent a valuable behavioral marker to complement pre-emptive screening routines, the present data concurrently invoke a latent endophenotypic liability spanning positive-like schizotypal traits and poor audiovisual integration. As the sub-second temporal regime in which multisensory processing unfolds maps onto E/I imbalances timescales reported in schizophrenia (Uhlhaas & Singer, 2010), brain oscillations represent candidate biomarkers supporting these dynamics, with alpha rhythms being the most plausible among them due to their role in pacing cortical excitability (Jensen & Mazaheri, 2010) and setting the temporal resolution of perceptual sampling (VanRullen, 2016).

Chapter 5: The Role of Alpha Oscillations among the Main Neuropsychiatric Disorders in the Adult and Developing Human Brain: Evidence from the Last 10 Years of Research

5.1 Introduction

Neuropsychiatric disorders are currently one of the most important sanitary emergences to watch for in high- and middle-income countries. Recent data collected on the European population (Trautmann et al., 2016) reports that approximately 165 million people are affected each year by mental disorders, and it is estimated that more than 50% of the general population in middle- and high-income countries will suffer from at least one mental disorder at some point in their lives. Some pieces of evidence (Vigo et al., 2016) suggest that these results may be an underestimation, which would further increase these numbers. This would have enormous consequences from an economic perspective, and in terms of years of life lived with disability. This burden involves children as well, especially those from economically developed countries, even though an increase in other countries is soon expected (Baranne & Falissard, 2018). Nonetheless, despite its relevance, it is still difficult to make a proper diagnosis because of the vast range of manifestations and overlap among the symptoms that may exist even inside the same cultural group, making these symptoms somewhat elusive to behavioral inspection (Kohrt et al., 2014; Pies, 2007; Sadock et al., 2009). In fact, despite the availability of numerous disorder assessment scales, the misdiagnosis rates are still high, with some reports indicating that over one third of patients are misdiagnosed (Ayano et al., 2021; Phillips & Kupfer, 2013; Stahnke, 2021; Vermani et al., 2011). This has obvious consequences on the patient's well-being. Therefore, it is crucial to find a more reliable way of accurately making differential diagnoses, thus enabling prompt and proper intervention.

To this aim, various efforts have been put towards identifying neural markers capable of discriminating between neuropsychiatric disorders, treatment response, and the outcome prediction (Rivera et al., 2022; Yahata et al., 2017). The electroencephalogram (EEG) has been very helpful, since it allows the brain electrical activity to be recorded in a totally non-invasive manner, with a relative fast montage and a high temporal precision (Bathelt et al., 2014; Rosenberg et al., 2015). For these reasons, it has been widely used to assess brain function in both the healthy and pathological populations. Indeed, the EEG is actually used in several clinical settings with diagnostic and prognostic purposes (Di Gregorio, La Porta, et al., 2022; Jaworska et al., 2019). In the research field, it is commonly used to link a modulation in its signal during a task execution (ERP, event related potential) to a specific cognitive

process (Horvath et al., 2018; Norton et al., 2021). Further, it is possible to investigate the cognitive functions through the analysis of the brain's oscillatory activity.

5.1.1 The Use of Alpha Rhythm for the Study of the Cognitive Functioning

Since Hans Berger's (Berger, 1929) early studies, it has become evident that oscillatory patterns can be extracted from the brain's electrophysiological signal, resulting from the nearly simultaneous firing of large ensembles of neurons. This rhythmic activity has been differentiated into five main functional categories, according to its frequency (Başar, 2013; Mahjoory et al., 2020): delta (δ ; 0.5–3 Hz), theta (θ ; 4–7 Hz), alpha (α ; 8–13 Hz), beta (β ; 14–30 Hz), and gamma (γ ; 30–50 Hz). Their power is progressively reduced by increasing frequency, with a $1/f$ ratio (Bak et al., 1987).

These rhythmic oscillations can be detected by analyzing the signal obtained from the spontaneous brain activity, or in response to a sensory stimulation, internally or externally driven (Başar, 2013). Thus, these frequencies have been linked to sensory and cognitive aspects, such as perception, attention, memory, or even consciousness (Gupta & Chen, 2016; Karakaş & Barry, 2017; Ward, 2003). Consequently, their disruptions have been associated with alterations such as the ones occurring in brain lesions or neuropsychiatric disorders (Başar, 2013; Başar & Güntekin, 2013). It follows that the brain's oscillatory activity can possibly represent an electrophysiological marker of these conditions, in which, although there is a biological connotate, it is still difficult to make a diagnosis after a behavioral evaluation. In particular, alpha oscillations have been linked to several cognitive processes such as memory, attention, distractor suppression, or even language (Klimesch, 2000; Ward, 2003).

Alpha oscillations are the most prominent rhythm in the human electroencephalographic signal (Klimesch, 1999). A significant modulation of the alpha amplitude after external or internal events is called event-related synchronization (or desynchronization) (ERS/ERD), and is ascribable to an increase (or a decrease) in the rhythmic activity of a large number of neurons. Alpha synchronization seems to have a role in maintaining an active and adaptive inhibitory mechanism during perceptual suppression of upcoming information (Jensen & Mazaheri, 2010). This inhibitory mechanism is enacted through a reduction in the cortical excitability that lessens the processing capacity of a particular area which is irrelevant to the ongoing processing (Klimesch, 2012; Sigala et al., 2014). Therefore, a synchronization within the alpha band may be an electrophysiological correlate of an information suppression mechanism (Pfurtscheller et al., 1996). Moreover, alpha amplitude has an important role in predictive processes, since the ability to predict the identity (Mayer et al., 2016) or even the probability of occurrence (Tarasi, di Pellegrino, et al., 2022) of the incoming stimulus modulates alpha power, which plays a role in preparing the brain for forthcoming stimulus perception

(Romei et al., 2010; Samaha et al., 2017). Indeed, in the perceptual decision-making domain, alpha power appears to drive choice bias, as alpha ERD correlates with the adoption of a liberal criterion, increased decision confidence, and visual awareness (Iemi et al., 2017). On the other hand, it has been causally demonstrated (Di Gregorio, Trajkovic, et al., 2022) that the frequency of the maximum power within the alpha band (i.e., individual alpha frequency, IAF) is a critical parameter in defining sensory accuracy. Indeed, reducing (or, otherwise, increasing) IAF would result in a worsening (or an improvement) of the individual's accuracy level (Cecere et al., 2015; Cooke et al., 2019; Minami & Amano, 2017). Altogether, these results highlight the functional role of alpha activity in perceptual and cognitive processes. Moreover, the oscillatory activity can be used as a connectivity index between two or more brain regions, comparing the synchronization in phase or in amplitude over the areas of interest (Friston, 2011). This kind of information is particularly useful when considering the oscillatory activity within the alpha band, given the empirical evidence supporting its involvement in diverse cognitive functions. It follows that the alpha-based indices can be used to assess cognitive functioning in a broad range of pathological conditions (Douw et al., 2010; Lejko et al., 2020; Morand-Beaulieu et al., 2021). In particular, neuropsychiatric diseases seem to be associated with anatomical and functional changes in the brain architecture, including connectivity alterations (Fingelkurts et al., 2007; Hinkley et al., 2011). For instance, a reduction in the alpha power over the occipital regions is reported in children with Attention Deficit Hyperactivity Disorder (ADHD) (Bozhilova et al., 2022; Lenartowicz et al., 2018). This alteration seems to interfere with the processing of relevant and irrelevant stimuli, contributing to the attentional deficits in ADHD patients. Therefore, the behavioral symptoms of these disorders seem to be accompanied by alterations in the alpha-band oscillatory activity. For this reason, alpha-based parameters have been useful for the diagnosis of diverse neuropsychiatric disorders, as highlighted by the number of publications linking anomalous alpha activity to these conditions. In particular, among the conditions included in the DSM-5, the literature mostly focused on disorders such as schizophrenia, depression, ADHD, and autism. This also emphasizes the relevance of alpha band parameters as potential neuromarkers when exploring the disorders' expression. Thus, a better understanding of the role of alpha waves for the manifestation of the symptoms would help to better comprehend the disorder and its associated biotypes. This could allow for a proper diagnosis and help to build more effective treatments and interventions.

However, even if the EEG-derived indices are commonly used in the clinical practice, there is still a lack of agreement about the diagnostic accuracy of these measures. In fact, even if there are plenty of EEG indices available in the literature, the results are often conflicting, if not opposing (Lefebvre et al., 2018). This is mostly caused by the heterogeneity of the studies and the different pathological biotypes (Loo et al., 2018), instead of the fast technological and methodological advances which this

field of research has witnessed in the last few years. Indeed, while sometimes these new indices confirm the previous results, other times, they do not. Thus, the aim of the present work is to examine the existing literature to find reliable indices that would support the operator during the diagnosis and intervention procedures. To better identify how these disorders differ at the neural level, we took into account both local and connectivity electrophysiological indices within the alpha band, in order to depict the issue from a broader perspective (see Table 5.1).

Table 5.1 Table showing the main electrophysiological indices used for the review, along with a brief description.

Table of EEG Indices		
Index	Full Name	Description
ERD/ERS	event-related synchronization/desynchronization	Amplitude up/down-modulation in response to a specific event, due to a synchronized activity of a large number of neurons
FAA (PAA)	frontal (or posterior) alpha asymmetry	Relatively higher alpha power recorded from the left (as compared to the right) hemisphere over frontal (or posterior) regions
IAF	individual alpha frequency	The frequency bin displaying the highest power value within the alpha band (8–13 Hz)
ITC	intertrial coherence	The degree of oscillatory phase-synchronization across different trials
PAC	phase amplitude coupling	Coupling between the phase of slower oscillations with the amplitude of faster oscillations (i.e., reflecting integrative mechanisms of neural activity within the brain)
PSD	power spectral density	Measure of signal's power content versus frequency

Hence, given the abundance of work referring specifically to alpha oscillations, we aimed to summarize the literature regarding the main neuropsychiatric disorders in both adult and developing age groups which have emerged over the last 10 years. This work's objective is to give the reader an overall perspective on how the alpha-based indices can be useful when investigating neuropsychiatric conditions, to help isolate the core features that better depict them. This may help with finding more reliable diagnostic and prognostic indices for each condition. For this reason, we excluded from the current work articles including patients with multiple diagnoses, or investigating comorbidities. Furthermore, while inspecting the publications, we also excluded those investigating drug effects or animal studies, in order to focus specifically on those studies which could help to define a more concise view of these conditions.

5.2 Schizophrenia Spectrum Disorder (SSD)

Although over a hundred years have passed since Kraepelin's pioneering works on dementia praecox, the nosographical profile of Schizophrenia Spectrum Disorder (SSD) still displays some core clinical features that place this disorder among the most debilitating psychiatric syndromes. These hallmark symptoms include psychotic-like manifestations, such as delusions and hallucinations (positive symptoms), amotivation, anhedonia, and social withdrawal (negative symptoms), along with severe deficits in the cognitive (i.e., attention, working memory [WM], executive functions) and perceptual domain (Edition, 2013). Inquiries aiming to elucidate the pathophysiological mechanics behind the emergence of SSD have recently focused on providing an oscillatory account of the aforementioned impairments, implying that such deficiencies might be engendered by a systematic failure to temporally integrate local neural activities into large-scale networks (Uhlhaas, 2013; Uhlhaas & Singer, 2015). These considerations substantiate a conceptual framework based on the notion of SSD as a disconnection syndrome, where an aberrant decrease (or increase) in cross-regional synchronization might be responsible for the behavioral abnormalities witnessed in SSD patients (Stephan et al., 2009). Accordingly, it has been proposed that this rhythmic dysconnectivity may elicit primary deficits at a cognitive and perceptual level, whereas the subsequent pathological attempts at their resolution should lead to the onset of positive symptomatology (Uhlhaas & Singer, 2015).

On a molecular level, such oscillatory alterations are construed as a by-product of a malfunctioning of neurotransmitters' dynamics. For instance, changes in inhibitory mechanisms mediated by gamma-aminobutyric acid (GABA)ergic interneurons (especially parvalbumin-positive cells) and reduced efficiency of N-methyl-D-aspartate receptors (NMDAR) have been tied to the emergence of SSD symptoms, which has also been associated with dopaminergic disturbances in mesolimbic and mesocortical loci (Pittman-Polletta et al., 2015). While the complex interplay between these different dysregulations has been suggested to mainly affect activity in the gamma band, mounting evidence garnered in the last few years points toward their involvement in the generation of alpha rhythms as well (Lemercier et al., 2017; Lozano-Soldevilla et al., 2014; Puig et al., 2014).

5.2.1 Resting State Data

A seemingly common finding in SSD patients is a slightly reduced parieto-occipital spontaneous alpha power (resulting in an increased cortical excitability) as compared to healthy individuals (Başar et al., 2016; Garakh et al., 2015). This kind of evidence has been replicated in several studies exploiting

resting-state data, which showed a tendency toward a reduction in local alpha activity as measured via power spectral density (PSD, i.e., the signal's power content versus frequency) not only posteriorly, but also in frontal and central regions (Canali et al., 2015; Garakh et al., 2015; Goldstein et al., 2015; J. W. Kim et al., 2015). Moreover, a direct link has been found between this decrease in alpha power at the parietal and left frontotemporal sites and the gravity of the positive SSD symptomatology (Candelaria-Cook et al., 2020; Mitra et al., 2017). Accordingly, treatments capitalizing on alpha-tuned transcranial alternating current stimulation (tACS), which were administered to patients experiencing auditory hallucinations, were proven to restore such imbalances by boosting resting alpha power, consequently reducing the severity of hallucinatory symptoms (Ahn et al., 2019). However, recent evidence appears to depict a more nuanced portrait of the matter. While some studies described no reduction in terms of posterior alpha activity in SSD patients (Freche et al., 2020; M. Murphy & Öngür, 2019; Yeum & Kang, 2018), one reported higher parieto-central alpha power in medicated patients as compared to healthy controls (Hong, Summerfelt, et al., 2012). Such an increase was also outlined by data collected in three additional papers, focusing on, rather than task-positive regions (i.e., neural areas more active during attention-demanding tasks), task-negative areas, which are known to increase their level of excitability at rest (Fox et al., 2005). A globally heightened spectral power was reported in SSD individuals (Nakhnikian et al., 2020; Narayanan et al., 2014) when compared to controls, whereas in a similar work, the same abnormal increase was found with regard to an alpha component located over parietal and temporal areas largely overlapping with the posterior portions of the Default Mode Network (DMN) (Nakhnikian et al., 2021). Interestingly, spectral inquiries carried out on DMN sites via EEG and magnetoencephalography (MEG) showed comparable results, namely increased alpha power in the medial prefrontal and posterior cingulate cortices (mPFC and PCC) of SSD patients (J. S. Kim et al., 2014; Koshiyama et al., 2021).

Another oscillatory parameter that can be extrapolated from resting-state power analyses is IAF, namely the exact frequency within the alpha band at the maximum amplitude value. The existing literature suggests that a faster (rather than slower) IAF entails better perceptual acuity and efficiency (Bertaccini et al., 2022; Di Gregorio, Trajkovic, et al., 2022), with individuals displaying pronounced schizotypal traits characterized by slower IAFs (Trajkovic et al., 2021). Findings gathered over the last decade unilaterally uphold previous knowledge, namely slower resting-state IAFs in SSD patients (Freche et al., 2020; Koshiyama et al., 2021; M. Murphy & Öngür, 2019; Nakhnikian et al., 2020; Yeum & Kang, 2018), with the degree of deceleration positively correlating with visuo-attentional performance and scorings at cognitive scales (Ramsay et al., 2021). Furthermore, faster IAFs in SSD individuals undergoing multisession cognitive training was found to predict protocol outcome (i.e., responders vs. non-responders). Along this line of reasoning, it has also been found that occipital IAFs

of patients affected by negative symptoms cycle more slowly than in healthy participants, while the opposite held for individuals with SSD displaying positive symptoms (Garakh et al., 2012). Accordingly, IAFs in both groups of patients correlated with the severity of symptomatology, as measured via behavioral scales (Goldstein et al., 2015).

At-rest connectivity metrics have also been largely exploited to gain some insights into the network architecture of SSD patients. Heightened synchronization within the alpha band has been reported in first-episode schizophrenic patients, with cortical hubs sited along frontocentral, occipital, and right temporo-parietal regions displaying the highest levels of interconnections, which was negatively correlated with scorings at cognitive scales (T. Liu et al., 2019). In a similar study, alpha coherence parameters were also found to be enhanced both in an inter- and intra-hemispheric manner in SSD patients (Kam et al., 2013). Notably, synchronization measures gathered from DMN nodes are in line with such results (i.e., similar or increased inter-areal alpha coupling in SSD; Baenninger et al., 2017; J. S. Kim et al., 2014; Nakhnikian et al., 2021). On the other hand, several studies provided a different perspective on the way alpha oscillations behave on a network level in SSD. Evidence for globally reduced alpha synchrony over frontal areas has been outlined by means of different indices, such as phase-locking value (PLV) and phase-lag index (PLI), in patients compared to healthy controls, with a concurrent increase in the information flow from occipital to anterior sites (and a decrease in the opposite direction; Olejarczyk & Jernajczyk, 2017). A study adopting non-negative matrix factorization, as well as both energy and entropy measures of connectivity, in individuals with SSD unveiled a general decrease in alpha-band coherence within four spread clusters centered on the bilateral cingulate, left temporal-parietal, precuneal-PCC, and right prefrontal cortices (Phalen et al., 2020). These patterns of reduced rhythmic interaction were reported to be associated with patients' psychiatric symptoms. Another work uncovered attenuation of inter-hemispheric alpha connections in SSD (but not healthy individuals) at multiple sites (frontal, parietal, and temporal) (Yeum & Kang, 2018). A decrease in alpha-tuned inter-hemispheric anterior connectivity and frontoposterior cross-talking was also highlighted in two further studies adopting connectivity analyses (Di Lorenzo et al., 2015; Lehmann et al., 2014).

To summarize, a significant slowdown of IAFs appears to be a core pathological feature characterizing SSD. As for oscillatory power, spontaneous alpha activity appears to be decreased and increased in SSD patients over, respectively, task-positive and task-negative regions (figure 5.1). On a network level, dysregulations in both directions (higher vs. lower connectivity) in various neural clusters have been found, perhaps due to the different methodological approaches adopted (scalp- or source-based computations), or sample variability (first-episode vs. chronic or medicated vs. unmedicated patients).

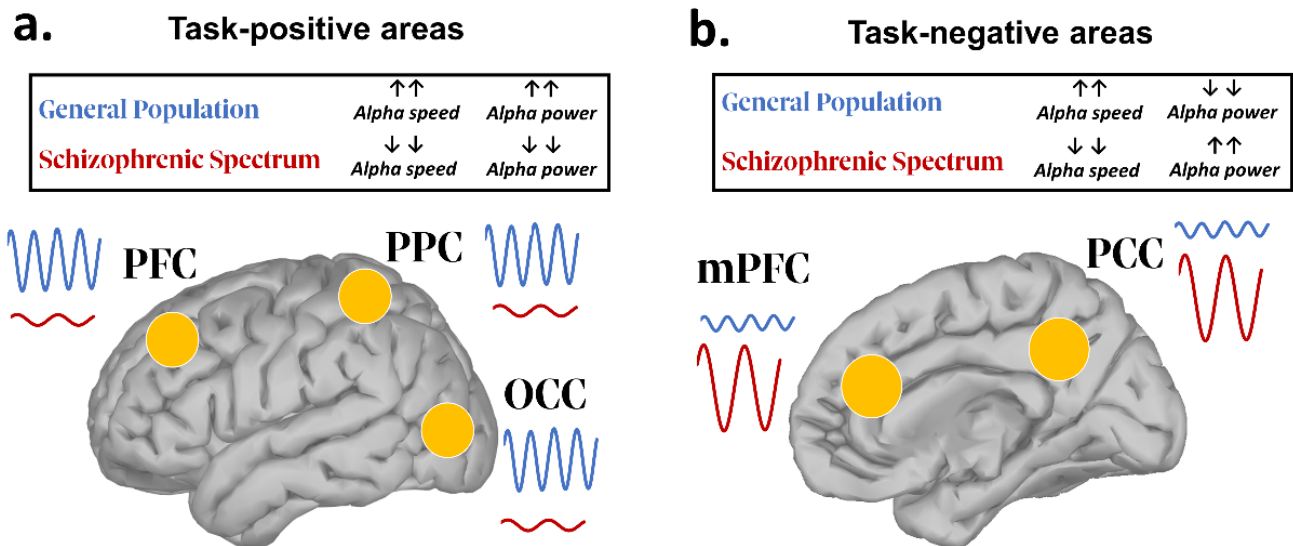


Figure 5.1 Graphical representation summarizing the main findings on resting-state alpha power in SSD (relative to healthy individuals). The left panel (a) depicts alpha oscillatory patterns relative to task-positive areas, while the right panel (b) depicts those relative to task-negative regions (largely overlapping with DMN's nodes). Upward and downward arrows indicate respectively an increase or a decrease in alpha power or frequency speed. As for the former areas, alpha power is decreased, while the latter show an overall increase of such oscillatory index. PFC (prefrontal cortex); PPC (posterior parietal cortex); OCC (occipital cortex); mPFC (medial prefrontal cortex); PCC (posterior cingulate cortex).

5.2.3 Perceptual Impairments

Alpha oscillatory dynamics in SSD have been scrutinized in patients asked to perform perceptual tasks. Indeed, a plethora of deficits involving sensory processing has been reported in SSD, the severity of which has been hypothesized to trigger the onset of positive symptomatology (Postmes et al., 2014; Uhlhaas & Singer, 2015). Auditory hallucinations correspond to the most salient psychopathological manifestation in SSD. As such, defective mechanisms in the rhythmic signaling underlying auditory perception have been widely investigated to pinpoint some of the putative features driving this kind of hallucinations. Auditory steady-state response (i.e., the electrical response recorded from the auditory cortex to the entrainment induced by repetitive acoustic stimuli) paradigms have been frequently employed to probe the electrophysiological malfunctioning in SSD (Parker et al., 2019). These studies reported aberrations in the low frequency bands (theta and alpha) in SSD (as compared to controls) during the task, such as lower evoked power, intertrial coherence (ITC), and increased theta–alpha phase–amplitude coupling (PAC; Edgar et al., 2014; Hirano et al., 2018; Parker et al., 2019). Similar tasks capitalizing on the presentation of multiple pairs of auditory stimuli yielded interesting results about whether and how alpha oscillations mediate perceptual impairment in auditory-related sensory gating. Specifically, evoked alpha power over posterior and midline sites has been shown to undergo a reduced suppression in response to the administered acoustic pairs in SSD as compared to controls

(Carolus et al., 2014; Hamm et al., 2012; Hong, Summerfelt, et al., 2012), with the degree of (deficient) suppression being associated with GABAergic levels over frontocentral areas (L. M. Rowland et al., 2013). However, evidence for a demeaned alpha suppression over midline posterior areas, which tended toward a relative increase (i.e., more alpha suppression) over frontocentral sites, has also been reported in SSD (Başar-Eroğlu et al., 2013). Moreover, audio-verbal training was found to be effective in boosting such impaired alpha suppression in response to the second (but not the first) acoustic stimulus in each pair, leading to an oscillatory improvement that correlated with better scoring on verbal learning scales (Popov et al., 2015). Impaired sensory gating was also shown to be accompanied by reduced frontocentral alpha ITC between the first and second auditory stimulus, which was inversely correlated with the negative symptoms assessed using a behavioral scale (Keil et al., 2016). Consistent with this finding, a lower alpha-tuned inter-hemispheric coherence between temporal and parietal electrodes was outlined during the completion of a passive auditory task in patients with SSD experiencing auditory hallucinations (as compared to controls and SSD patients not affected by such symptoms). Likewise, aberrant rhythmic patterns within the alpha band have also been found through paradigms presenting a series of standard acoustic stimuli intermingled with deviant tones. Two studies showed that SSD patients exhibit lower ITC and evoked power than healthy participants over central regions in response to standard tones, with the magnitude of the power increase among patients correlating with verbal learning and working memory capacities (M. Lee et al., 2017, 2018). However, higher evoked alpha power, after both standard and deviant stimuli, was also reported (Hong, Moran, et al., 2012). Overall, alpha rhythmic activity appears to be less reactive and susceptible to task-relevant suppression in patients engaged in perceptual tasks, which suggest both an over-increased power at rest and diminished control during the performance.

5.2.4 Cognitive Deficits

Impaired cognition is an additional feature enriching the already complex clinical phenotype of SSD. Subtle derangements at this level often tend to occur many years before the onset of psychotic symptoms, fueling the idea that delusions and hallucinations might represent a pathological attempt to make sense of erratic and vague information provided by deficient cognitive mechanisms (Uhlhaas & Singer, 2015). While it remains to be clarified whether these deficits result from a disruption of lower-level perceptual mechanisms, various inquiries were set to further illuminate the oscillatory contributions to such phenomena. The auditory oddball task has been among the most widely adopted paradigms to disentangle the neurophysiological correlates underpinning the way in which patients with SSD handle novel stimuli and cope with irrelevant information. For instance, SSD patients and

individuals at a high risk of developing psychosis were found to display a reduced posterior alpha ERD as compared to healthy controls in response to target stimuli (Kayser et al., 2014; Núñez et al., 2017). On the other hand, a similar study capitalizing on MEG recordings reported a significant decrease in alpha ERS over occipital and posterior midline regions (Fujimoto et al., 2012). Transcranial magnetic stimulation (TMS) treatments administered along the left frontoparietal axis to restore these disbalances showed that, in most SSD patients, an increase in task-related alpha power (recorded after, as compared to before, the TMS protocol) occurred in response to both rare and frequent stimuli. This degree of spectral increase also displayed a slight association with improvements in positive and negative symptomatology, as assessed via behavioral scales (Aubonnet et al., 2020).

Alpha ERD/ERS dysregulations in SSD have been explored even via working memory (WM) paradigms. Indeed, individuals with SSD exhibit a reduced contralateral alpha suppression (ERD-like response) in trials with higher cognitive loads. This aberrant reduction correlated with worse WM performance both between (lower SSD relative to controls) and within (lower SSD with less alpha suppression relative to those displaying greater reduction) groups. In the latter case, a significant relationship with diminished contralateral ERD and the psychiatric symptoms was also uncovered (Coffman et al., 2020). Furthermore, a comparable reduction in contralateral alpha ERD, coupled with impaired behavioral performance, was reported in SSD in two similar studies (Erickson et al., 2017; Kustermann et al., 2016), while weaker inter-areal connectivity within the alpha range has been outlined between occipital regions and several temporo-parietal and frontal clusters (the magnitude of which was associated with the severity of positive symptoms) (Sklar et al., 2022).

Maladaptive alpha dynamics also appear to arise in SSD individuals instantiating inhibition-related mechanisms (or a release from inhibition). Patients with SSD showed higher alpha ERD over frontal and temporal sites during the inhibitory task (Cooper & Hughes, 2018). Conversely, reduced alpha suppression over sensorimotor cortices was also found in SSD during incongruent trials of a Stroop task (in association with slower reaction times) (Popov et al., 2019).

Lastly, mounting evidence suggests that a disruption in alpha dynamics might also be involved in social cognition impairments (i.e., poor empathy judgment and mentalizing skills, along with pathological social withdrawal) (M. F. Green et al., 2015). Specifically, SSD patients engaged in a facial emotion recognition task displayed lower alpha power and higher connectivity within the alpha band over frontocentral sites, together with lower accuracy in recognizing both happy and fearful emotional expressions (Popov et al., 2014). When performing an ecological face-to-face interaction with a confederate, the SSD group displayed an alpha connectivity increase undetected in healthy controls during the more affiliative task condition (*closeness* condition). Such an increase was found to be positively correlated with negative symptoms (L. Y. Li et al., 2021). Aberrant modulation of

alpha power in SSD was also noted during the Ultimatum Game, a social decision-making task involving a fair split of a sum of money between other humans or a computer (Gabay et al., 2014). Patients displayed a more robust upregulation of alpha power over midfrontal spots during the anticipation phase when playing with a computer vs. a human agent. This power difference was proven to be negatively correlated with positive symptoms (Billeke et al., 2015). Moreover, in a self-referential memory task, SSD displayed higher scores when presented with self-related items (as compared to neutral or other-related items), which was paralleled by a demeaned alpha ERS over the midline and right frontocentral regions during the encoding phase, and a massive reduction (relative to healthy subjects) in long-range alpha synchronization across multiple cortical electrodes (Jia et al., 2019).

Altogether, these findings (Table 5.2) resemble those concerning perceptual processing, namely a pervasive dysregulation in the way alpha oscillations instantiate phasic fluctuations in event-related cortical excitability (ERD vs. ERS). Regarding connectivity metrics, the results are more interspersed, even though they seem to point toward a reduction in long-range alpha coherence across different cognitive tasks, suggesting a bioelectrical disruption in the way higher-level neuronal firing modulates the activity of lower areas.

Table 5.2. Table representing the main electrophysiological findings in SSD, with the methods and the studies who contributed to them.

Schizophrenia Spectrum Disorder (SSD)		
Studies	Analytic Method	Main Findings
Yeum & Kang, 2018; Murphy & Öngür, 2019; Freche et al., 2020; Nakhnikian et al., 2020; Koshiyama et al., 2021; Ramsay et al., 2021;	Resting state IAF	Slower IAF over posterior regions
Canali et al, 2015; Garakh et al, 2015; Goldstein et al, 2015; Kim et al, 2015; Başar et al., 2016; Mitra et al, 2017; Candelaria-Cook et al, 2020;	Resting state PSD	Posterior and frontal Alpha power reduction
Kim et al, 2014; Koshiyama et al, 2021; Nakhnikian et al., 2021;	Resting state PSD	Alpha power increase in the DMN
Kam et al, 2013; Lehamann et al, 2014; Kim et al, 2014; Popov et al, 2015; Di Lorenzo et al, 2015; Baenninger et al, 2017; Olejarczyk & Jernajczyk, 2017; Yeum & Kang, 2018; Jia et al., 2019; Liu et al., 2019; Phalen et al., 2020; Li et al., 2021; Nakhnikian et al., 2021; Sklar et al., 2022;	Functional connectivity	Aberrant long-range functional connectivity
Fujimoto et al., 2012; Hamm et al, 2012; Hong et al, 2012; Hong et al, 2012; Başar-Eroğlu et al., 2013; Carolus et al, 2014; Kayser et al, 2014; Lee et al, 2018; Lee et al, 2017; Núñez et al., 2017; Aubonnet et al, 2020;	Auditory evoked response	Aberrant Alpha ERD/ERS over posterior and frontocentral areas

5.3. Major Depressive Disorder (MDD)

Major depression has been described as a psychiatric syndrome whose core features entail persistently low mood and anhedonia, coupled with sleep and psychomotor disturbances, fatigue, or loss of energy. Alterations in the affective domain might also involve feelings of worthlessness or guilt and suicidal thoughts, suggesting a pervasive tendency toward negative self-referential thinking and ruminations. In addition, subclinical cognitive deficits (i.e., diminished ability to concentrate, impaired attentional and memory functioning) have often been reported in patients suffering from this disorder (Edition, 2013).

Oscillatory insights into the pathophysiological dynamics underlying MDD suggest that individuals diagnosed with this disorder exhibit rhythmic aberrations, encompassing lower frequency bands, which is likely due to alterations occurring at cortical and subcortical loops that coalesce into a neuropathological phenotype known as thalamocortical dysrhythmia (Canali et al., 2015; Fingelkurts & Fingelkurts, 2015; A. Leuchter et al., 2013). Consistent with this notion, MDD patients display higher alpha power levels over the left (relative to the right) frontal lobe, an oscillatory pattern called frontal alpha asymmetry (FAA; figure 5.2) (Eidelman-Rothman et al., 2016). Given the inverse relationship between alpha rhythms and cortical excitability, this electrophysiological abnormality has been framed within the approach–withdrawal model (Davidson et al., n.d.), where an increased activation of the right vs. left frontal cortices has been thought to occur in individuals more prone to behavioral withdrawal vs. approach (i.e., proneness toward a negative vs. positive affective style). As such, FAA has been deemed as one of the most reliable biomarkers (although for a different account, see Horato et al., 2022; Kołodziej et al., 2021; van der Vinne et al., 2017)) indexing MDD-related affective asymmetries responsible for symptoms such as hopelessness or helplessness and anhedonia (de Aguiar Neto & Rosa, 2019; Eidelman-Rothman et al., 2016; Fingelkurts & Fingelkurts, 2015).

Aside from FAA, while it has been recently proposed that MDD might be also characterized by interhemispheric asymmetries over posterior sites (i.e., posterior, or parietal, alpha asymmetry, PAA) (Fingelkurts & Fingelkurts, 2015), interareal communication seems to be altered as well. For instance, MDD patients displayed higher alpha-band coherence within the DMN and between anterior midline areas and the frontoparietal network (Alamian et al., 2017; Northoff, 2016). These aberrant patterns of interregional cross-talking are assumed to underlie many functional dysregulations, putatively

resulting in ruminative thoughts, increased self-focus, and a reduced ability to concentrate and properly deploy attentional resources (Northoff, 2016).

Thus, a general disruption in alpha rhythms, occurring on several different levels, seems to crucially contribute to the pathogenic mechanics behind MDD syndrome and some of its associated affective and cognitive symptoms.

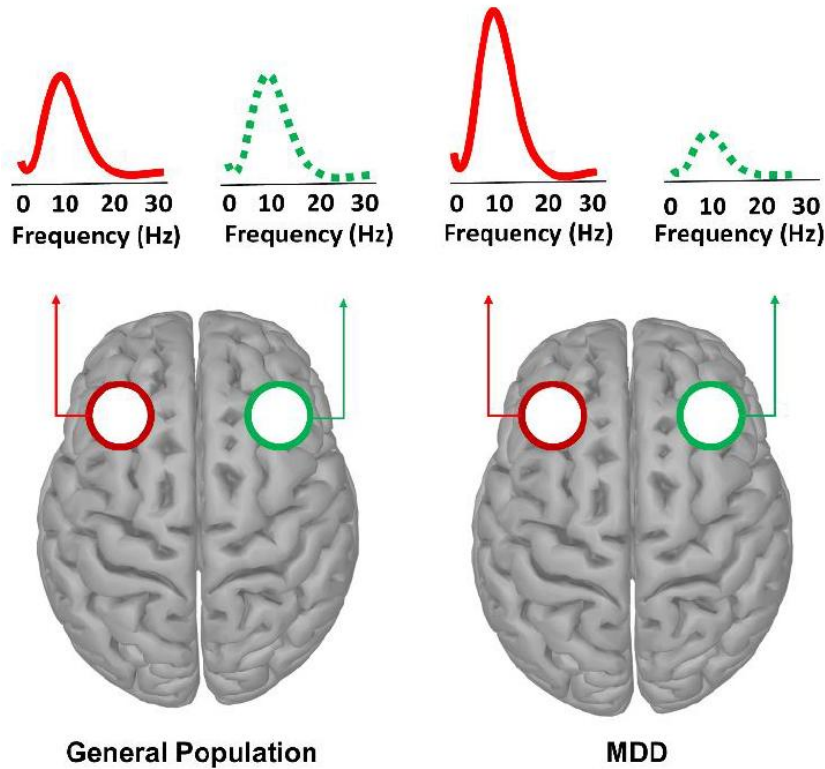


Figure 5.2 Schematic depiction of FFA patterns witnessed in depressive patients. Relative to healthy individuals (left panel), MDD patients (right panel) display higher relative alpha power over the left (vs. right) frontal cortex.

5.3.1 Resting State Data

Much of the resting-state literature gathered over the last decade has been devoted to the investigation of FAA, with the aim of affirming its role as a neuromarker able to provide an early diagnosis in individuals at risk, but also to anticipate the clinical outcomes. A stronger activation in the alpha band of the right frontal cortex in MDD was replicated in several studies (Auerbach et al., 2015; Barros et al., 2022; Cantisani et al., 2016; Jaworska et al., 2012; Jesulola et al., 2017; Koo et al., 2019; Kustubayeva et al., 2020; C. R. Quinn et al., 2014), some of them showing a robust relationship between the degree of FAA and scores on depression behavioral scales (Y. Park et al., 2019; Smith et al., 2018). FAA has also been proven to predict treatment effectiveness. For instance, FAA seems to display a negative correlation with sensitivity to specific psychotherapeutic protocols (Gollan et al.,

2014), while bifrontal alpha-tuned tACS was capable of reducing both alpha power over the left prefrontal cortex (i.e., asymmetry decrease) and the depressive symptoms (Alexander et al., 2019; Riddle et al., 2022).

Lateralized patterns of rhythmic activation have been reported over posterior sites as well. Although not as straightforward as FAA, PAA appears to be a recurrent oscillatory feature of MDD (Fingelkurts & Fingelkurts, 2015). Specifically, alpha power was found to be enhanced over the left parietal cortex of female patients suffering from MDD (Jaworska et al., 2012), whereas a sample of depressed adolescents tested in a different study displayed an opposite lateralization trend, which was associated with rumination and anhedonia symptoms (Umemoto et al., 2021). Further, MDD patients less sensitive to deep-brain stimulation treatments seem to show an increased parietal alpha activity over the left hemisphere, with the magnitude of PAA negatively correlating with behavioral depression scores (Quraan et al., 2014). In addition, anodal transcranial direct-current stimulation (tDCS) over the dorsomedial PFC was shown to induce a greater reduction in anxiety scores in patients displaying lower and higher baseline alpha power, as recorded from, respectively, the left parietal lobe and the precuneus (Nishida et al., 2019).

Apart from oscillatory asymmetries, canonical spectral aberrations within the alpha band have also been described in patients exhibiting suicidal ideations (Benschop et al., 2019). Higher parieto-central alpha power was also found to characterize elders suffering from late-life depression (Wu et al., 2022), and to better discriminate MDD individuals from healthy participants (P. F. Lee et al., 2018). Moreover, a positive clinical outcome in depressed patients has been associated with a decrease in frontal alpha power triggered by 10-Hz repetitive TMS protocols and electroconvulsive therapy (Hill et al., 2021; Woźniak-Kwaśniewska et al., 2015). However, some studies also reported lower posterior oscillatory power within the alpha band in MDD (Kan & Lee, 2015; A. Wolff et al., 2019), the degree of which was linked with depression severity and attentional impairments (Jiang et al., 2016; Keller et al., 2020). Conversely, symptomatologic improvements in MDD have been proven to correlate with frontal and midline alpha power increases stemming from alpha-tuned repetitive TMS protocols (I. A. Cook et al., 2019; Noda et al., 2013).

Resting-state paradigms have also been exploited to address whether and how MDD might alter rhythmic connectivity dynamics. To begin with, proneness to brooding rumination appeared to go along with reduced alpha–gamma PAC over posterior brain areas (J. Wang et al., 2022), and global reduction in functional connectivity within the alpha band has been proven to correlate with depression severity (Mohammadi & Moradi, 2021). In a network-based study adopting both nodal and global measurements, lower alpha connectivity was uncovered in MDD. Additional analyses also revealed decreased nodal clustering in several cortical hubs spread over frontal regions, as well as the temporal

lobe and the visual cortex (Shim et al., 2018). Multi-layer analyses run on MEG data to explore interareal oscillatory cross-talking showed similar results, namely a decrease in alpha connectivity in depressed participants (Nugent et al., 2020). Conversely, alpha-tuned repetitive TMS protocols were shown to ignite an increase in connectivity in MDD, displaying symptom improvements (Corlier et al., 2019). Still, these results are challenged by plenty of data suggesting an opposite (positive) relationship between levels of alpha connectivity and depression severity. Increased interhemispheric (central) and intrahemispheric (right frontocentral) alpha coherence was found to discriminate depressed individuals from those diagnosed with bipolar disorder (Tas et al., 2015). Similarly, MDD displays higher alpha coupling, linking frontopolar loci to the temporal and parieto-occipital regions (A. F. Leuchter et al., 2012). Moreover, depressed patients also displayed increased cross-regional alpha connectivity between the ventromedial PFC and both the left mPFC and left dlPFC, as well as between the subgenual anterior cingulate cortex (ACC) and the left dlPFC (Olbrich et al., 2014; Q. Wang et al., 2019). Furthermore, positive outcomes yielded by antidepressant-based treatments have been associated with weaker alpha oscillatory connectivity bridging the insular cortex to the rostral ACC (Minami et al., 2022), whereas the magnitude of the TMS-driven decrease in spectral correlation metrics relative to the left hemisphere was shown to be correlated with clinical ameliorations (A. F. Leuchter et al., 2021).

Taken together, resting-state data concur in assigning FAA (and to a lesser degree PAA) a pathophysiological role in the emergence of MDD. As for more generic impairments in oscillatory power and connectivity, the aforementioned patterns appear more difficult to interpret. These controversial findings might be construed as the result of heterogeneous clinical samples in terms of age or gender, not to mention the different frequency bins (within the canonical alpha band) adopted throughout the analyses. Lastly, a scenario where MDD might exhibit diverging rhythmic phenotypes should not be ruled out; this jeopardizes a unified interpretation of the matter.

5.3.2 Cognition, MDD and Alpha Rhythms

Oscillatory fingerprints underpinning impaired alpha activity in MDD are not restricted to the resting brain. Electrophysiological investigations during cognitive tasks are consistent with the notion that cortical circuits responsible for attentional deployment, memory storage, and executive functions display demeaned activation in MDD (Northoff, 2016). For instance, during the auditory oddball task, MDD patients who exhibited lower IAFs and alpha power at rest were shown to upregulate such parameters during tasks in response to deviant stimuli (A. Wolff et al., 2019), along with increased

event-related alpha phase synchronization between frontocentral and parieto-occipital electrodes in response to target stimuli during a visual oddball paradigm (Y. Li et al., 2016).

With regard to the WM domain, MDD patients displayed poorer behavioral performance on a Sternberg task, which was associated with decreased posterior alpha power during the retention period (Bailey, 2014; O. W. Murphy et al., 2019). Moreover, lower increases and decreases in alpha phase synchronization within, respectively, the frontoparietal route and occipito-central cortical clusters have been reported in MDD during the n-back task (Y. Li et al., 2017).

Altered patterns of alpha activity appear to also underlie impairments in inhibitory mechanisms, as measured using Go/No-Go tasks. For instance, both reaction times and accuracy rates were reported to be significantly lower in depressed patients displaying suicidal behavior. These data were linked to abnormally high alpha power levels recorded from the ventromedial PFC and ACC during, respectively, Go and No-Go trials (Dai et al., 2022). Further, mindfulness-based therapeutic protocols have been reported to enhance task-related alpha ERD and left frontoparietal coherence during the same task, with the degree of oscillatory realignment shown to correlate with clinical ameliorations (Schoenberg & Speckens, 2015).

Defective emotional processing is an additional symptomatological feature characterizing major depression, with disrupted alpha rhythm dynamics contributing to this pathological phenomenon. In a sample composed of MDD patients with and without dysphoria, higher bilateral frontal alpha power was reported in response to both pleasant and unpleasant emotional stimuli only in MDD patients with dysphoric symptoms (Messerotti Benvenuti et al., 2019). During an emotion self-regulation study employing happy emotion induction training, a power decrease in the upper alpha band over the frontal and temporal sites was reported during the first session of the protocol. Intriguingly, changes in task-related FAA (asymmetry decrease) resulting from such self-regulation training were proven to correlate with scoring at the behavioral scales (Zotев et al., 2016). Similarly, bifrontal alpha tACS applied to MDD patients was reported to attenuate left alpha power, and thus FAA, during the passive viewing of emotionally positive images (Riddle et al., 2022). In addition, a weaker posterior alpha ERD was found in MDD patients engaged by WM items superimposed on negative emotional pictures, whereas the opposite pattern was witnessed when positive emotional pictures were presented in the background (Segrave et al., 2012). Biases in emotional processing have also been investigated through face recognition paradigms. For instance, FAA appeared to unfold in MDD in response to both happy and sad faces (Koller-Schlaud et al., 2020). Moreover, alpha–gamma PAC unveiled an attenuated interplay between right-lateralized cortical (i.e., orbitofrontal cortex) and subcortical (i.e., thalamus and amygdala) neural nodes in non-responders to antidepressant treatments, which was likely to reflect abnormal sensitivity to negative emotional stimuli (Dai et al., 2022).

Lastly, impaired alpha activity has been proven to play a pivotal role in higher cognitive abilities. Patients with MDD were found to display FAA patterns when performing a reinforcement learning task, the occurrence of which has been deemed to underlie losses in approach-related motivation (Gheza et al., 2019). Reduced alpha power over the left hemisphere was also reported during a multi-stage decision-making task in MDD patients (Kustubayeva et al., 2020), while a neurofeedback training was able to boost alpha power as measured during the completion of a counting task over the ACC and parieto-occipital sites (Escolano, Navarro-Gil, Garcia-Campayo, Congedo, De Ridder, et al., 2014).

In brief, task-relative alpha dysregulations tend to be often witnessed in MDD. Aside from FAA, generic alterations in oscillatory power and inter-regional communication have been found to underpin different cognitive deficits. However, the direction of these alterations is still unclear (Table 5.3), and seemingly depends on each individual's pathophysiological biotype, as well as the specific cognitive process.

Table 5.3 Table representing the main electrophysiological findings in the MDD, with the methods and the studies who contributed to them.

Major Depressive Disorder (MDD)		
Studies	Analytic Method	Main Findings
Jaworska et al, 2012; Quinn et al, 2014; Auerbach et al, 2014; Fingelkurts & Fingelkurts, 2015; Cantisani et al, 2016; Jesulola et al, 2017; Smith et al, 2018; Koo et al, 2019; Park et al, 2019; Kustubayeva et al, 2020; Barros et al, 2020;	Resting state PSD	Frontal Alpha asymmetry
Jaworska et al, 2012; Quraan et al, 2014; Fingelkurts & Fingelkurts, 2015; Umemoto et al, 2021;	Resting state PSD	Posterior Alpha asymmetry
Kan & Lee, 2018; Jiang et al, 2016; Lee et al, 2018; Benschop et al, 2019; Wolff et al, 2019; Keller et al, 2020; Wu et al, 2022;	Resting state PSD	Aberrant posterior Alpha power
Leuchter et al, 2012; Olbrich et al, 2014; Tas et al, 2015; Northoff et al, 2016; Alamian et al, 2017; Li et al, 2017; Nugent et al, 2020; Wang et al, 2019; Nugent et al, 2020; Mohammadi & Moradi, 2021; Minami et al, 2022;	Functional connectivity	Aberrant short and long-range functional connectivity
Bailey, 2014; Murphy et al, 2019; Kustubayeva et al, 2020; Dai et al, 2022.	Evoked response during WM and attentive tasks	Aberrant Alpha power over posterior (reduced) and midfrontal (increased) areas

5.4 Autism Spectrum Disorder (ASD)

Autism spectrum disorder (ASD) is a complex neurological and developmental disorder characterized by impairments in social cognition and interaction other than sensory and perceptual abnormalities (Association, 2013; Kessler et al., 2016). The behavioral and cognitive symptoms associated with ASD are extremely heterogeneous, and the diagnosis is based on different patterns of behavior, including: (a) persistent deficits in social communication and social interaction, such as socio-emotional reciprocity, non-verbal communication, or difficulties adjusting behavior according to various social contexts; (b) restricted interests, repetitive patterns of behavior, such as stereotyped motor movements, inflexible adherence to routines, or unusually intense interests (Association, 2013).

5.4.1 *The Role of Alpha Oscillations in ASD's Symptomatology*

Studies on the neural underpinnings of ASD show functional and anatomical alterations within the perceptual neural network (Dickinson et al., 2018; Han et al., 2017; Tarasi, Trajkovic, et al., 2022). ASD individuals showed alterations in long-range structural and functional connectivity (rather than in a local areas) (R. Delorme et al., 2013; Han et al., 2017; Khan et al., 2013; J. J. Wolff et al., 2017). Specifically, ASD individuals seem to display a reduction in interhemispheric long-range synchronization within the alpha band. Indeed, it has been demonstrated that ASD individuals have a reduction in the alpha phase coherence between temporal regions (Dickinson et al., 2018). Other authors (Riva et al., 2019) showed that frontal alpha asymmetry in 6-month-old children correlates with ASD diagnosis at 24 months. Similarly, connectivity measures within the alpha band have also been linked to sensory symptoms assessed using behavioral scales (Han et al., 2017). These results point toward a decrease in long-range cross-talking, although additional evidence also reports an increase in short-range connectivity among the ASD population (figure 5.3) (Dickinson et al., 2018; Han et al., 2017; T. Zhou et al., 2020). In general, these connectivity patterns seem to significantly differ from the ones found in neurotypical individuals, reflecting an atypical brain network development in ASD. Specifically, while neurotypicals show a strengthening of long-range connections and a weakening of short-range ones with aging, the opposite tendency can be seen in ASD (Dickinson et al., 2021; Ghanbari et al., 2015). Furthermore, several studies based on connectivity measures (Tarasi et al., 2021; Tarasi, Trajkovic, et al., 2022; Ursino et al., 2022) highlight the role of the directional interactions among brain areas in ASD. In more detail, ASD individuals show a prevalence of ascending connections from posterior to anterior areas, pointing to a tendency to convey more bottom-up information. Altogether, and consistent with previous literature (Courchesne

et al., 2007; Wass, 2011), these pieces of evidence highlight electrophysiological abnormalities in ASD (i.e., reduced interhemispheric connectivity over temporal and frontal regions). Since these aberrant modulations appear at early stages of development, they tend to be accompanied by anatomical disturbances, including atypical axon numbers, synaptogenesis, and pruning (Courchesne & Pierce, 2005; T. Zhou et al., 2020). Altogether, these alterations seem to significantly contribute to the perceptual deficits and clinical manifestations of ASD.

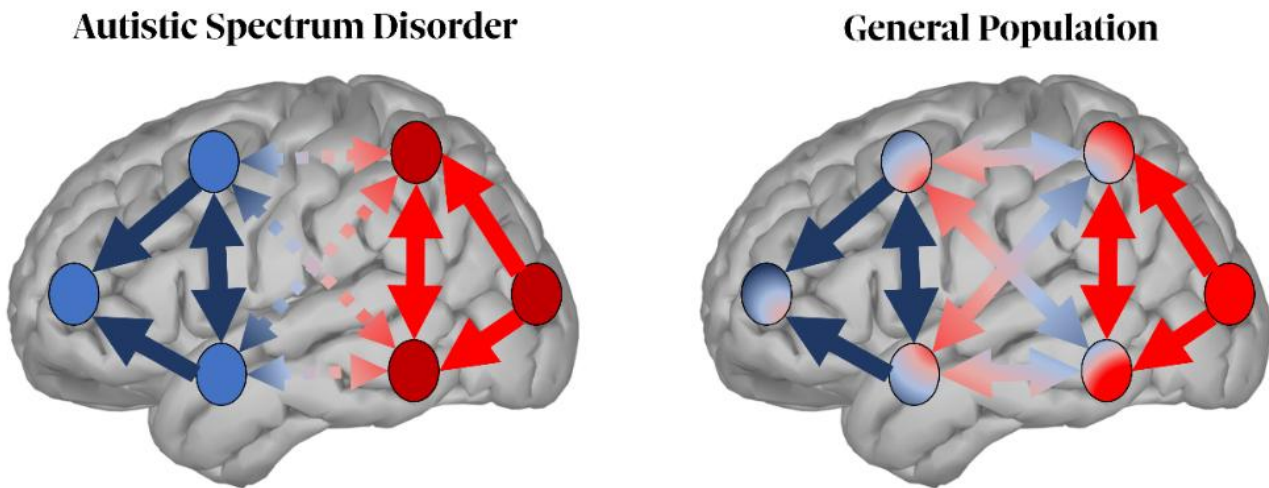


Figure 5.3 Imbalance in alpha connectivity in ASD relative to typically developing individuals. Persons with ASD show a local increase in connectivity in both posterior and anterior areas, while long-range connectivity between these two regions is reduced (dashed lines). Conversely, neurotypical individuals show the opposite pattern, resulting in a minor local integration (shaded circles).

A large number of studies also associated brain oscillatory activity with ASD symptoms. Specifically, Machado and colleagues (Machado et al., 2015) investigated the role of PSD in sensory elaboration in ASD, using a visual and audiovisual passive task. They reported a reduction in alpha power and an increase in slow-delta, high-beta, and gamma bands. This seems to be mainly due to the role that the alpha phase plays for the integration of cortical information, supporting executive function and the response to sensorial stimuli via the modulation of neuronal excitability (Palva & Palva, 2011). Coherently, Han et al. (Han et al., 2017) reported that brain connectivity within the alpha band correlates with symptom severity in ASD, specifically with the “sensory stimuli and relating behavior” subscale of the Autism Behavior Checklist. This alteration in brain activity may be responsible for a disruption in the excitatory/inhibitory balance and, consequently, may affect the neural response, leading to biased behavioral responses to sensory stimuli. Such imbalance could partly explain the unusual interest in simple objects characterizing people with ASD (Han et al., 2017; Palva & Palva, 2011). In line with this evidence, studies addressing how ASD individuals allocate attentional

resources have revealed abnormal processing of the upcoming stimuli. Specifically, during an intersensory attention task, in which the suppression of a distractor is relevant to reaching good performance levels, ASD individuals do not show the anticipatory power increase in the alpha band over parieto-occipital areas that is seen in neurotypical individuals before the distracting stimuli (J. W. Murphy et al., 2014). The lack of this preparatory activity has been associated with impaired performance due to the presence of task-irrelevant sensory information. Furthermore, people with ASD did not exhibit any posterior alpha desynchronization (with the resulting reduction in power) during the appearance of a relevant target, which was associated with impaired behavioral performance and increased ASD symptomatology (Keehn et al., 2017). Thus, these aberrant alpha power modulation patterns seem to be linked to impairments in perceptual suppression of irrelevant sensory information, contributing to difficulties in focusing on relevant stimuli (Han et al., 2017; Palva & Palva, 2011).

Another EEG measure linked to ASD symptoms is the mu–alpha suppression, i.e., a reduction in the alpha power over sensorimotor areas during action execution or observation of actions and facial expressions (Niedermeyer & Da Silva, 2005). Consistent with the mirror neurons hypothesis, mu suppression reflects the internal simulations of others’ actions, allowing one to better understand their intentions (Wood et al., 2016). Several studies (Ewen et al., 2016; A. Liu et al., 2018) have shown less consistent mu–alpha suppression in ASD, which is possibly related to social deficits.

In conclusion, due to its heterogeneous manifestations, ASD can be challenging to diagnose using behavioral scales. The findings described here indicate that some of its symptoms can be linked to specific neural alterations, thus legitimatizing the search for neural markers of ASD. Thus, finding an electrophysiological correlate of ASD would considerably support and ease the diagnostical evaluation.

5.4.2 EEG Indices for an Early ASD Diagnosis

Despite the significant number of electrophysiological measures available in the literature, there is still a lack of concordance regarding which index would best represent an anatomical marker of ASD to assist an early diagnosis (Kessler et al., 2016; Matlis et al., 2015). In fact, several MEG and EEG studies have reported anomalies in one or more frequency bands in ASD, linking these indices to symptom severity. Yet, the results are often conflicting (Carter Leno et al., 2021; Cornew et al., 2012; Fauzan & Amran, 2015; M. D. Gregory & Mandelbaum, 2012; Kareem Abd & Kadhim, 2022; Lefebvre et al., 2018; Levin et al., 2020; Ronconi et al., 2020; Takesaki et al., 2016). This seems to be attributable to the great discrepancies between experimental design and procedures, as well as sample discrepancies (e.g., some studies were conducted on children, while others on adults, some on persons

with a low- or high-functioning profile, under or without medications, etc.) (Cornew et al., 2012; Edgar et al., 2019; Mohammad-Rezazadeh et al., 2016; J. Wang et al., 2013).

An EEG study from Matlis and colleagues (Matlis et al., 2015), conducted on a large sample of children with ASD, showed a robust reduction in the peak alpha-ratio (i.e., reduced posterior to anterior power ratio) in persons with ASD. The authors also used this index as an electrophysiological marker for ASD, reaching high accuracy levels. These results suggest that ASD individuals may have higher power values over the anterior areas, which correlates with behavioral inhibition and sociability (Knyazev, 2010; Knyazev et al., 2012). A recent study (Dickinson et al., 2021) used the EEG data obtained from the spontaneous brain activity in 3-month-old infants to predict a later ASD diagnosis. This study highlighted that the best predictors of a later ASD diagnosis at 18 months are a lower frontal and a higher fronto-temporal connectivity. These results are consistent with the literature indicating the presence of hypoconnectivity within the frontal regions, which is in line with the executive and social difficulties among the ASD population (Just et al., 2012; Lombardo et al., 2011). Similarly, Orekhova et al. (Orekhova et al., 2014) demonstrated that high-risk 14-month-old infants later diagnosed with ASD showed higher alpha-based connectivity over the fronto-central areas. These results are in line with the aforementioned studies (Fair et al., 2009; Supekar et al., 2009; T. Zhou et al., 2020) suggesting that ASD individuals are associated with a shift from early white matter maturation during infancy to hypoconnectivity with aging.

Altogether, these data suggest the presence of an excitation–inhibition unbalance in the neural excitability in persons with ASD (Kessler et al., 2016; Rubenstein & Merzenich, 2003; Simon & Wallace, 2016). This feature could be responsible for a modified signal-to-noise ratio, resulting in an altered sensorial experience. In fact, due to the abnormal levels of cortical excitability, these individuals could be characterized by hypo- or hyper-responsiveness to sensorial stimuli, thus affecting several cognitive and perceptive domains. Therefore, such electrophysiological alterations may underlie perceptual alterations, contributing to explanations for some of the distinctive symptoms of ASD. The gamma band has been demonstrated to have a key role in these dynamics, given its involvement in the binding of perceptual information into one coherent whole via the integration of responses from near areas (Singer & Gray, 1995). However, the results involving the measurement of the gamma frequency are often conflicting, since its large frequency spread makes it difficult to track the phase between brain areas (Kessler et al., 2016). To avoid these difficulties, it can be useful to use cross-coupling indices, in which the phase of a lower frequency oscillation in one area has been shown to modulate the amplitude of a higher frequency in another area (Canolty & Knight, 2010). Due to its involvement in top-down processing and the perceptual experience (Arnal & Giraud, 2012; van Driel et al., 2014), alpha power has been demonstrated to be a promising index for the study of ASD-related

difficulties. In addition, this index is highly sensitive to alterations in long-range connectivity (Engel et al., 2001; Jensen et al., 2015). Thus, integrating both frequencies using the alpha–gamma PAC could provide an accurate depiction of the local and global connectivity (Palva & Palva, 2011). Several studies report altered alpha–gamma PAC among the ASD population (Berman et al., 2015; Khan et al., 2013; Seymour et al., 2019), achieving a diagnostic accuracy of 90% (Khan et al., 2013). However, while Berman and colleagues (Berman et al., 2015) found an increased alpha–gamma PAC within the ASD group, other studies (Khan et al., 2013; Seymour et al., 2019) reported the opposite result. This discrepancy is likely due to differences in the experimental designs (resting state vs. visual task EEG recording) (Berman et al., 2015; Khan et al., 2013; Seymour et al., 2019). In general, as suggested by Kessler et al. (Kessler et al., 2016), alterations in the alpha–gamma PAC may reflect an imbalance between excitatory/inhibitory activity in the perceptual brain network, resulting in a hypo- or hyper-sensitivity to various classes of stimuli and, thus, different clinical manifestations among the ASD population. This explanation could clarify the conflicting results (Table 5.4) about the alpha–gamma PAC, and then help to understand the nature of the perceptive alterations in individuals with ASD.

Table 5.4. Table representing the main electrophysiological findings in the ASD, with the methods and the studies who contributed to them.

Autistic Spectrum Disorder (ASD)		
Studies	Analytic Method	Main Findings
Murphy et al, 2014; Machado et al, 2015; Keehn et al, 2017;	Task-induced PSD	Impaired modulation of Alpha power
Knyazev et al, 2012; Matlis et al, 2015; Riva et al, 2019;	Topographical distribution of Alpha power	Aberrant Alpha power in frontal regions
Khan et al, 2013; Berman et al, 2015; Seymour et al, 2019;	PAC	Aberrant Alpha–Gamma PAC
Khan et al, 2013; Orekhova et al, 2014; Ghanbari et al, 2015; Han et al, 2017; Wolff et al, 2017; Dickinson et al, 2018; Zhou et al 2020;	Functional connectivity	Aberrant short- (enhanced) and long-range (reduced) functional connectivity
Ewen et al, 2016; Liu et al, 2018.	Evoked response during motor tasks	Less suppressed Mu–Alpha ERD/ERS over sensorimotor areas

5.5 Attention Deficit Hyperactivity Disorder (ADHD)

ADHD is a neurodevelopmental disorder defined by two main pathological clusters (Association, 2013): (A) marked difficulties in the deployment and maintenance of the attentional focus (likely due to ineffective suppression of distracting stimuli) during most daily-life activities; (B) hyperactivity and poor impulsiveness control (i.e., logorrheic behavior, interrupting or intruding on others, blurting out answers before questions are over, squirming in seat). These two different core symptoms might occur separately or jointly, and have been associated with impairments in sensorimotor mechanisms, reward processing, affective self-regulation, and executive functions (Cortese et al., 2012; Willcutt et al., 2005). While the onset of such symptoms occurs before the age of 12, they tend to persist in adulthood, often in comorbidity with anxiety disorders, depression, or substance abuse (Franke et al., 2018; McCarthy et al., 2012).

5.5.1 *The Role of Alpha Oscillations in ADHD's Symptomatology*

EEG analyses have played a pivotal role in the exploration of ADHD oscillatory biomarkers (Fingelkurts et al., 2007; Hinkley et al., 2011; Lejko et al., 2020). Although some findings might appear to be controversial due to the heterogeneity of ADHD phenotypes, existing literature suggests that individuals diagnosed with ADHD exhibit several alterations in oscillatory mechanisms crucial for cognition (see for instance (Michelini et al., 2022)). Mid-frontal theta (Bickel et al., 2012) and motoric beta alterations are often reported (Neuper & Pfurtscheller, 2001; Spitzer & Haegens, 2017) together with impairments involving posterior alpha rhythms. In particular, it has been observed that the anticipation of visual distractors is linked to an alpha activity decrease over the visual cortex in typically developing individuals, whereas the anticipation of relevant stimuli increases it (Klimesch, 2012; Lenartowicz et al., 2018). Moreover, an increase in the alpha power has been reported over relevant regions during high-demanding cognitive tasks, which is thought to suppress external inputs in order to support the relevant ones (Lenartowicz et al., 2018).

Consequently, ADHD's symptoms may depend on abnormal oscillatory neural activity. Such alterations may also help to explain the WM deficit in ADHD. For instance, Lenartowicz and colleagues (Lenartowicz et al., 2019) recorded EEG activity in a large sample of ADHD children during a spatial WM task. EEG parameters associated with encoding, vigilance, and maintenance functions were analyzed. During the encoding, reduced occipital alpha power was reported, while the maintenance phase was accompanied by a greater power increase in the alpha band, interpreted as a compensatory response to weak alpha activity during the previous encoding stage. Such a failure in

the encoding process was associated with poorer reading comprehension and executive functioning, as well with more severe ADHD symptomatology. Similarly, Hasler and colleagues (Hasler et al., 2016) found reduced alpha and theta anticipatory activity in adults with ADHD when engaged in bottom-up and top-down attentive tasks. Such patterns were thought to reflect dysfunctional neural dynamics underlying the suppression of distractors and the prioritization of relevant information (figure 5.4). The reduced ability to inhibit task-irrelevant stimuli may prompt or result from the enhanced tendency to mind-wander in ADHD. Some studies (Bozhilova et al., 2020, 2022) linked alpha and theta reduction to spontaneous mind-wandering, namely the attentional shift from the task at hand to inner and unrelated thoughts (Mooneyham & Schooler, 2013). The reduced ability to inhibit task-irrelevant stimuli may prompt or result from the enhanced tendency to mind-wander, and may trigger some of the core cognitive symptoms characterizing ADHD. In line with these considerations, Bozhilova and colleagues (Bozhilova et al., 2020) asked adults with ADHD to perform a Go/No-Go task, while mind-wandering reports and EEG data (relative to both response execution and inhibition) were collected. The authors reported a higher error rate in the ADHD group and increased reaction time variability, along with reduced event-related alpha and beta suppression during No-Go trials. A hierarchical regression model applied to these measurements unveiled that ADHD diagnosis and proneness to mind-wandering might share a common oscillatory deficit, consistent with the notion that mind-wandering may be a supplemental pathological facet of this disorder. These pieces of evidence have been further supported by a later study (Bozhilova et al., 2022), in which the authors reported how the reduction in the alpha and theta modulation in ADHD patients during WM and attentional paradigms is linked to mind-wandering episodes. Altogether, these findings suggest that alpha band alterations responsible for the impaired inhibition of task-irrelevant information might also underlie the increase in mind-wandering episodes.

Accordingly, a review by Lenartowicz and colleagues (Lenartowicz et al., 2018) highlighted how such attenuation in alpha suppression during visuo-attentional tasks is primarily linked to the ADHD inattentive profile, along with atypical lateralization patterns. Neurotypical individuals engaged in visuo-attentional paradigms show inter-hemispheric modulations in posterior alpha power. In particular, ERD is commonly reported in the hemisphere contralateral to the attended stimulus, while ERS is reported ipsilaterally. This inter-hemispheric imbalance is altered in ADHD patients, who do not display atypical modulations over posterior regions (Vollebregt et al., 2016). Similar results have been replicated by several different studies (Guo et al., 2019, 2020; Longarzo et al., 2020; Mazaheri et al., 2014; Ter Huurne et al., 2017; Yordanova et al., 2013). Specifically, Guo et al., (Guo et al., 2019) adopted a visuospatial attentional task in which the stimulus onset could be primed by a cue consisting of a gaze pointing toward either the left or right hemifield. The authors reported that, in the

control group, an alpha lateralization with ERD was present in the hemisphere contralateral to the hemifield containing the to-be-attended upcoming stimuli, while children diagnosed with ADHD did not exhibit such a lateralization. This aberrant modulation was more pronounced in the left hemisphere, and was proven to correlate with both behavioral performance and severity of the inattentive symptoms. Interestingly, this lateralization pattern has been observed even over the sensorimotor areas when employing a motor task (Ter Huurne et al., 2017). In this case, a reduction in the mu–alpha power over sensorimotor regions was reported to occur within the hemisphere contralateral to the hand performing the task in the neurotypical group, but not in ADHD. Moreover, in the ADHD group, a correlation was found between the aberrant lateralization in the oscillatory pattern and both the behavioral performance and difficulties to control disruptive motor activity and attentional processes in daily life.

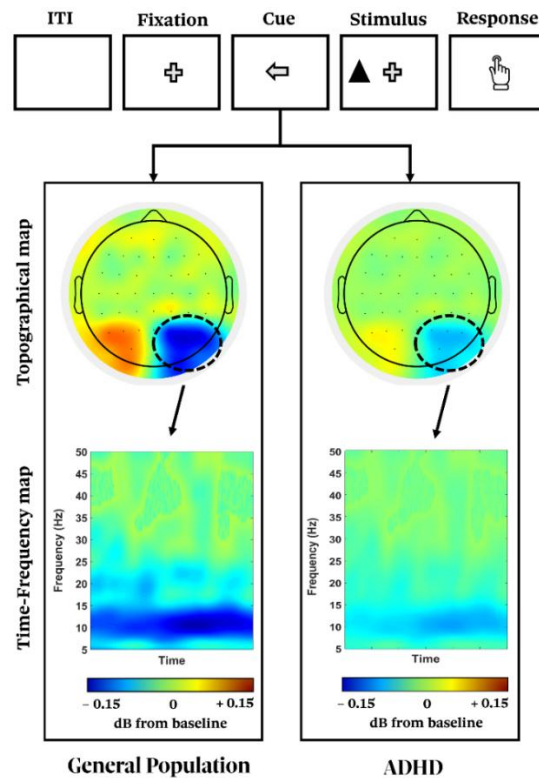


Figure 5.4 Simulated data showing a demeaned modulation in the inhibitory alpha power in ADHD (relative to controls) during the anticipation of a target stimulus in a visual task. Noteworthy, the lack of modulation comprises both contralateral ERD and ipsilateral ERS.

Altogether, these results emphasize once more how the pathophysiological mechanisms triggering the symptoms of such a disorder might ensue from a deficient modulation of posterior alpha power, which may hinder the proper suppression of distracting information and, as a consequence, the allocation of attentional resources toward relevant stimuli. An interesting line of research, consequently, attempted to artificially modulate alpha activity with the aim of inducing shift in performance and in the symptoms' severity in individuals with ADHD.

5.5.2 Normalizing Alpha Power Using the Neurofeedback Technique

As mentioned above (Guo et al., 2019; Lenartowicz et al., 2018; Vollebregt et al., 2016), imbalanced alpha oscillations are an important biomarker of ADHD symptomatology. Accordingly, many authors used neurofeedback to normalize alpha power imbalances in ADHD patients. Neurofeedback-based protocols consist of training sessions where the participants learn to self-modulate their brain oscillations through real-time feedback, with the aim of concurrently reshaping specific behavioral routines (Arns et al., 2014; Loo & Makeig, 2012). The effectiveness of such approach in ADHD patients has been demonstrated by Escolano and colleagues (Escolano, Navarro-Gil, Garcia-Campayo, Congedo, & Minguez, 2014), who were able to enhance fronto-midline upper alpha power in ADHD children undergoing 18 training sessions. The authors reported improvements in neuropsychological tests assessing WM, concentration, and impulsivity. Indeed, boosting alpha power appeared to generate a rebound effect that entailed a robust task-related alpha power decrease. A similar approach has been employed in another study (Deiber et al., 2020) in which the authors induced a rebound effect through a neurofeedback protocol aimed at desynchronizing the alpha power during a Go/No-Go task. This resulted in a subsequent power normalization, and in improvements in terms of motor inhibition. Furthermore, results highlighting the relevance of alpha desynchronization in attentive visual paradigms (Lenartowicz et al., 2018) have been adopted to reduce the power in this frequency range via neurofeedback protocols in ADHD individuals, prompting significant improvements to sustained attention (Mishra et al., 2021).

In conclusion, the literature revealed how some electrophysiological features such as the posterior alpha suppression seem to be linked to the occurrence of ADHD symptomatology (Lenartowicz et al., 2018, 2019; Loo et al., 2018; Vollebregt et al., 2016). These findings are further strengthened by neurofeedback studies, which highlighted how normalizing these aberrant oscillatory patterns could benefit ADHD patients. Altogether, these pieces of evidence (Table 5.5) underline the benefits of looking into oscillatory activity in the alpha band, as well as how this kind of information can be used to induce an amelioration.

Table 5.5 Table representing the main electrophysiological findings in ADHD, with the methods and the studies who contributed to them.

Attention Deficit Hyperactivity Disorder (ADHD)		
Studies	Analytic Method	Main Findings
Mazaheri et al, 2014; Hasler et al, 2016; Vollebregt et al, 2016; Lenartowicz et al, 2018; Guo et al, 2019, Guo et al, 2020; Lenartowicz et al, 2019;	Topographical distribution of Alpha power during attentional tasks	Aberrant Alpha ERD/ERS lateralization

Yordanova et al, 2013; Lenartowicz et al, 2019;	Topographical distribution of Alpha power during motor tasks	Reduced Mu–Alpha ERD/ERS lateralization
Bozhilova et al, 2020; Bozhilova et al, 2022.	Evoked response during spontaneous mind wandering and tasks	Reduced Alpha ERD/ERS

5.6 General Conclusions

The present work aimed to review the last 10 years of research on the role of alpha oscillations among the main neuropsychiatric disorders, such as SSD, MDD, ASD, and ADHD, to summarize the high volume of publications on these topics. The main findings suggest that individuals with SSD may display, in task-positive regions, a reduction in both the alpha power and frequency compared to healthy individuals, while in task-negative areas, the oscillatory power appears to be increased (J. S. Kim et al., 2014; Ramsay et al., 2021). Further, FAA has proven to be a valuable proxy of MDD emergence, since these patients seem to display an increase in the alpha power over the left frontal hemisphere, and a decrease in the right one compared to controls (Fingelkurts & Fingelkurts, 2015; Jaworska et al., 2012). In individuals with ASD, ground evidence suggests the presence of an imbalance in the alpha band's neural connectivity, with a local increase in short-range connectivity in both the posterior and anterior networks, while the long-range connectivity between these two regions is reduced (Courchesne & Pierce, 2005; Dickinson et al., 2018; Han et al., 2017). Lastly, a lower modulation of contralateral alpha ERD and ipsilateral alpha ERS has been found in ADHD during the anticipation of target stimuli in a visual task, when compared to typically developing individuals (Bozhilova et al., 2022; Lenartowicz et al., 2018).

Nonetheless, robust electrophysiological biomarkers of neuropsychiatric disorders are still difficult to identify. This seems to be due to the enormous differences in the clinical conditions and their behavioral manifestations. Furthermore, in the studies we considered, several methodological discrepancies emerged. In particular, some studies use high-density EEG while others do not, resulting in a range between 16 and 256 electrodes, and, similarly, important discrepancies can be found regarding the number of individuals included in the studies. Other relevant discrepancies concern the participants' age (children vs. adults), the disorder onset (first or not), whether the person is under treatment (behavioral/pharmacological), or the choice to record the EEG signal during a task or in a resting state condition. Moreover, a consistent heterogeneity can be seen in the biotypes included in the research (for instance, considering the inattentive, the hyperactive, or both subtypes in the ADHD sample). Altogether, these factors might lead to discrepancies in the scientific literature, despite

searching for the same condition. Thus, even the line of research focusing specifically on the role of alpha bands found conflicting results with small differences in the experimental methodology.

The current work also highlights how the availability of several EEG indices to address the same issue allows for a deeper understanding of certain specific aspects of the phenomena. Indeed, most of these measures are often based on the investigation of different alpha parameters, not allowing for a direct comparison between studies. This is often regarded as controversial evidence, making it difficult to draw parallels even with regard to studies sharing methodological similarities. Therefore, herein, we emphasize the importance for future research to adopt a standardized methodological procedure, allowing for a better comparison of these fragmented pieces of evidence. Such an approach might also help provide an overall conclusion regarding the magnitude of the effects found herein. This may strengthen our highlights, allowing researchers and clinicians to use the aforementioned finding to plan more effective evidence-based treatments tailored to each specific clinical phenotype. In this paper, we attempted to circumscribe these conditions and their electrophysiological peculiarities, for example by excluding from the current work studies investigating comorbidities. Forthcoming studies should fill this gap, since tracing links between these pathological conditions would provide a more exhaustive picture, possibly illustrating how these behavioral and neurophysiological features overlap. This would also help us to understand which alpha-based indices better explain the commonalities between these disorders.

In conclusion, the last 10 years of research have brought several proofs on the role of alpha oscillations in neuropsychiatric disorders. In particular, alterations in the alpha power and frequency have been reported in patients with SSD (J. S. Kim et al., 2014; Ramsay et al., 2021), whereas FAA has been proven to be able to discriminate MDD from healthy controls (Fingelkurts & Fingelkurts, 2015; Jaworska et al., 2012). Furthermore, an imbalance in the alpha band brain connectivity between long- and short-range regions has been observed in ASD (Courchesne & Pierce, 2005; Dickinson et al., 2018; Han et al., 2017). Finally, ADHD seems to display reduced alpha power during stimuli processing relative to controls (Bozhilova et al., 2022; Lenartowicz et al., 2018).

Hence, the alpha band indices may represent reliable and practical measures to support the clinician during the diagnosis formulation, the choice and the evaluation of a treatment, or the assessment of the symptoms.

Abbreviations:

ACC	Anterior cingulate cortex
ADHD	attention deficit hyperactivity disorder
ASD	autism spectrum disorders
dIPFC	dorsolateral prefrontal cortex
DMN	default mode network
DSM-5	diagnostic and statistical manual of mental disorders
EEG	electroencephalogram
ERD	event-related desynchronization
ERP	event related potential
ERS	event-related synchronization
FAA	frontal alpha asymmetry
IAF	individual alpha frequency
ITC	intertrial coherence
MDD	major depressive disorders
MEG	magnetoencephalography
mPFC	medial prefrontal cortex
OCC	occipital cortex
PAA	posterior/parietal alpha asymmetry
PAC	phase amplitude coupling
PCC	posterior cingulate cortex
PFC	prefrontal cortex
PPC	posterior parietal cortex
PSD	power spectral density
SSD	schizophrenia spectrum disorder
tACS	transcranial alternating current stimulation
tDCS	transcranial direct-current stimulation
TMS	transcranial magnetic stimulation
WM	working memory

Chapter 6: Rhythmic TMS as a Feasible Tool to Uncover the Oscillatory Signatures of Audiovisual Integration.

6.1 Introduction

How human perceptual systems handle signals gathered by our sensorium is pivotal to adaptive behavior. Relatedly, multisensory integration is perhaps the most demanding among the environmental challenges perception has to cope with (Calvert et al., 2004; Wallace et al., 2020). Bayesian theories posit that two main questions should be addressed for observers to efficiently accommodate modality-diverging inputs into a meaningful percept. First, they must ascertain whether such inputs share a common source (Körding et al., 2007; Shams & Beierholm, 2010). If so, they then need to evaluate how reliable are they in sensory terms (Angelaki et al., 2009; Knill & Pouget, 2004). Any failure to resolve either of these problems is likely to prompt misperceptions, fueling maladaptive responses and, in the long run, abnormal behavior (Hornix et al., 2019; Wallace et al., 2020).

To date, translational evidence is suggestive of far-reaching deficits in cross-modal processing across clinical phenotypes such as autism (Stevenson et al., 2014), dyslexia (Facoetti et al., 2010), and schizophrenia (Ross et al., 2007), in which hallucinations are the first-rank symptom. However, as novel biobehavioral models of perceptual decision-making emphasize (Tarasi, Trajkovic, et al., 2022), episodes of disrupted multisensory integration could be witnessed in healthy subjects as well. It is the case of cross-modal illusions, where the simultaneous (or near-simultaneous) occurrence of stimuli differing in modality misleads the observer either into perceiving a non-existing phenomenon, or not perceiving an existing one. Noteworthy examples are the McGurk effect (McGurk & Macdonald, 1976), the Rubber-Hand illusion (Botvinick & Cohen, 1998), and the Ventriloquist effect (Alais & Burr, 2004), which have been construed as a by-product of a sensory system overruling the other one it is interacting with. Along this line of literature lies also what has been referred to as the Sound-Induced Flash Illusion (SIFI, (Shams et al., 2000)).

In the SIFI, the presentation of a single flashing dot coupled with temporally close pairs of acoustic stimuli has been found to drive observers into reporting a second, illusory flash. As clarified by additional inquiries on the matter, the closer in time acoustic inputs occur, the likelier the SIFI (and vice versa) (Hirst et al., 2020; Shams et al., 2002). These dynamics subsume the broader functional architecture of cross-modal interplay, in which the sensory primacy of audition over vision has been thought to shape the latter's temporal binding windows (TBW). The cortical spots most likely to host these kind of operations have been proven to lie on both the occipital and temporal lobes, as well as

the pathways in between (Murray, Thelen, et al., 2016; Van Atteveldt et al., 2014). The former hosts the primary visual cortex, whose hemodynamic responses and structural integrity have been shown to predict SIFI proneness (de Haas et al., 2012; Watkins et al., 2006). Furthermore, anatomical evidence hints at a rich network of synaptical afferents branching out from primary auditory cortices to the occipital pole (Cappe et al., 2009; Meredith et al., 2009). Under this perspective, when temporal neurons fire in response to an acoustic stimulation (i.e. beeps), the resulting signals were shown to dictate windows of occipital excitability (i.e. TBWs) phase-locked at 10 Hz (Romei et al., 2007; Romei, Rihs, et al., 2008; Romei, Gross, et al., 2012).

Cognitive electrophysiology via electroencephalography (EEG) has been thus embraced to better detail the oscillatory underpinnings of this phenomenon, with a specific focus on posterior alpha rhythms (8-12 Hz). Away from cortical idling, phasic fluctuations within this frequency band have been proven to index cortical excitability (Ergenoglu et al., 2004; Romei, Brodbeck, et al., 2008; Romei, Rihs, et al., 2008), as well as deploy attentional resources via sensory gating (Jensen & Mazaheri, 2010; Klimesch et al., 2007), and route in a feedback fashion top-down predictions along the cortical hierarchy (Mayer et al., 2016; Samaha et al., 2015; Tarasi, di Pellegrino, et al., 2022; Zanto et al., 2011). Alpha oscillations have also been assumed to scaffold perception with a temporal frame, parsing the ever-flowing stream of visual events into discrete epochs, by virtue of their cycling rate (VanRullen, 2016; Varela et al., 1981). As principled by the discrete sampling hypothesis account, the faster (or slower) these rhythms oscillate, the higher (or lower) the observers' visual sampling rate, and their perceptual or cognitive accuracy (Bertaccini et al., 2022; Di Gregorio, Trajkovic, et al., 2022; Samaha & Postle, 2015, but see Buergers & Noppeney, 2022 for a different perspective).

Altogether, these assumptions are of uttermost relevance to the understanding of the SIFI. Indeed, the likelihood of reporting an illusory percept during SIFI paradigms was found to dramatically increase (vs decrease) for stimulus onset asynchronies (SOAs, i.e., the temporal spacing between auditory inputs within each acoustic pair, roughly corresponding to the inter-beep interval) lower (vs higher) than 100 ms (i.e. the average length of an alpha cycle) (Cecere et al., 2015). Spectral inquiries informed by such pieces of evidence substantiate a mechanistic scenario wherein specific prestimulus alpha features seem to be predictive of SIFI outcomes (Lange et al., 2014). In particular, the speed at which posterior alpha waves resonate (i.e. IAF, defined as the local power spectrum peak within the frequency band spanning from 7 to 13 Hz (Klimesch et al., 1993)) was shown to be intertwined with SIFI-related performance, with faster rhythms entailing a finer sampling rate, and reduced temporal windows wherein the illusion is experienced (Cecere et al., 2015; Keil & Senkowski, 2017).

The case for a causative contribution of alpha waves to the SIFI was further bolstered via transcranial alternating-current stimulation (tACS). When delivered at the proper frequency rate, tACS ignites a

physiological response known as “entrainment” (i.e. fine-tuning of endogenous neuronal firing to a frequency imposed by an external oscillator) (Bender et al., 2019; Helfrich, Schneider, et al., 2014; Thut, Schyns, et al., 2011; Wolinski et al., 2018). Crucially, entrainment allows for amplitude modulation, and to either up- or down-shift oscillatory peak frequencies toward faster or slower cycling rates (Herrmann et al., 2013; Romei, Thut, et al., 2016). Concerning the SIFI, entrainment-based paradigms confirmed that prestimulus alpha rhythms orchestrate multisensory synergisms, by dictating the observer’s perceptual sampling rate via their frequency peak (Cecere et al., 2015). However, no actual evidence linking the behavioral readouts of this illusory phenomenon with tACS-driven changes to IAF’s speed has been gathered so far, as it is still a matter of lively debate whether any online EEG recording is viable when delivering such protocol (Kasten & Herrmann, 2019; Neuling et al., 2017). Of note, slower IAFs coupled with higher proneness to the SIFI (i.e. wider TBWs), have been recursively found in individuals lying along the schizophrenic continuum (Ferri et al., 2018; Haß et al., 2017; Ramsay et al., 2021; Trajkovic et al., 2021), with the degree of impairment in both domains proportionate to the severity of positive symptomatology. These findings reinvigorate the translational virtue of combining cross-modal tasks, such as the SIFI, with electrophysiology and neurostimulation. A promising tool that might serve this purpose is transcranial magnetic stimulation (TMS). TMS-based protocols entail the release of transient magnetic bursts over a distinct scalp region, which perturb the electric homeostasis of the cortical mantle lying underneath (Rossi et al., 2021). Besides being a safe and non-invasive technique, TMS has been shown to stand as a worth supplementation of tACS (Thut, Veniero, et al., 2011; Trajkovic et al., 2022). This approach harnesses the entraining nature of rhythmic-TMS (rhTMS), and has often been capitalized upon the same way as tACS (Coldea et al., 2022; Riddle et al., 2019, 2020; Romei et al., 2011; Romei, Thut, et al., 2012), and paired with online EEG recordings. As of today, combined rhTMS-EEG was used to uncover what resonating frequencies are best suited for, respectively, optimal propagation of motoric signals (Romei, Bauer, et al., 2016), auditory working memory performance (Albouy et al., 2017), and visual detection (Stengel et al., 2021; Vernet et al., 2019). With regard to the latter, causal evidence for the mechanistic contribution of alpha waves to visual sampling (i.e. discrete sampling hypothesis) has recently been provided through TMS-driven rhythmic entrainment (Di Gregorio, Trajkovic, et al., 2022). All in all, rhTMS appears to be endowed with many convenient features for charting the oscillatory mechanics that govern perception, multisensory integration, and, more narrowly, the SIFI. However, two main issues hinder the implementation of rhTMS routines in audiovisual tasks, and both concern the physics relative to TMS. First, each magnetic pulse the machine emits is concurrent with a loud clicking noise, which might peak up to 80 decibels. As audiovisual tasks such as the SIFI revolve around illusory visual experiences conveyed by timed acoustic stimuli, a crucial question to be

addressed is whether TMS-associated clicks impact or not the perceiver's proneness to double-flash reports, either by enhancing or most likely disrupting the illusory percept. Relatedly, every magnetic pulse elicits cutaneous sensations and muscle twitches over the scalp. Given the impact somatosensations have on the illusion itself (Cooke et al., 2019; Fotia et al., 2021; Violentyev et al., 2005), it remains to be tested the degree to which rhTMS interacts or not with the SIFI, prompting unintended changes to the illusory rate.

In light of these considerations, the translational meaning of the SIFI as a proxy of multisensory deficits along the schizotypal continuum, the orchestrating role ascribed to posterior alpha rhythms in regard, and the potential rhTMS-based investigations retain to explore such a relationship, we seek to clarify whether some preconditions fundamental to the adoption of this protocol are met. Namely, we want to ascertain whether TMS-induced clicking noise and cutaneous sensations might somehow perturb the behavioral readouts of the SIFI. We did so by tracking accuracy rates (i.e., inverse proneness to the illusion) of healthy individuals asked to perform a SIFI paradigm under different temporal conditions, while Sham and rhTMS were delivered (in a block-wise fashion) to the occipital pole at frequency rates matching the IAF, during the prestimulus time window. Importantly, as long as each of the aforementioned stimulation conditions are proven to exert no influence on the occurrence of the illusion, robust evidence will be provided for the feasibility of rhTMS as a tool to gather clinical insights into the oscillatory markers behind multisensory impairments witnessed in individuals suffering from schizophrenia.

6.2 Methods

6.2.1. Participants

All the experimental sessions were carried out at the Center for Studies and Research in Cognitive Neuroscience in Cesena (Italy). A total of 27 healthy and right-handed volunteers (22 females, mean age 23.11 ± 2.06 s.d. years old), naïve as to the purpose of the study, were recruited from a broader population of individuals who already participated in EEG studies performed at our laboratory between the end of 2022 and the beginning of 2023. Written informed consent was obtained from all the participants prior to the experimental testing, which was conducted in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna (Prot. 140758, 9 October 2018). All participants reported normal or corrected-to-normal vision, no history of psychiatric or neurological disorder, as well as no counterindication with respect to TMS protocols. No monetary compensation was provided for those who took part in the study.

6.2.2. Procedure

Each experimental session had a duration of approximately 70 minutes, and progressed as follow. Upon signing the informed consent, participants were seated on a chair, 57cm distant from a 17" CRT monitor (refresh rate 60 Hz, 1280x1024 resolution), in a dim-lighted and sound-attenuated room. An electrodeless EEG cap, arranged according to the 10-10 international system (i.e., 64 electrode spots), was fitted in order to pinpoint the location over the scalp (i.e., the occipital pole, electrode Oz) to be targeted via rhTMS. After receiving detailed instructions concerning the task, participants performed five interleaved blocks of a within-subjects SIFI paradigm. As literature shows (Shams et al., 2000), the SIFI entails the report of a second (i.e., illusory) visual percept, when a single flashing dot is coupled with pairs of interleaved acoustic stimuli. Such effect is reliant on the temporal spacing between auditory inputs (i.e., SOAs), whose length has been proven to modulate the propensity to experience the illusion (Cecere et al., 2015; Shams et al., 2000). On average, SOAs shorter vs longer than 100 ms have been associated with an increase vs decrease in the proneness to the SIFI. As such, the SIFI task herein employed was characterized by three distinct SOAs (i.e., 50, 100 and 150 ms), presented in a randomized order across trials within each block. This allowed us to cover, respectively, three different behavioral scenarios: higher (i.e., 50 ms SOA), medium (i.e., 100 ms SOA), and lower (i.e., 150 ms SOA) likelihood of a double-flash report.

Importantly, each block differed in terms of stimulation conditions from all others. Participants completed a Baseline block (no stimulation provided), along with Sham and active rhTMS, both administered according to two different protocols: "overlapping" and "non-overlapping" (see Section 6.2.5 below), where the occipital pole was stimulated with an output frequency matching the IAF. This was done following a pseudorandomized counterbalanced order across individuals. That is, the Baseline block could occur, respectively, at the beginning, in the middle, or at the end of each experimental session. Likewise, the order of Sham and active rhTMS blocks was pseudorandomized following a counterbalanced design across subjects, which, however, was implemented independently from that adopted for the Baseline blocks (figure 6.1, a). This allowed to prevent any practice-induced bias from differentially perturbing behavioral measurements relative to a specific condition.

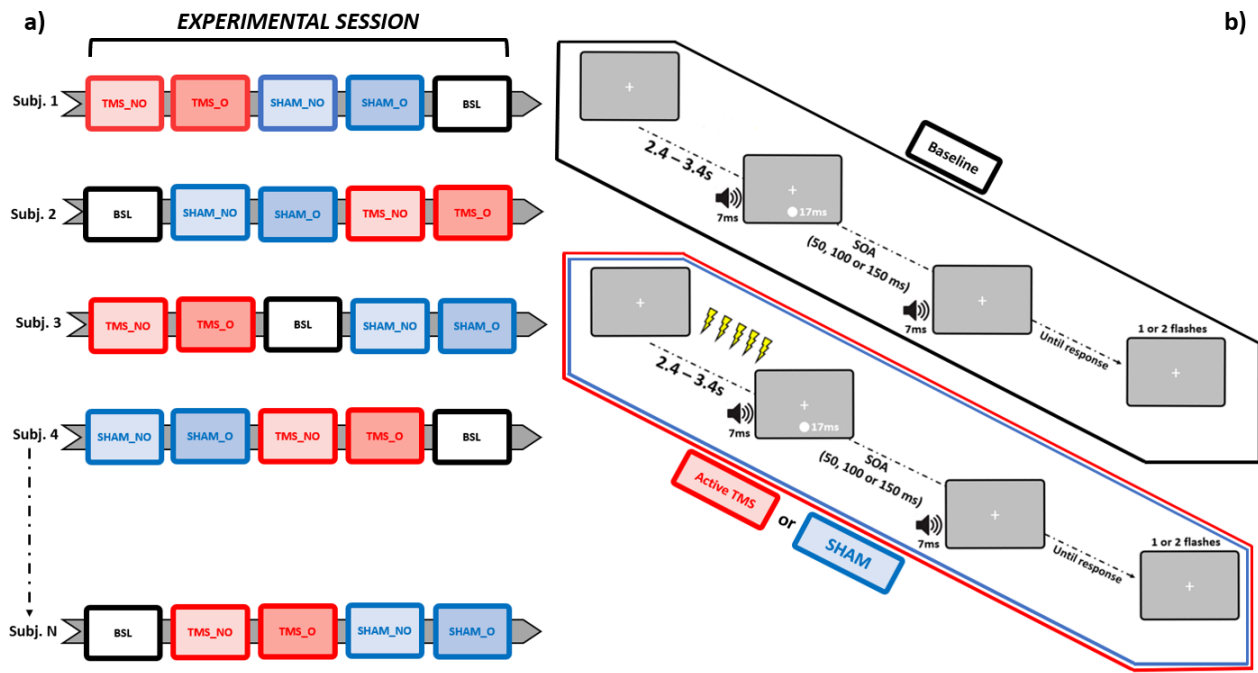


Figure 6.1 Schematic representation of, respectively, the pseudorandomized-counterbalanced design adopted for this study (**panel A**), and the trial structures relative to the SIFI task, sorted as a function of each stimulation condition (**Panel B**). BSL = Baseline, SHAM_NO = non-overlapping Sham, SHAM_O = overlapping Sham, TMS_NO = non-overlapping TMS, TMS_O = overlapping TMS.

6.2.2.1 SIFI Task

The SIFI was ran on a Matlab-equipped (version 2015b, MathWorks) Windows machine via Psychophysics Toolbox (version 3.0). Each trial started with a fixation cross presented on a grey background at the center of the screen. After a random time interval spanning from 2400 to 3400 ms, a single visual stimulus (white-colored circle subtending 2 degrees of visual angles, 5 degrees of visual angles below the fixation cross) was presented for the duration of a refresh rate (~17 ms for a 60 Hz monitor), simultaneously with a 7ms-long acoustic stimulus (~88 db sinusoidal tone at 3500 KHz, sampling rate 44.1 KHz) emitted from a pair of stereo PC speakers placed at both sides of the screen. After a SOA of either 50, 100, or 150ms, a second 7ms-long acoustic stimulus was emitted. At the end of each trial, participants were asked to report (by pressing a key button with their right hand), whether they saw 1 vs 2 flashes. Each trial's response type was stored for the subsequent statistical analyses. Let it be further highlighted that what resulted from this procedure was that, in every trial within each experimental session, one flash only was actually presented. As such, the occurrence of 2-flashes reports was to be ascribed to the illusory drive exerted by the SIFI itself. Every block consisted of 75 trials, equally distributed according to the three aforementioned SOAs (i.e., 25 trials per each SOA, presented in a randomized order), for a total of 375 trials per experimental session. During those experimental blocks (4 out of 5) in which rhTMS (either Sham or active) was delivered, magnetic

trains were discharged within the prestimulus time window. Namely, the temporal span immediately prior to the onset of the audiovisual pair (figure 6.1, b).

6.2.2.2 EEG Recordings

To control for the impact of both the Sham and active rhTMS protocols on the perceived illusion, participants' IAFs (as assessed from electrode Oz) were computed by resorting to resting state EEG data (rsEEG) previously recorded at our lab. According to the sampling rate hypothesis, stimulation at the IAF should not have any impact on the illusion rate, so that any modulation of the SIFI should be of non-cortical origin, and therefore similarly observed for both the Sham and active stimulation.

EEG data were recorded at rest, while participants seated on comfortable chairs in a dim-lighted and sound-attenuated room. rsEEG data had a varying duration spanning from 2 to five 5 minutes, and were recorded in the eyes-open condition (i.e. participants were asked to continuously stare at a fixation cross presented on a screen), using a 64 active Ag/AgCl electrodes cap (ActiChamp, Brain Products, Gilching, Germany), arranged according to the 10-10 international system. The software Brain Vision Recorder (Brain Products Italia Srl, Putignano, Italy) was used to record the electroencephalogram at 1000 Hz, at each electrode. Electrodes were online referenced to the FCz electrode, and impedance levels were kept below 10 k Ω . After the impedance check, and prior to the recording, the EEG trace was visually inspected to make sure no artifacts from non-physiological sources (e.g., power lines noise, bad electrode contact) were not contaminating the signal. This check was reiterated while rsEEG recording was ongoing, with a particular focus on occipital channels.

6.2.2.3 Rhythmic Transcranial Magnetic Stimulation (rhTMS)

Magnetic pulsations discharged during both the Sham and active rhTMS blocks were generated by a TMS machine (TMS Rapid, Magstim Company, Whitland, UK), and administered via a 70 mm figure-of-eight coil. Five interleaved biphasic pulses (maximum field strength ~ 1.55 T) were delivered over the cortical spot corresponding to the Oz electrode (as localized using the electrodeless EEG cap participants had to wear), during each trial's prestimulus time window. The coil was held tangentially to the scalp, with an orientation set to induce currents running in a posterior-anterior direction during active rhTMS blocks (figure 6.2, a). Conversely, Sham stimulation was performed by holding the coil orthogonally to the scalp. This latter orientation allowed us to keep the source from which pulses were emitted (and thus the clicking noise) as close as it was when delivering active rhTMS, whilst preventing the stimulation to be actually deployed. Maximal stimulator output (MSO) was set at 57%, an intensity level near to those associated with induction of visual phosphenes when TMS is delivered

to occipital loci (Romei, Thut, et al., 2012; Silvanto et al., 2005). TMS was administered in a rhythmic fashion by pacing the release of magnetic bouts according to the IAF. In brief, the inter-pulse interval (IPI, estimated in ms) within each train was set in order to mimic the speed at which the individual's alpha waves intrinsically oscillate ($IPI = 1000 / IAF$). Crucially, both Sham and active rhTMS have been delivered following two different timing protocols. In the “overlapping” blocks (e.g., SHAM_O and TMS_O), every train was discharged such that the last magnetic bout within was released in overlap with the presentation of the audiovisual pair, in line with most literature employing entrainment protocols (Albouy et al., 2017; Di Gregorio, Trajkovic, et al., 2022; Romei, Bauer, et al., 2016; Romei et al., 2011; Romei, Thut, et al., 2012; Ruzzoli & Soto-Faraco, 2014; Stengel et al., 2021; Vernet et al., 2019). On the other hand, in the “non-overlapping” blocks (e.g. SHAM_NO and TMS_NO) the last magnetic pulse in each train was transmitted an IPI prior to the presentation of the audiovisual pair (figure 6.2, b). Since rhTMS-induced entrainment after-effects are rather short-lived (Thut, Veniero, et al., 2011), this approach enabled us to disentangle whether trains delivered in overlap with the audiovisual pair (i.e. ensuring the soundest entrainment) might perturb or suppress the SIFI, as compared to “non-overlapping” trains. Germane to this, as our focus was also to clarify to which degree TMS-generated clicking noise might interact with the perception of task-related acoustic stimuli, we quantified the loudness of rhTMS clicks via a digital phonometer. This operation returned an intensity value of around 78 decibels, which prompted us to set the output of both the PC speakers at a slightly higher level (88 decibels, see Section 6.2.3). Timing and output parameters relative to the Sham and active rhTMS protocols were dictated in real-time through an automated routine implemented in MatLab, and a TriggerBox device (EMS medical) connecting the operating PC with the TMS machine.

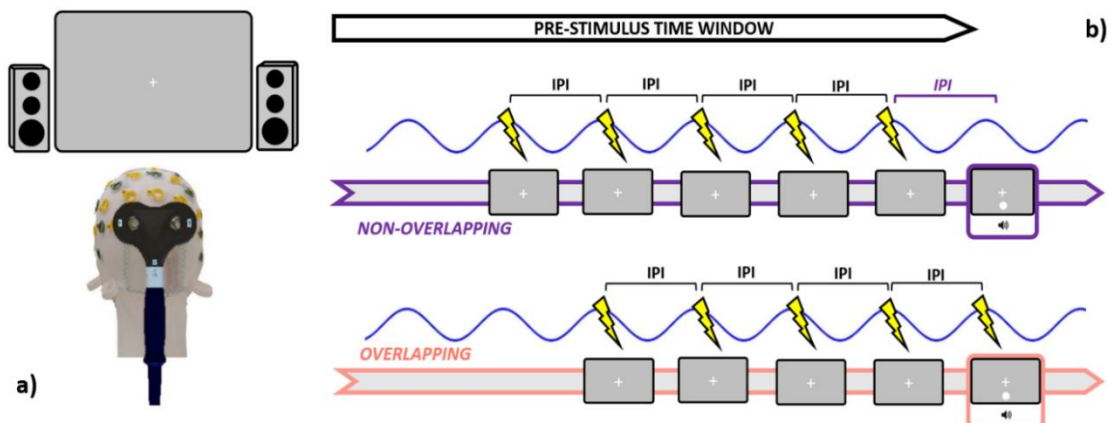


Figure 6.2 Graphical summary relative to the stimulation specifics. Panel **a)**: participants were seated 57cm distant from the screen, while active TMS was delivered to the occipital pole (electrode Oz) with the coil held tangentially to the scalp. Panel **b)**: during the prestimulus time-window, both Sham and Active TMS were delivered right before the occurrence of the audiovisual pair. In the non-overlapping conditions, the last pulse within each train was administered an IPI prior to the audiovisual onset, while in the overlapping conditions the last pulse was emitted simultaneously with the audiovisual pair. IPI = inter-pulse interval (1000/IAF).

6.2.3 Data Analyses

6.2.3.1 EEG Data Preprocessing and Individual Alpha Frequency (IAF) Peaks Extraction.

Preprocessing of rsEEG data was performed via EEGLAB (A. Delorme & Makeig, 2004). Signals from every channel were offline re-referenced to the average activity of all electrodes. Next, linear filtering was applied through a high-band pass of 1 Hz, and a low-band pass of 40 Hz, which allowed us to minimize power line noise and motor artifacts. Filtered data underwent a further visual inspection, where temporal segments containing residual noise at occipital channels were rejected and spherically interpolated. After these preliminary quality checks, power spectral density (PSD) estimate was performed, per each individual, on filtered data recorded from electrode Oz using Welch's method (*pwelch* MatLab function). Resting-state signals were parsed into 2 seconds segments with 25% degree of overlap. To reduce spectral leakage, a Hann-window was implemented on each segment, which was zero-padded to a length of 10 seconds to increase the frequency resolution up to 0.1 Hz. Each segment's power spectrum was then computed via Fast Fourier Transform, and averaged together with power spectra relative to all other segments. This procedure yielded the PSD estimate at each frequency bin, and was reiterated for Oz rsEEG data of every participant. Lastly, a custom-made MatLab algorithm was implemented to extract the IAF from PSD estimate computed over rsEEG signals. This routine was designed to search for the frequency component within the narrowband spanning from 8 to 13 Hz that showed the highest power estimate. The output of this computation was double-checked by visually inspecting the PSD plot, to ensure the estimated peak was representing a deviation from the $1/f$ scaling of the EEG spectral activity.

6.2.3.2 Behavioral Data

Behavioral measurement kept track of performance accuracy (i.e., the inverse proneness to the SIFI: the higher the accuracy rates, the lower the propensity to experience the illusion), which was computed separately per each experimental block (i.e., each stimulation condition: Baseline, SHAM_NO, SHAM_O, TMS_NO, and TMS_O) as a function of the SOA (50, 100, and 150 ms). As one flash only was presented in every trial, accuracy rates were thus calculated as the ratio between the amount of correct responses (1-flash reports, being 2-flashes reports illusory in nature) over the total amount of trials. Such procedure yielded 15 distinct accuracy rates (one per each SOAs and stimulation condition), which were then entered into the statistical analyses.

6.2.3.3 Statistical Analyses

All statistical analyses were performed via jamovi 2.3.21 (the jamovi project, 2021) and JASP 0.16.4 (the JASP team, 2022). We first approached our behavioral data by preliminarily analyzing accuracy rates at Baseline. This was done to ascertain whether the SIFI actually occurred at the group level (i.e., decreasing proclivity to report an illusory percept as the SOAs increased). To this aim, a repeated measure ANOVA (rmANOVA), having one within-subjects factor with three levels (corresponding to the three SOAs) was ran on mean accuracy rates. After, in order to address the main questions upon which the rationale of the current study rests, a further rmANOVA was performed. This analysis was designed to have stimulation condition (Baseline, SHAM_NO, SHAM_O, TMS_NO, and TMS_O) and SOAs (50, 100, and 150 ms) as within-subjects factors, and mean accuracy rates as the dependent variable. This course of action enabled us to clarify whether rhTMS might be a convenient tool to investigate SIFI-related mechanics, by testing for example whether the entrainment protocol set at IAF modulates, as compared to Baseline, the illusion or not (providing a first causal demonstration against vs in favour to the sampling rate hypothesis); or rather, disrupts the illusory phenomenon, due to any by-product thereof (clicking noise, cutaneous sensations).

As the key scope of this study was to detail whether (and how) any of the stimulation protocols might differentially disrupt the occurrence of the illusion, the results yielded by this 5 x 3 rmANOVA were further explored via Bayesian Informative Hypotheses (BAIN). Compared to null-hypothesis testing, this approach allows us to directly evaluate how well a statistical model (built upon an hypothesis of interest) explains the experimental data. This could be achieved through the Bayes theorem by computing, per each hypothesis, the posterior model probability (PMP). Such parameter, whose values span from 0 to 1, returns an estimate about the extent to which the associated model (as compared to a set of competing hypotheses) finds support from the empirical data. Accordingly, the higher the PMP, the higher the probability that the underlying hypothesis might be the best suited to describe the experimental evidence. Moreover, BAIN provides the possibility to contrast two distinct models (i.e., two distinct hypotheses), by comparing their relative PMPs and assessing whether one of them, relative to the other, has a higher probability of explaining the data (Hojtink et al., 2019; Degni et al., 2022). In light of this statistical pipeline, a preliminary analysis performed on G*Power (parameters: effect size $f = 0.25$; α error probability = 0.05; power = 0.80; number of groups = 1; number of measurements = 15) returned an optimal sample size of 21 subjects for this kind of experimental design, which brought us to recruit 27 volunteers.

6.3. Results

6.3.1 Accuracy Rates

Before moving to the core analyses, we first checked whether our data replicated findings regarding the SIFI, by running on accuracy rates at Baseline a one-way rmANOVA with SOAs (3 levels: 50, 100 and 150 ms) as a within-subjects factor. Results show a significant main effect of SOAs ($F_{2,52} = 22.6$, $p < .001$, $\eta_p^2 = .465$), which was further elucidated via post-hoc analyses using Bonferroni corrections. This procedure confirmed the occurrence of the SIFI at the group level, as accuracy rates at 150ms SOA ($M = .653$, $S.E.M. = .058$, $95\% C.I. = [.553 .773]$) proved to be significantly higher (all p -values $< .001$) than those relative to SOAs of 100ms ($M = .471$, $S.E.M. = .058$, $95\% C.I. = [.352 .590]$) and 50ms ($M = .307$, $S.E.M. = .050$, $C.I. = [.204 .410]$). Likewise, accuracy rates at 100ms SOAs displayed significantly higher values as compared to those at 50 ms (p -value $< .05$). These data replicate findings relative to the differential impact that SOAs exert on the illusion, with larger SOAs decreasing the likelihood of perceiving a second, illusory flash (results depicted in figure 6.3).

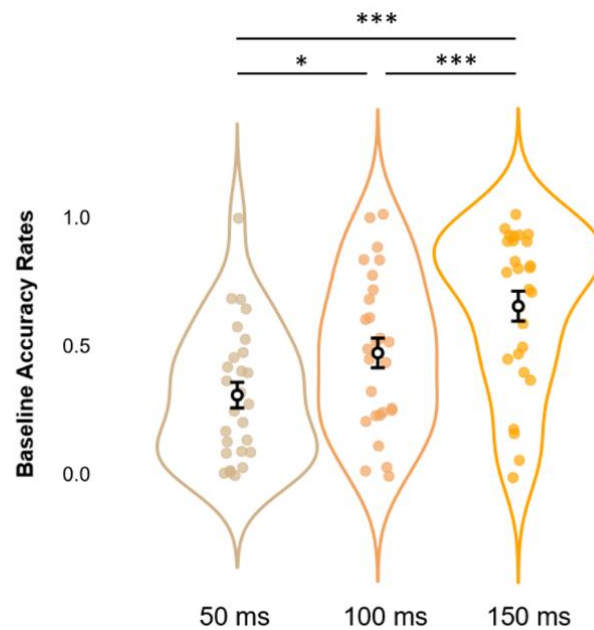


Figure 6.3 Estimated marginal means (error bars expressed as 95% standard errors), and violin plots relative to Baseline Accuracy Rates. The graph shows observed Accuracy Rates scores (x-axis), sorted as a function of each different SOA (50,100,150 ms ; y-axis). * = $p < .05$, *** = $p < .001$

We next performed our main analysis on accuracy rates, to clarify whether rhythmic stimulation at occipital loci, delivered via Sham and active protocols, differentially affected or not the proneness to the SIFI. To this end, a 3 x 5 rmANOVA with SOAs (3 levels: 50, 100 and 150 ms) and Condition (5 levels: Baseline, SHAM_NO, SHAM_O, TMS_NO, and TMS_O) as within-subjects factors, and

mean accuracy rates as dependent variable, was performed. Whereas a significant and robust main effect of SOAs was returned ($F_{2,52} = 34.13, p < .001, \eta^2 p = 0.568$), the analysis did not yield any main effect of Condition, nor any significant interaction of SOAs*Condition (all F -values $_{(4,104)(8,208)} < 2.31$, all p -values $> .05$, all $\eta^2 p < 0.081$).

Post-hoc analyses via Bonferroni corrections confirmed the effects observed in the Baseline condition alone. Independently of Condition, we compared within-subjects levels relative to the significant main effect of SOAs. Results suggest a pattern where Condition-collapsed accuracy rates at 150ms ($M = .663, S.E.M. = .045, 95\% C.I. = [.570 .755]$) appear to be higher (all p -values $< .001$) than those at 100ms ($M = .508, S.E.M. = .050, 95\% C.I. = [.404 .611]$), and 50ms ($M = .316, S.E.M. = .046, 95\% C.I. = [.222 .410]$). In the same vein, Condition-collapsed accuracy rates reported for 100ms SOAs were shown to be significantly higher (p -value $< .001$) as compared to those at 50ms SOAs. All the above-mentioned results are depicted in figure 6.4

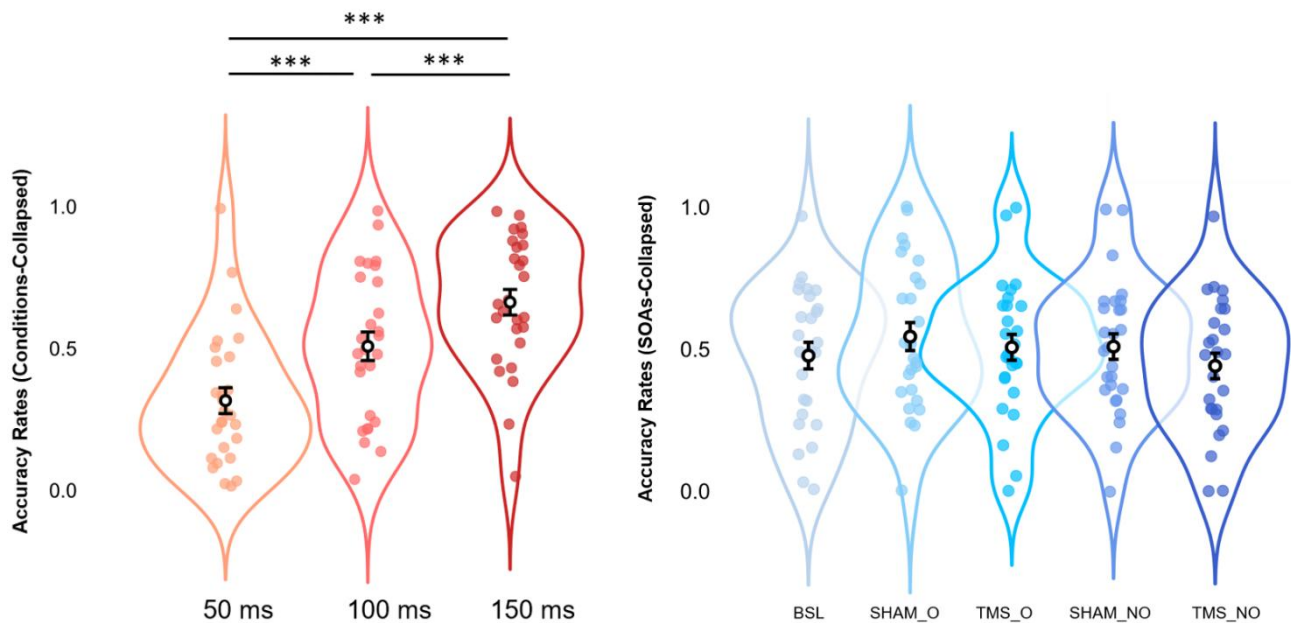


Figure 6.4 Estimated marginal means (error bars expressed as 95% standard errors), and violin plots relative to Condition-collapsed Accuracy Rates (leftmost panel), and SOAs-collapsed Accuracy Rates (rightmost panel). All graphs show observed Accuracy Rates scores (x-axes), sorted as a function of each different SOA (50,100,150 ms ; y-axes relative to the leftmost panel) or stimulation condition (BSL, SHAM_O, TMS_O, SHAM_NO, TMS_NO; y-axis relative to the rightmost panel). *** = $p < .001$

In light of the null findings revealed by the 5x3 rmANOVA regarding the effects of the stimulation protocols on the occurrence of the illusion, we implemented BAIN to better detail whether the equality constrained hypothesis (i.e., similar mean accuracy rates across stimulation conditions) indeed retains the highest probability to describe our data. As such, we developed six different hypotheses about mean accuracy rates, and the PMPs thereof were then tested against each other. The first hypothesis

(i.e. the one which we were focusing on) followed the results returned by the 5x3 rmANOVA, assuming that no significant difference in terms of accuracy rates (i.e. inverse proneness to the illusion) should be witnessed across conditions:

$$\mathbf{H_1: Baseline = SHAM_NO = SHAM_O = TMS_NO = TMS_O}$$

The second hypothesis was a broad one, and posited that, while no difference should be expected between active and Sham stimulation conditions (as well as between overlapping and non-overlapping stimulation protocols) the associated accuracy rates might be higher (i.e. reduced proneness to the illusion) than those relative to Baseline:

$$\mathbf{H_2: Baseline < SHAM_NO = SHAM_O = TMS_NO = TMS_O}$$

The third and fourth hypotheses trailed the second one, as they assume in a more specific fashion that an increase in mean accuracy rates (as compared to Baseline) might be at work, depending on whether Sham or active TMS was delivered:

$$\mathbf{H_3: Baseline < SHAM_NO = SHAM_O < TMS_NO = TMS_O}$$

$$\mathbf{H_4: Baseline < TMS_NO = TMS_O < SHAM_NO = SHAM_O}$$

Likewise, the fifth and the sixth hypotheses posited that an increase in mean accuracy rates (as compared to Baseline) should be expected as a function of whether the stimulation protocols, regardless of their active or Sham nature, were administered so as to overlap or not with the occurrence of the first audiovisual pair:

$$\mathbf{H_5: Baseline < SHAM_NO = TMS_NO < SHAM_O = TMS_O}$$

$$\mathbf{H_6: Baseline < SHAM_O = TMS_O < SHAM_NO = TMS_NO}$$

Results show that H_1 retained the highest relative probability ($PMPb = .743$), as compared to H_2 ($PMPb = .126$), H_4 ($PMPb = .060$), H_5 ($PMPb = .058$), H_3 and H_6 (both $PMPb$ values = $.006$), and H_u ($PMPb = .000$), which corresponds to unconstrained hypothesis representing any other set of relationships between the parameters other than those explicitly formulated (i.e. a “fail-safe” model that place no constraints on the parameters and mitigate the risk of selecting a set of bad hypotheses (Hoijsink et al., 2019; Van Lissa et al., 2021)). Accordingly, H_1 also displays the highest Bayes Factor ($BF.u = 921.501$), as compared to all other hypotheses hereby outlined (all $BF.u$ values < 155.935). Namely, when contrasting each of our hypotheses with H_u , H_1 corresponds to the model under which it appears more likely to report the patterns observed in our data, or else, the model receives the strongest support from our experimental evidence. All the above mentions results are depicted in figure 6.5.

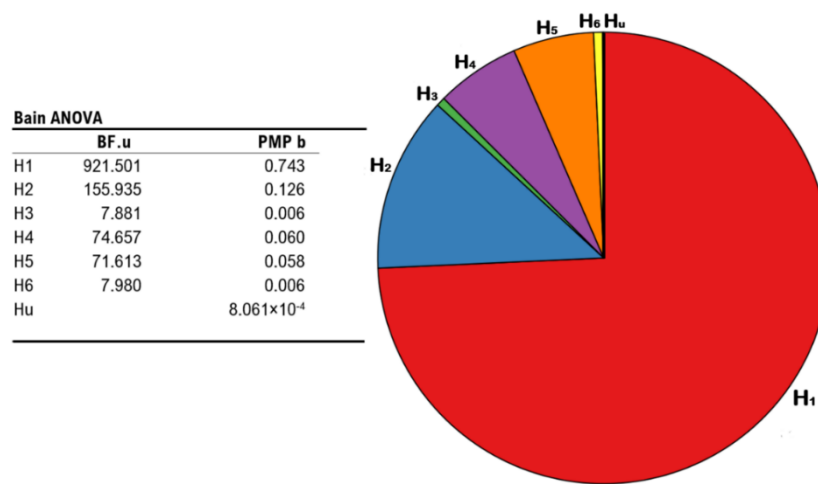


Figure 6.5 Results from BAIN regarding the impact of different stimulation protocols on the occurrence of the illusion. Leftmost panel: summary table showing Bayes Factors of each hypothesis vs the unconstrained hypothesis ($BF.u$), and posterior model probabilities of each model ($PMP b$), including the unconstrained hypothesis. Rightmost panel: pie chart of the posterior model probabilities relative to all six models (H_1 , H_2 , H_3 , H_4 , H_5 and H_6) including the unconstrained hypothesis (H_u).

6.4. Discussion

In this study we aimed to elucidate whether rhTMS may stand as a reliable tool with the potential to probe the cortical mechanics underlying the SIFI. In this regard, we investigated to which extent TMS-induced clicking noise and cutaneous sensations might perturb the occurrence of the illusion, as compared to Baseline. We addressed these experimental questions by delivering trains of interleaved magnetic pulses over the occipital pole during the prestimulus time window, at a frequency rate matching the IAF of individuals asked to perform the SIFI task. This was done with regard to both Sham and active rhTMS following two distinct protocols, such that the last pulse within each train

could either overlap or not with the occurrence of the audiovisual pair. Mean accuracy rates relative to each stimulation condition were tracked as behavioral proxies of the differential impact one of the stimulation conditions might exert on the SIFI.

To begin with, wide interindividual variability appears to subsume the SIFI. In our sample, we witnessed both illusion-prone participants (i.e., displaying accuracy rates close to 0 across different SOAs), as well as illusion-immune participants (i.e., displaying accuracy rates close to 1 across different SOAs). These data highlight how subjective in nature the SIFI is, and the degree to which the associated phenomenal outcomes might change as a function of individual factors (Hirst et al., 2020). Some of them have been linked to training conditions (Di Luzio et al., 2021), pathological aging (S. Chan et al., 2015), and most of all, clinical and subclinical neuropsychiatric conditions such as autism spectrum disorder (Stevenson et al., 2014), schizophrenia (Haß et al., 2017), and marked schizotypal traits (Ferri et al., 2018). At the empirical level, these two latter cases epitomize a biobehavioral continuum along which alterations within the perceptual (and phenomenal) domain qualitatively change depending on how severe the syndromic landscape is (Ettinger et al., 2014; Tarasi, Trajkovic, et al., 2022). Illusions entail misperceiving one or more properties of an actual object, whereas no such object exists at all (even though reported) when hallucinatory episodes occur (Macpherson & Batty, 2016). Accordingly, proneness to illusions such as the SIFI was found to be increased in both schizophrenic patients and individuals with high schizotypal traits (Ferri et al., 2018; Haß et al., 2017), whilst hallucinations are a syndromic hallmark of schizophrenia only. In brief, the worse the clinical scenario, the broader the phenomenal alterations. These pieces of evidence emphasize the translational meaning of the SIFI as a reliable index of multisensory deficits, which should be capitalized on to illuminate the putative pathomechanisms arbitrating the individual's trajectory toward a neuropsychiatric phenotype or another.

Away from these preliminary considerations, our analyses yielded rather intriguing results. First, we replicated findings concerning the reliance of the SIFI on different SOAs. Data collected at Baseline confirmed a higher propensity to double-flash reports (i.e., lower accuracy rates) for inter-beep delays around 50ms (Shams et al., 2000), with progressively increasing accuracy rates (i.e., lower proneness to the SIFI) as the SOAs got wider (Cecere et al., 2015; Ferri et al., 2018). The larger the inter-beep delays, the easier and more accurate the cross-modal integration.

Such findings provided a convenient departure point toward an in-depth inquiry about the impact different stimulation conditions may exert on the SIFI, as compared to Baseline. According to our results, none of the TMS protocols significantly perturbed the illusory rate. On the one hand, we delivered the Sham stimulation to assess whether TMS clicks might interfere with the ongoing perceptual processing of acoustic stimuli. We found no evidence for either an enhancement or

suppression of the double-flash report across each SOA, as compared to Baseline. Likewise, active rhTMS was administered to test for unintended changes to the illusory experience due to somatosensory sensations that come along with the stimulation. No such evidence was found either. In addition, this allowed to discount for a perceptual bias effect potentially induced by the rhTMS delivered precisely at IAF as causative for the illusory rate report, i.e., an alternative account to the sampling rate hypothesis (see (Buergers & Noppeney, 2022)). Both the Sham and active protocols were also set to either overlap or not with the occurrence of the audiovisual pair. As the former condition was proven to instantiate the maximal oscillatory entrainment (Di Gregorio, Trajkovic, et al., 2022; Thut, Veniero, et al., 2011; Trajkovic et al., 2022), we aimed to ascertain it did not prompt any differential alteration to the SIFI, as compared to the non-overlapping stimulation. Again, no difference between conditions could be found. These patterns were further corroborated via Bayesian statistics, which confirmed that the best-suited model to explain our observed data was indeed one where none of the stimulation protocols had an impact on the occurrence of the illusion. Taken together, these findings provide novel evidence about the feasibility of rhTMS-based interventions in the cortico-rhythmic scrutiny of audiovisual integration. That is, the experimental by-products engendered by rhTMS (i.e., clicking noise and somatosensations) do not jeopardize the occurrence of the illusion, whose cortical underpinnings could be thus further explored by means of this protocol. This is of uttermost significance in translational terms, as it implies that rhTMS could be capitalized on (in forthcoming studies) to gather clinical insights into the electrocortical signatures driving multisensory impairments witnessed in psychosis-prone individuals. Such considerations hold true especially with regard to the combination of rhTMS and EEG recordings.

Although EEG and neuromodulation have been separately exploited to this end (Cecere et al., 2015; Keil & Senkowski, 2017), no attempt to combine these techniques has been carried out until now, due to tACS-induced artifacts contaminating EEG signals (Kasten & Herrmann, 2019). The findings herein supplied pave instead the way to forthcoming inquiries in which both behavioral and electrocortical insights into the SIFI could be gained. Indeed, TMS (as compared to tACS) retains some favourable biophysical properties that ushered in the development of pipelines aimed at denoising EEG recordings from TMS-induced artifacts (Bertazzoli et al., 2021; Hernandez-Pavon et al., 2022; Rogasch et al., 2017). As such, TMS-EEG has progressively become a reliable approach to address what more oscillations can tell us about neural dynamics and their psychological correlates (Miniussi & Thut, 2010; Thut & Miniussi, 2009). TMS-EEG co-registration has so far been employed to explore the hodological architecture of the cortical connectome (Bortoletto et al., 2015), and whether any causal interplay between distinct neural nodes therein may occur under specific physiological or cognitive conditions (Massimini et al., 2005). Despite being focused on the response of local rhythms to an

external oscillator, online EEG matched with rhTMS fall within this framework as well (Albouy et al., 2017; Di Gregorio, Trajkovic, et al., 2022; Romei, Bauer, et al., 2016; Thut, Veniero, et al., 2011). When conflated with our results, these notions streamline the implementation of combined rhTMS-EEG to test for the oscillatory underpinnings of the SIFI. This even more so applies if the clinical significance of specific alpha features (i.e., IAF) to specific psychiatric disorders is factored in (Ippolito et al., 2022).

Aside from these considerations, our main analyses are also suggestive of an even stronger impact of SOAs on the likelihood of experiencing the illusion. Akin to what has been outlined at Baseline, wider inter-beep delays (as compared to narrower ones) come with a lesser proclivity to double-flash reports (Cecere et al., 2015; Hirst et al., 2020; Shams et al., 2000). This evidence remarks the robustness of the SIFI, and the extent to which this phenomenon is reliant on the cross-modal interplay between audition-relayed priors and occipital excitability (Meredith et al., 2009; Mishra et al., 2007; Romei, Rihs, et al., 2008). The more the former are conveyed within a temporal frame outpacing the spontaneous excitatory cycles (i.e. TBWs) of the visual cortex, the worse the multisensory operations are instantiated.

Germane to this notion, it could be argued that active rhTMS tailored at the IAF should have prompted an increase in alpha power and a reduction in cortical excitability, which might have in turn modulated the probability of reporting the illusion (Cecere et al., 2015; Romei, Brodbeck, et al., 2008; Romei, Rihs, et al., 2008). Our data provide no evidence in the support of such claim. These results might be construed borrowing distinct empirical and theoretical perspectives. For instance, the inverse relationship between the amplitude of alpha rhythms and the proneness to the illusion across SOAs was reported in one study only (Cecere et al., 2015) and has barely replicated ever since. Furthermore, the tie between transient fluctuations in posterior alpha power and visual performance has been recently couched within a broader conceptual framework accounting for signal detection theory (SDT) measurements, rather than accuracy per se (Samaha et al., 2020). While perceptual sensitivity (i.e., d') should be dictated by the cycling speed of occipital alpha waves (Di Gregorio, Trajkovic, et al., 2022), amplitude bursts in the same frequency band are assumed to channel sensory biases (i.e. response criterion) (Iemi et al., 2017) and shape metacognitive abilities (Samaha et al., 2017). As our experimental design was primarily planned to measure the feasibility for the application of the rhTMS protocol in testing the neural underpinnings of the SIFI without altering its phenomenological experience across individuals, it does not allow us, in its current form, to extract SDT-derived indices. Therefore, it remains an open question whether rhTMS modulation of either alpha power or frequency may causally impact the observer's sensory bias vs. perceptual sensitivity, when engaged in multisensory paradigms like the SIFI. Nevertheless, we have provided convincing evidence here that

this protocol is viable to causally test for the functional role of different oscillatory parameters in determining the SIFI. Moreover, although we could not disentangle with the current paradigm whether any modulation in the proneness to the illusion could be determined by a perceptual bias or change in perceptual sensitivity, the lack of any modulation by the active compared to the Sham stimulation speaks in favour of the absence of a perceptual bias phenomenon as far as the entrainment at IAF is concerned. Indeed, according to the sampling rate hypothesis, this effect should be expected for stimulation at a faster or slower pace than IAF, a hypothesis that can be causally tested using the protocol hereby validated. Such reasoning has some beneficial implications concerning the functional scrutiny of cortical rhythms unfolding outside the canonical boundaries of the alpha band as well. That is, rhTMS-driven entrainment could be deployed not only to up- or down-shift the alpha peak (i.e., $IAF \pm 1$ or 2 Hz; Di Gregorio, Trajkovic, et al., 2022; Cecere et al., 2015) but also to recruit neuronal pools oscillating, for instance, within the theta (i.e., around 5 Hz) or beta (i.e., around 20 Hz) range. Akin to what aforementioned about alpha activity, this would allow us to causally probe how pivotal the contribution of these rhythms is to cross-modal operations, trailing empirical findings recently gathered (from occipital sensors) by means of both audiovisual and visuo-tactile paradigms (Cooke et al., 2019; Fotia et al., 2021; Ronconi et al., 2023; Y. Noguchi, 2022).

To conclude, we herein replicated results regarding the robustness of the SIFI as an illusory event, and the degree to which it relies on interindividual variability and distinct temporal dynamics (i.e., SOAs). Moreover, we also provided evidence for the viability of rhTMS-based protocols to explore this phenomenon. Namely, that TMS-induced clicks and somatosensations do not significantly alter the occurrence of the illusion. These findings lay the foundations for future inquiries set to question (by means of rhTMS-EEG coregistration) the causal contribution of specific electrocortical features (i.e., alpha, and theta and beta frequency and amplitude) to perceptual metrics of cross-modal integration such as visual acuity and response bias.

Chapter 7: Assessing the Causal Role of Occipital Alpha Frequency in Audiovisual Perceptual Sensitivity vs Response Bias and the Mediating Role of Personality Traits along the Schizotypal Continuum

7.1 Introduction

Everyday life floods our perceptual machinery with manifold streams of data, which are often multisensory in nature. To cope with such a massive informational intake, efficient cross-modal operations must be instantiated to rearrange modality-diverging inputs into unified and coherent percepts (Noppeney, 2021; Stein & Stanford, 2008). Empirical evidence is supportive of a mechanistic model wherein temporal sensitivity plays a pivotal role in optimizing how, and to what extent, signals encoded by distinct sensory channels are partitioned or merged together, depending on whether their asynchronies exceed (or not) some degree of temporal tolerance, known as the *temporal binding window* (TBW; Wallace & Stevenson, 2014a, 2014b). Meaningful insights into the dynamics subtending this construct have largely been gathered by means of audiovisual tasks, many of which leveraging illusion-inducing paradigms (Alais & Burr, 2004; McGurk & Macdonald, 1976). Chief among them is the renowned *Sound-Induced Flash Illusion* (SIFI; Shams et al., 2000), in which paired acoustic tones, overlapping with a (single) flashing visual stimulus, mislead the observer into reporting two (rather than one) flashes. A sensory primacy of audition over vision has been proposed as the key driver of the phenomenon, with signals relayed through the former modality biasing visual cortex excitability during audiovisual interplay (Cappe et al., 2012; Murray, Thelen, et al., 2016; Romei et al., 2007; Romei, Gross, et al., 2012; Romei, Rihs, et al., 2008; Van Atteveldt et al., 2014). Consistently, stimulus onset asynchronies (SOAs, the temporal lags between the first and the second tone within each pair) act as the psychophysical determinants mediating this cross-modal illusion: the more the acoustic inputs occur in temporal proximity, the higher the propensity for the SIFI (Shams et al., 2000, 2002). Experimental reports suggest the likelihood of experiencing the double-flash illusion to be tied with SOAs spanning (on average) less than 100 ms (Shams et al., 2000), although wide inter-individual variability spanning perceptual training, expertise, age, cognitive functioning and neurodevelopmental disorders, among other factors, has been well documented (Hirst et al., 2020). For instance, clinical and subclinical profiles prone to positive symptoms (i.e., delusions and hallucinations), such as patients diagnosed with schizophrenia or individuals displaying pronounced schizotypal traits, exhibit a higher predisposition (as compared to healthy individuals) toward the SIFI even when SOAs exceed 100 ms (Ferri et al., 2018; Haß et al., 2017), implying broader TBWs.

Recent inquiries set to detail SIFI-related cortical substrates concur on the occipital pole serving as the core region that orchestrates many processes which this illusion stems from, by hosting a functional hub where sensory and higher-order streams funnel into (Cappe et al., 2009; Hirst et al., 2020; Mishra et al., 2007; Murray, Thelen, et al., 2016; Romei, Gross, et al., 2012; Watkins et al., 2006). Away from being a neural spot devoted to vision only, this site has been associated with computations regarding multisensory events (Beauchamp, 2005; Bolognini, Rossetti, Casati, et al., 2011; Calvert et al., 1999; Ghazanfar & Schroeder, 2006; Mercier et al., 2013; Murray, Thelen, et al., 2016; Romei et al., 2007; Shams et al., 2001), as well as top-down information conveyed by parieto-frontal spots (Bressler et al., 2008; Lauritzen et al., 2009). Given the fine-grained temporal backbone that audiovisual interactions rely upon (i.e., TBWs spanning ~100 ms), bioelectric mechanics in the electroencephalographic (EEG) alpha range (7-14 Hz, 70 - 130 ms per cycle) have been regarded as the most likely candidate to instantiate such operations. Predominantly occipital in their topography, alpha rhythms engage in phasic fluctuations known to up- and down-regulate cortical excitability (Dugué et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Romei, Brodbeck, et al., 2008; Romei et al., 2007) and route inter-areal exchange of predictive inputs (Bastos et al., 2015; Fries, 2005; Mayer et al., 2016; Tarasi, di Pellegrino, et al., 2022). Further, prestimulus alpha frequency (i.e., the speed at which these rhythms oscillate, right before stimulus onset) has been thought to supply perception with a temporal frame that parses incoming visual signals into discrete events (e.g., snapshots), thereby dictating boundaries for perceptual awareness (Cecere et al., 2015; Di Gregorio, Trajkovic, et al., 2022; Samaha & Postle, 2015). Each alpha wave would thus represent a building block of conscious experience, acting as a perceptual cycle whose oscillatory speed sets an observer's visual sampling rate (Coffin & Ganz, 1977; Kristofferson, 1967; VanRullen, 2016; Varela et al., 1981). Of note, this electrophysiological index bears trait-like features (Gasser et al., 1985; Salinsky et al., 1991) shown to parametrize perceptual audiovisual performance. The propensity to experience the SIFI was found to negatively correlate with the individual alpha frequency (IAF) recorded from parieto-occipital loci: the slower the IAF, the wider the TBW, and the greater the number of illusory percepts (Cecere et al., 2015; Keil & Senkowski, 2017). Evidence for a tie between IAFs and SIFI-related TBWs has been further reinvigorated by data revealing slower IAFs in patients suffering from schizophrenia or displaying schizotypal traits (as compared to healthy individuals), namely, those clinical and subclinical populations performing poorly (i.e., more prone to the illusion) at the SIFI (Ippolito et al., 2022; O. W. Murphy et al., 2019; Ramsay et al., 2021; Trajkovic et al., 2021).

As straightforward as the relationship between TBWs and IAFs was proved to be (i.e., supporting the notion that each recurrent alpha cycle should provide a discrete sampling window), whether the SIFI might be entirely due to poor cross-modal sensitivity (enlarged TBWs), rather than a phenomenon

partly mediated by perceptual bias (global horizontal shift in the psychometric curve) is still to be determined (but see recent insights from Deodato & Melcher, 2023; Y. Noguchi, 2023; Samaha & Romei, 2024). To this end, it may be helpful to probe this twofold account within a formal decision-making framework such as that outlined by Signal Detection Theory (SDT, Stanislaw & Todorov, 1999). When couched into the domain of psychophysics, SDT provides a valuable model tracking the contribution to performance accuracy provided by perceptual sensitivity (d'), which returns the sensory precision of a given system in disentangling the actual signal from noise, and response criterion (c), which instead estimates how much a given system is biased toward a specific response by priors, rather than the actual sensory evidence, when issuing a decision. Regarding SIFI paradigms, and TBW more broadly, seminal SDT-oriented efforts aimed at scrutinizing whether occipital IAFs might predict (either by shaping perceptual sensitivity or fueling aprioristic response biases) the individual's proneness to report an illusory percept (i.e., inverse accuracy in terms of behavioral performance), yielded controversial pieces of information, and failed to replicate existing findings (Buergers & Noppeney, 2022). Methodological differences in both the experimental design and data analysis must be factored in when construing such results (Samaha & Romei, 2024). Even so, a unifying interpretation of the matter is heavily constrained by the correlational nature of their associated study design.

In this preregistered study (<https://osf.io/u93az/resources>), we seek to address what still remains an open question: that is, whether perceptual sensitivity and/or response bias, as assessed during audiovisual tasks, *causally* relies on the speed of occipital alpha oscillations, and to which degree personality traits along the schizotypal axis might mediate such relationship. We did so by recording EEG activity from healthy participants screened for their schizotypal traits, who were asked to perform a 2AFC version of the SIFI paradigm. Causal manipulation of prestimulus alpha frequency was achieved on-line via the entrainment-inducing properties of rhythmic Transcranial Magnetic Stimulation (rhTMS; Di Gregorio et al., 2022; Thut et al., 2011), such that in each trial the IAF was up- or down-shifted prior to stimulus onset, following a block-wise fashion. We expect that rhTMS-driven changes in prestimulus alpha frequency should map onto perceptual acuity dynamics, rather than response bias, with IAFs entrained to a faster vs slower pace entailing greater vs lower audiovisual sensitivity (lesser vs more false alarms; i.e., 2-flashes reports in 1 flash trials).

7.2 Methods

7.2.1 Participants

892 healthy individuals from the general population were screened for their schizotypal traits. From this database, a total of 60 participants (38 females, mean age: $23.93 \text{ years} \pm .47 \text{ Standard Error of Mean, [S.E.M.]}$) were recruited. All participants reported normal or corrected-to-normal vision, normal hearing, and no history of substance abuse or other (neuro)psychiatric disorders, as well as no contraindication with respect to TMS-based protocols (Rossi et al., 2021). Participants gave written consent prior to completing the personality screening and the experimental session, and all were naïve to the actual purpose of the study. Sample size estimation was performed via G*Power 3.1 software (alpha level = 0.05, power = 0.80; Faul et al., 2007) and following a recent meta-analysis on the topic (Samaha & Romei, 2024).

7.2.2 Procedure

Each participant (screened as for his/her/their schizotypal traits) was asked to partake in two distinct (yet identical in structure) experimental sessions, separated by at least 2 days. Both sessions were carried out in a dim-lighted and sound-attenuated room, and progressed as follows. First, a set of 64 Ag/AgCl electrodes was mounted on each participant according to the 10–10 international system. Next, they performed a preliminary titration procedure involving a modified SIFI task (mSIFI) in which, along with two interleaved acoustic stimuli, either one or two flashes were presented (i.e., 2AFC). In this phase, we implemented a staircase procedure in order to identify, on a per-participant basis, a threshold SOA associated with a performance accuracy of around 70%. After the completion of the titration phase, 3-minute resting-state EEG data (rsEEG) were recorded both under eyes-open and eyes-closed conditions, to extract the IAF for the subsequent rhTMS protocols (Di Gregorio, Trajkovic, et al., 2022; Trajkovic et al., 2022). By means of this information (i.e., threshold SOA and IAF), six experimental blocks, interleaved by small breaks of around 5 minutes, were then carried out. That is, participants performed six blocks of the mSIFI paradigm (i.e., main task) titrated at the individual's threshold level (i.e., employing the threshold SOA only), while EEG activity was continuously recorded. Following a block-wise pseudorandomized order, rhythmic entrainment was engendered via rhTMS delivered during the prestimulus time window according to three stimulation protocols differing in terms of frequency: IAF-1Hz, IAF, IAF+1Hz, along with their corresponding frequency-matched Sham protocols.

7.2.2.1 Schizotypal Traits Screening

Schizotypal traits screening was performed via Qualtrics (a web-based data collection system) using the Italian version of the Schizotypal Personality Questionnaire (SPQ; Raine, 1991). This instrument comprises 74 items requiring binary responses (e.g., *Yes* vs *No*: all items endorsed *Yes* are scored 1). Items assess behavior, thoughts, and attitudes typically associated with schizotypal personality. The 74 items are also pooled into 9 subscales (e.g., Odd or Eccentric Behavior, Social Anxiety, Ideas of Reference, Suspiciousness, etc.), reflecting behavioral and cognitive–perceptual clusters described in the DSM-5. The sample of 60 individuals recruited to participate in the study displayed an overall mean SPQ score of 18.3 ± 1.56 *S.E.M.* However, as our key experimental focus was on the putative impact positive schizotypal sub-traits may exert on audiovisual metrics, we devised, per each participant, a positive sub-traits score (PositiveSub) composed of the summed scores relative to the subscales evaluating, respectively, Odd Beliefs or Magical Thinking, and Unusual Perceptual Experiences (mean PositiveSub score: $4.03 \pm .55$ *S.E.M.*). Note that, as a personality questionnaire, high scores do not indicate a diagnosis of a schizotypal spectrum disorder but rather the presence of schizotypal traits in otherwise healthy individuals.

7.2.2.2 Apparatus and Stimuli

Visual stimuli consisted of solid light-grey [RGB: 136,136,136] disks overlaid on a grey [RGB: 127,127,127] background, subtending 1.5 degrees of visual angle, and displayed at 4.3 degrees of visual angle below a white fixation cross at the center of the screen. Stimuli were presented at 57 cm viewing distance on an 18” CRT monitor (Elo TouchSystems Entuitive, refresh rate 120 Hz, 1024x768 screen resolution) for the brief (flashing) duration of one refresh rate (nominally ~ 8.3 ms, although way shorter due to CRT phosphor decay rate; Elze, 2010). Auditory stimuli were sinusoidal pure tones (frequency: 5 kHz; sampling rate: 44.1 kHz) lasting 3 ms and delivered via paired stereo speakers located on both sides of the monitor, thus allowing for coincidental spatial perception of visual and auditory stimuli (Ferri et al., 2018). Stimuli presentation and behavioral responses recording were controlled via an automated routine running on a Windows machine equipped with Matlab (2019b; MathWorks) and the Psychophysics Toolbox (version 3.0.14; Brainard, 1997).

7.2.2.3 *mSIFI Task (Titration).*

All trials started with a small fixation cross continuously displayed at the center of the screen. After a random temporal lag of 500–1500 ms, a solid-grey disk and an acoustic tone were simultaneously delivered. While a second auditory tone was always played at 20 different SOAs from the onset of the first one, ranging from 24 to 181 ms (with each interval corresponding to an increment of one refresh rate: 8.3 ms), only in half the trials was a second disk presented, in overlap with the second auditory stimulus. This course of action enabled us to replicate the perceptual fingerprints of the SIFI (1 flash, two sounds; 1F2S) in 50% of trials, whereas in the other half, two disks paired with two acoustic tones occurred (2F2S). Let it be noted that we hereby chose to include 2S trials only (rather than 1S or 0S trials) to reduce as much as possible any further confound on the response criterion produced by sound-induced biases. Upon stimuli presentation, participants were asked to report, regardless of the number of sounds, whether they saw 1 vs 2 flashes (i.e. disks), by pressing specific key buttons, after which an inter-trial interval of 500 ms followed (figure 7.1, a). For each participant, an adaptive staircase procedure devised according to an up/down (i.e., SOA) rationale informed by the participant's perceptual accuracy was implemented. This procedure was set to identify, at the individual level, the SOA associated with a threshold accuracy rate around 70%. To this end, up to a maximum of 21 staircase reversals, for a total amount of 200 trials (i.e., 20 blocks) were adopted. Specifically, each block was composed of 10 trials: 5 1F2S and 5 2F2S (presented in randomized order). The threshold SOA was identified either when the staircase reached the same SOA at least 3 times, or by averaging the SOAs relative to the last 3 reversals.

7.2.2.4 *mSIFI Task (Main Task: Threshold SOA and rhTMS)*

The main task was composed of six different blocks whose trials structure closely resembled that employed during the titration phase (except for time-lags, which now randomly varied from 2500 - 3500 ms, due to safety issues regarding the TMS protocol; Rossi et al., 2021). Namely, both 1F2S and 2F2S trials progressed as described above, with the crucial exception that one SOA only (i.e., threshold SOA) was adopted here (i.e., the one computed via staircase procedure and associated with the individual's performance accuracy of around 70%). Each of the 6 blocks was made up of 40 1F2S trials and 40 2F2S trials (presented in a randomized order), for a total of 80 trials per block, resulting in 480 trials overall. Throughout the main task, EEG activity was continuously recorded, and during each trial's prestimulus time window (i.e., the temporal window preceding the occurrence of the first audiovisual pair, and immediately following the random time-lags) a 5-pulse TMS train was delivered,

such that the last magnetic bout within the train overlapped with the first audiovisual pair (based on previous literature; Bertaccini et al., 2023). Depending on the specific block, the stimulation parameters changed in order to differentially entrain prestimulus alpha oscillations (figure 7.1, b), either by not modulating their frequency rate (IAF), slowing it down (IAF-1Hz), or speeding it up (IAF+1 Hz). Each of these three blocks was paired with a corresponding frequency-matched Sham block (i.e., one per stimulation frequency), to control for any spurious effect ascribable to the practicalities of the protocol. Importantly, we adopted pseudo-randomized and counterbalanced design across participants to control for the order in which stimulation protocols were administered.

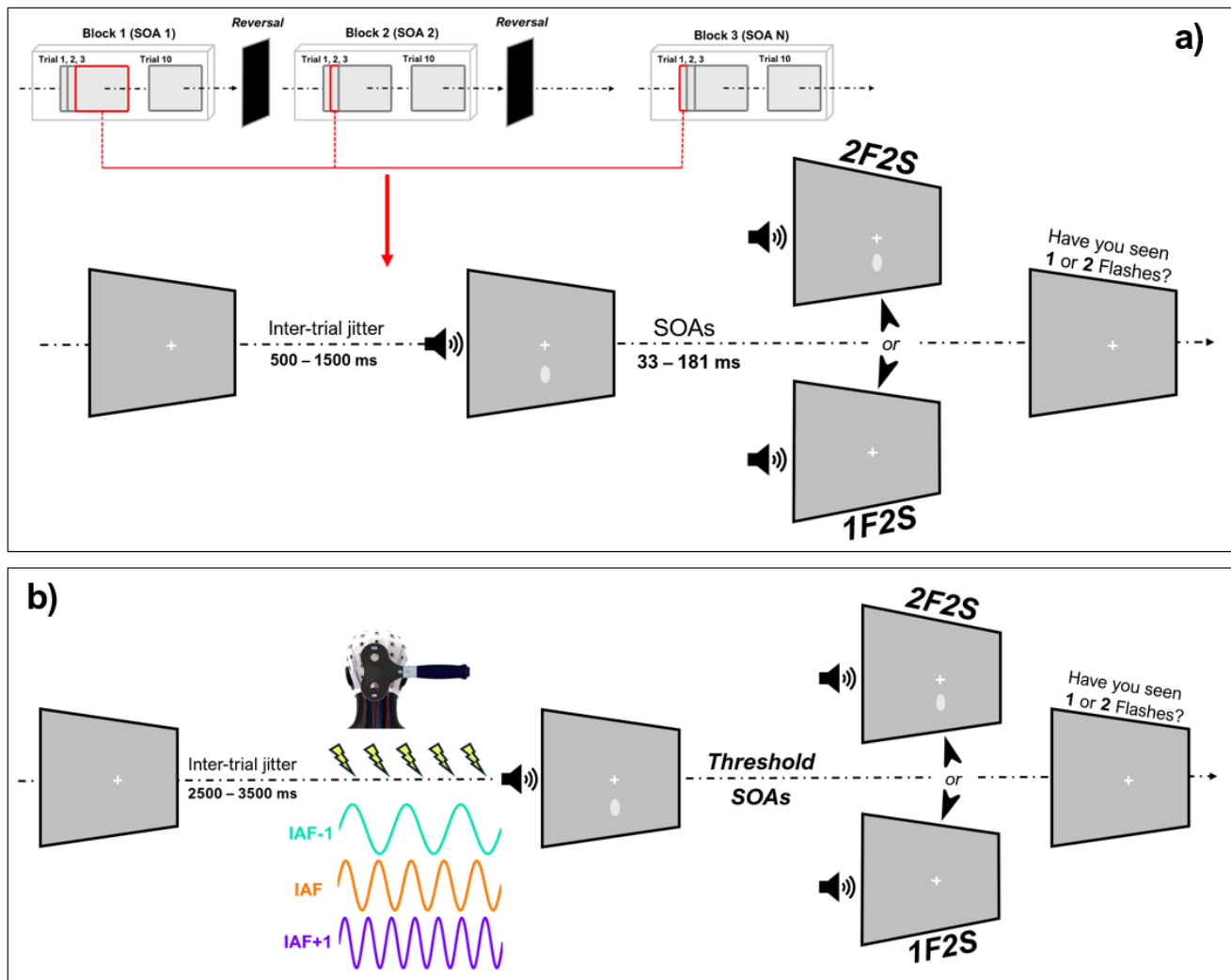


Figure 7.1 Graphical depiction of the experimental tasks. **a) Titration procedure:** after the EEG cap was fitted, each participant performed a titration procedure devised to extract the threshold SOAs to be employed during the main task. The up-or-down staircase was allowed to achieve a maximum of 21 reversals. The directionality thereof was dictated by the accuracy rate relative to the prior block, which comprised 10 trials (5 1F2S trials, 5 2F2S trials). Each trial started with a fixation cross randomly lasting between 500 ms and 1500 ms, followed by the occurrence of the first audiovisual pair. After a SOA that varied across blocks depending on reversals directionality, either a second audiovisual pair (2F2S) or a second acoustic tone only (1F2S) were emitted, with participants asked to report how many visual stimuli were presented (1 flash vs 2 flashes). **b) Main task:** trials structure resembled that from the titration procedure, except for the usage of one SOA only (threshold SOA identified via staircase procedure), and a longer inter-trial jitter, upon which rTMS was delivered according to a protocol (active vs Sham) and frequency output (IAF-1Hz, IAF, IAF+1Hz) that were manipulated in a block-wise fashion, following pseudo-randomized and counterbalanced design across participants. All sessions featured a total of 6 blocks, each comprising 80 trials (40 2F2S trials and 40 1F2S trials).

7.2.2.5 EEG Recordings and Acquisition

Electrophysiological data were recorded at rest and during the main task via the Software Brain Vision Recorder (Brain Products, Munich, Germany) from 61 Ag/AgCl electrodes (Fp1, Fp2, AF3, AF4, AF7, AF8, F1, F2, F3, F4, F7, F8, FC1, FC2, FC3, FC4, FC5, FC6, FT7, FT8, C1, C2, C3, C4, C5, C6, T7, T8, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, P1, P2, P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, O1, O2, Fpz, AFz, Fz, FCz, Cz, CPz, Pz, POz, Oz) arranged according to the international 10-10 system. The right mastoid was used as reference, whilst the ground electrode was placed over the left cheek. EEG signal was band-pass filtered online between 0.01 and 100 Hz, and sampling rate set at 5000 Hz. The impedance of all electrodes was kept below 10 k Ω , except for ground, reference and Oz electrodes, whose impedance levels were carefully kept below 5 k Ω .

7.2.2.6 Transcranial Magnetic Stimulation.

Rhythmic entrainment was exogenously instantiated via a 70 mm figure-of-eight coil by delivering, during each trial's prestimulus time window, a stimulation train consisting of 5 interleaved biphasic pulses (maximum field strength ~ 1.55 T), generated by a TMS machine (TMS Rapid, Magstim Company, UK), right over the cortical spot corresponding to electrode Oz (Trajkovic et al., 2022). The coil surface was held tangentially to the scalp, with an orientation capable of inducing currents running in a posterior-anterior direction. Unlike active rhTMS conditions, in the Sham stimulation a $4 \times 4 \times 4$ cm foam-rubber cube was affixed to the center of the coil's stimulating surface, increasing coil–scalp distance to prevent cortical stimulation from being delivered. Stimulation intensity was set at 60% of the maximal stimulator output (MSO), a level associated with induction of visual phosphenes when TMS is delivered to occipital loci (Gerwig et al., 2003; Romei et al., 2007; Romei, Rihs, et al., 2008). TMS trains were administered in a rhythmic fashion by pacing pulses release according to the IAF (as measured over occipital areas via 3-minutes rsEEG recording, see *procedure*). In brief, the inter-pulse interval (IPI, estimated in ms) within each train was set in order to, respectively, not modulate alpha frequency rate ($IPI = 1000/(IAF)$), speed-up endogenous IAFs by 1Hz ($IPI = 1000/(IAF + 1)$), or slow them down by 1 Hz ($IPI = 1000/(IAF - 1)$). The same IPIs calculated for the active rhTMS protocols were adopted during their relative frequency-matched Sham blocks. Timing and outputs of rhTMS protocols were dictated by an automated routine implemented in MatLab (2019b, MathWorks) through a TriggerBox (EMS medical) connecting the operating PC with the TMS machine.

7.2.3 Analyses

7.2.3.1 Electrophysiological Data

All EEG analyses, from preprocessing to oscillatory metrics extraction, were performed in Matlab (2023b) via the EEGLAB toolbox (A. Delorme & Makeig, 2004) and custom-made algorithms.

rhTMS-based IAF Estimation - In order for the rhTMS parameters to be maximally effective in entraining alpha oscillatory activity, rsEEG data were employed to extract, on a per-participant basis, the IAF over the occipital lobe (Di Gregorio, Trajkovic, et al., 2022; Trajkovic et al., 2022). To this aim, 3-minute rsEEG were recorded (upon the titration procedure and prior to the main task) both under eyes-closed and eyes-open (gaze on a fixation cross presented over a screen) conditions, and re-referenced offline to the average of all electrodes before down-sampling at 500 Hz. We then applied a low-pass filter (30 Hz) and a high-pass filter (.5 Hz), after which power spectral density (PSD) was computed via Fast Fourier Transform on rsEEG data at electrode Oz, and the frequency peak displaying the local power maximum between 7 and 14 Hz under the eyes-open resting state condition was chosen as the IAF to be used during the subsequent rhTMS protocols. Importantly, if no clear peak in the alpha range was detectable, the same procedure was implemented on rsEEG data relative to adjacent electrodes (POz, O1, and O2). If no clear peak was detected from such electrodes either, PSD estimates at electrode Oz and the following IAF detection were performed on eyes-closed rsEEG data.

EEG Preprocessing - Identification and removal of TMS artifacts occurring during the main task was performed on EEGLAB via the TMS-EEG signal analyzer (TESA) toolbox (Rogasch et al., 2017), and based on previous literature (Di Gregorio, Trajkovic, et al., 2022; Trajkovic et al., 2022). To this end, we epoched EEG data from -2000 ms to 1000 ms around stimuli onset (i.e., the occurrence of the audiovisual pair). We applied linear detrending on each and every channel (EEGLAB function *eeg_detrend*), rhTMS pulse artifacts and evoked scalp muscles activity were removed by cutting-out signals around each TMS pulse (from -10 to + 10 ms), with missing samples being cubic-spline interpolated to minimize sharp non-stationarities likely to induce ringing artifacts. Down-sampling (from 5000 Hz to 1000 Hz) was then performed, followed by visual inspection of each epoch/channel, to ensure bad/noisy trials were discarded before further preprocessing steps. Next, we replaced interpolated signals with constant amplitude data, and ran an independent component analysis (ICA) via fastICA algorithm (Hyvärinen & Oja, 1997). This preliminary round of ICA was performed in order to selectively remove components bearing large amplitude artifacts such as those due to rhTMS-

evoked scalp muscle activity. After, a second cubic interpolation, and both pass-band (1-100 Hz) and stop-band (48 - 52 Hz) Butterworth filters were applied. Interpolated data were again removed, and a second round of ICA was carried out to clean the EEG signal from canonical artifacts (i.e., blinks, eye movements, and electrode noise). Then, we interpolated rhTMS pulse windows one last time, and re-referenced the denoised channels to the average of all electrodes. As a final step, all trials were once again visually inspected. We rejected and interpolated, respectively, trials containing residual rhTMS artifacts and channels over-contaminated by residual noise. Such procedure was applied to EEG data relative to both the active rhTMS and Sham blocks alike.

Instantaneous Alpha Frequency Estimation (iF) - To assess whether our rhTMS-based protocols succeeded in up- or down-regulating the oscillatory speed occipital alpha rhythms, we performed instantaneous frequency estimations (*iF*; Cohen, 2014; Samaha & Postle, 2015) over the prestimulus time window (from -800 ms to 0 ms) in which the stimulation protocols were administered. We endorsed a region-of-interest approach, by selecting a broad cluster of occipital electrodes (i.e., O1, Oz, O2, POz) that covered, along with the cortical spot where rhTMS was delivered (i.e., Oz), all surrounding sensors. De-noised epochs from each of these selected channels were filtered around the IAF (i.e., ± 2 Hz) via zero-phased, plateau-shaped band-pass filter (15% transition zones). We then Hilbert-transformed these filtered data in order to extrapolate instantaneous amplitude and phase angle time series from the resulting analytic signal. As such, instantaneous frequency estimates (in Hz) were extracted by performing, at each time point, temporal derivatives over the phase angle values. To account for noise-related non-stationarities embedded in the instantaneous frequency measurements, median filters were further implemented using ten different time windows ranging from 10 to 400 ms, after which trials and channels averaging was performed. This procedure was carried out per every individual as a function of the experimental condition (IAF-1, IAF, IAF+1, relative to both active rhTMS and Sham protocols), yielding time-resolved estimates of alpha frequency dynamics along the prestimulus temporal window.

Peak Alpha Frequency Extraction (on-task IAF) - As a control measure, beside *iF* estimates, we additionally employed a conventional time-collapsed metric for assessing rhTMS-driven changes to alpha rhythms speed. Namely, on-task individual alpha peak frequency (*on-task IAF*) relative to a peristimulus time window. First, denoised EEG epochs were trimmed from -450 to +150 ms (relative to stimuli onset) and channel-wise concatenated across our occipital cluster. Then, PSDs were computed over such signals using the Welch's method (Matlab function *pwelch*). To reduce spectral leakage, we tapered each segment with a 600-ms Hann window (0% overlap), and power spectra were zero-padded to yield 0.1 Hz frequency spacing. Of note, we chose a time segment straddling 150 ms

into the post-stimuli window to pinpoint the full-width of half maxima of the Hann taper from -300 to stimuli onset (i.e., roughly around the time segment where rhTMS effects should unfold the greatest across conditions). PSDs were then submitted to the Fitting Oscillations & One-Over-F (FOOOF) algorithm (Donoghue et al., 2020). FOOOF is a physiologically-informed toolbox that allows for the spectral parametrization of neuroelectric signals, achieved via iterative fitting steps. Each spectral profile fed to the algorithm is modelled as a mixture of both an aperiodic component (i.e., “1/f” slope) and true oscillatory activity (i.e., “knee-like” deviations, or “bumps”, sitting above said slope). FOOOF routines have been devised to disentangle such components, and return peak frequency estimates unbiased from background aperiodic activity. We thus entered our PSDs, channel by channel, into the FOOOF, to extract the frequency peak within the 7-14 Hz range with the largest aperiodic-adjusted power. Lastly, we retained as the cluster-level *on-task IAF* the mean frequency peak that resulted from averaging across each channel’s *on-task IAFs*. The aforementioned procedure was performed per each participant, and stimulation condition.

7.2.3.2 Behavioral Performance

Perceptual performance was tracked by adopting SDT measurements. Namely, we classified each individual’s response according to an equal variance Gaussian SDT model where 1-flash trials were treated as noise (catch trials) and 2-flashes trials as signal (target trials). As such, a 2-flashes report was binned, respectively, as a hit (H) in 2F2S trials, and a false alarm (FA) in 1F2S trials. Conversely, a 1-flash report was classified, respectively, as a correct rejection in 1F2S trials, and a miss in 2F2S trials. This classification was performed per each participant as a function of the experimental condition (IAF-1, IAF, IAF+1, as well as their relative frequency-matched Sham protocols). We leveraged these data to evaluate perceptual sensitivity (d'), response bias (c), and accuracy rates (ARs) relative to every session and stimulation condition, as follows (Stanislaw & Todorov, 1999):

- *Perceptual Sensitivity (d')* - The difference between z-scored hits and false alarms, according to the formula: $z(H) - z(FA)$, where the former represents the likelihood of reporting 2 flashes in target trials (hits), and the latter the likelihood of reporting 2 flashes in catch trials (false alarms). Larger d' values are indicative of better abilities in disentangling the actual audiovisual signal from noise, and vice-versa.
- *Response Bias (c)* – The negative half-sum of z-scored hits and false alarms, according to the formula: $-0.5*(z(H) + z(FA))$, where the former represents the likelihood of reporting 2 flashes in target trials (hits), and the latter the likelihood of reporting 2 flashes in catch trials (false

alarms). Positive c values are associated with conservative response criteria (less 2-flashes responses as compared to 1-flash response), while negative c values occur when a liberal response style is adopted (less 1-flash responses as compared to 2-flashes responses).

- *Accuracy Rates (ARs)* - The percentage of hits (2-flashes report in target trials) and correct rejections (1-flash report in catch trials) over the total amount of trials.

As a result, every participant was associated with three distinct behavioral indices (d' , c and ARs) per each TMS protocol (IAF-1Hz, IAF, IAF+1Hz, as well as their relative frequency-matched Sham protocols), which were then averaged across sessions.

7.2.3.3 Statistics

All statistical analyses relative to both electrophysiological and behavioral data were performed either via custom-made Matlab (2023b) algorithms, Rstudio (version 2024.09.1), Jasp (version 0.19.1.0) or jamovi (version 2.3.28).

Electrophysiological Data - As for instantaneous alpha frequency, to verify whether any significant difference in the prestimulus iF occurred as a function of the TMS protocol (IAF-1Hz vs IAF vs IAF+1Hz), condition comparisons within the time window spanning -800 ms to 0 ms (audiovisual pair onset) were performed via non-parametric cluster-based permutation testing in the time domain (Maris & Oostenveld, 2007). In brief, each participant's active-rhTMS iF estimates (i.e., IAF-1Hz, IAF and IAF+1Hz conditions) were timepoint-by-timepoint corrected using the associated frequency-matched Sham time series (e.g., active rhTMS IAF - Sham rhTMS IAF), returning three distinct frequency-wise Sham-corrected iF signals ($iF_{\text{IAF-1 Hz}}$ vs iF_{IAF} vs $iF_{\text{IAF+1 Hz}}$) per participant. Temporal clusters displaying neighboring significant differences ($p < .05$) were then identified, and selected, via one-way repeated-measures ANOVAs (rmANOVA: one level [Stimulation Frequency] with three factors: IAF-1Hz, IAF, IAF+1Hz) performed over such Sham-corrected data at each time point between -800 ms and 0 ms relative to stimulus onset. The corresponding F-ratios were then summed and stored as the cluster-level statistic (i.e., cluster mass). Next, we implemented random data permutation by shuffling Stimulation Frequency labels within each participant, to generate surrogate data distributions under the null hypothesis. For each permutation (2,000 iterations, $\alpha = .05$, F-threshold = 3.073), the highest cluster-based statistic was retained to derive a reference cluster-level statistic distribution via a Monte Carlo procedure. The proportion of values in this distribution exceeding the empirical (observed) cluster-based statistic served as the cluster-level p -value estimate, adjusted for multiple comparisons. We further explored prestimulus alpha frequency dynamics by

averaging across time points iF estimates within any significant temporal cluster(s), yielding (per each participant) time-collapsed Sham-corrected iF estimates, sorted as a function of the stimulation frequency (again, iF_{IAF-1} VS iF_{IAF} VS iF_{IAF+1}).

Lastly, to evaluate at a finer-grained level whether the putative iF changes align with the frequency output or the associated stimulation protocols, we endorsed Bayesian Informative Hypothesis testing (BAIN, Degni et al., 2022; Garofalo et al., 2024; Hoijsink et al., 2019). Compared to null-hypothesis testing, BAIN directly evaluates the extent to which a statistical model (built upon a hypothesis of interest) is the best suited to explain the experimental data, or else, what is the model receiving the strongest support from the empirical evidence at hand. This is achieved through the Bayes theorem by computing, for each competing hypothesis, the posterior model probability ($PMP.b$), which returns an absolute estimate about how supportive of a specific model empirical data are. This method provides a means to contrast different hypotheses to assay the relative probability of explaining the observed data. Importantly, regardless of the number of models set forth, BAIN also tests the probability of the unconstrained hypothesis, which represents any other set of relationships between the parameters differing from those explicitly formulated (i.e., a “fail-safe” model that places no constraints on the parameters and mitigate the risk of selecting a set of bad hypotheses, which includes the null-hypothesis as well). As such, we entered each participant’s time-collapsed iF into the BAIN, which was set to test three main hypotheses:

$$\mathbf{H}_1: iF_{IAF-1\text{ Hz}} < iF_{IAF} < iF_{IAF+1\text{ Hz}}$$

$$\mathbf{H}_2: iF_{IAF-1\text{ Hz}} < iF_{IAF} = iF_{IAF+1\text{ Hz}}$$

$$\mathbf{H}_3: iF_{IAF-1\text{ Hz}} = iF_{IAF} < iF_{IAF+1\text{ Hz}}$$

With $\mathbf{H}_1$ being the hypothesis of interest (i.e., the faster rhTMS frequency rates, the higher the iFs), while $\mathbf{H}_2$ and $\mathbf{H}_3$ represent alternative models that are likely to alternatively explain the main effect of Stimulation Frequency we predict to find. Of note, we adopted this very same statistical pipeline (with the exception of cluster-based permutation testing) with regard to *on-task* $IAFs$. Namely, each participant’s Sham-corrected *on-task* $IAFs$ were entered into a one-way rmANOVA (one level [Stimulation Frequency] with three factors: IAF-1Hz, IAF, IAF+1Hz). Any putative main effect of Stimulation Frequency was further explored via BAIN, using the same hypotheses set ($\mathbf{H}_1$, $\mathbf{H}_2$ and $\mathbf{H}_3$) employed for iF estimates. Finally, we tested whether iFs tracked *on-task* $IAFs$, by correlating (Spearman’s ρ) data from IAF-1Hz and IAF+1Hz conditions (i.e., where we indeed predicted an alpha frequency shift, unlike the IAF condition).

Behavioral Data - Akin to some of the electrophysiological statistical analyses, behavioral data relative to each participant's audiovisual sensitivity (d'), response bias (c) and accuracy rates (ARs) were Sham-corrected, to highlight the surmised differences between IAF-1Hz, IAF and IAF+1Hz across active rhTMS and Sham. Next, they were entered into three distinct one-way rmANOVAs (one for each behavioral index) with Stimulation Frequency (one factor with three levels, IAF-1Hz, IAF, IAF+1Hz) as the within-subjects factor; and, respectively, Sham-corrected d' , c and ARs as dependent variables. In addition, as we were interested in tracking any putative contribution of schizotypal traits to the behavioral outcome of rhTMS, the degree of positive sub-traits (PositiveSub, as assessed via the SPQ subscale indexing positive symptoms, *see Schizotypal Traits Screening*) were factored into each of the rmANOVAs, as covariate. Any significant interaction effect Stimulation Frequency*PositiveSub on behavioral metrics was further probed with separate linear mixed-effects models for each behavioral metric (y) : $y \sim \text{Stimulation Frequency (IAF-1Hz / IAF / IAF+1Hz)} \times \text{PositiveSubs} + (1|\text{participant})$. PositiveSub between-participants covariate was mean-centered, and because each participant contributed one observation per frequency level, random slopes for Stimulation Frequency were omitted (i.e., not estimable), while participant-specific random intercepts were retained. Fixed effects were tested with Type-III sums of squares and Satterthwaite degrees of freedom. We estimated marginal trends (covariate slopes) within each Stimulation Frequency level, and compared them via planned pairwise slope contrasts (IAF-1Hz vs IAF; IAF vs IAF+1Hz), with Bonferroni-adjusted p -values and 95% CIs.

7.3 Results

Experimental data reported in this section follow the format: *mean* $\pm$ *standard error of mean* (S.E.M.). Confidence intervals (C.I.) are 95% (two-sided).

7.3.1 Electrophysiological Data

7.3.1.1 Instantaneous Alpha Frequency (iF)

Because our primary focus was verifying whether any protocol-dependent shift on ongoing prestimulus alpha frequency occurred, we first ran cluster-based permutation testing (2000 iterations) over Sham-corrected iF estimates along a time-window ranging from -800 ms to 0 ms relative to stimuli onset. Preliminary one-way rmANOVAs performed over such temporal range returned a significant cluster of contiguous time points spanning from -377 ms to 0 ms (*empirical cluster mass* = 2579) that survived cluster-based permutations (surrogate threshold cluster mass = 901), implying a

reliable effect ($p < .001$) across our observed time series (figure 7.2, a). We proceeded further on by collapsing iF data across this significant temporal cluster ($iF_{IAF-1Hz} = -.004 \pm .001$ Hz; $iF_{IAF} = -.001 \pm .001$ Hz; $iF_{IAF+1Hz} = .016 \pm .008$ Hz), and then feeding them to the BAIN algorithm. Results show (figure 7.2. a: bottom-right inset) that, while H1 did not retain the highest relative probability ($PMP.b = .102$), the complementary hypotheses (i.e., H2 and H3) did ($PMP.b = .433$, and $PMP.b = .405$, respectively), even with the unconstrained hypothesis (i.e., Hu) factored in ($PMP.b = .059$). Accordingly, H2 and H3 displayed the largest Bayes Factors ($BF.u = 7.36$ and $BF.u = 6.78$) as compared to H1 ($BF.u = 1.74$). Namely, when contrasting H1, H2 and H3 with Hu, the former models appeared the most likely to depict the patterns observed in our data. In brief, iF patterns are suggestive of consistent stimulation-aligned shifts (i.e., H2 and H3) rather than a strict monotonic ordering across IAF-1 Hz, IAF, and IAF+1 Hz conditions (i.e., H1), supporting the proposition of directional shifts although with less evidence favouring a strict ordering.

7.3.1.2 On-task IAF

As a control measure introduced to keep track of iF estimates, we also leveraged a canonical time-collapsed approach to derive peristimulus alpha frequency speed. Namely, peak extraction (within the 7 -14 Hz range) from PSD relative to on-task EEG data (-450 ms to 150 ms). PSDs from each channel in our occipital cluster of interest were thus computed on a per participants basis, and then fed to the FOOOF algorithm, sorted as a function of the stimulation protocol. Next, the averaged occipital alpha peaks (per stimulation protocol and participant) were Sham-corrected ($on-task IAF_{IAF-1Hz} = -.191 \pm .070$ Hz; $on-task IAF_{IAF} = -.053 \pm .062$ Hz; $on-task IAF_{IAF+1Hz} = .124 \pm .069$ Hz) and submitted to a one-way rmANOVA (figure 7.2, b, top inset) that returned a significant main effect of Stimulation Frequency ($F_{2,118} = 5.38$; $p < .01$; $\eta^2_p = .084$; $BF_{10} = 10.9$). Follow-up BAIN analyses revealed a pattern mirroring what was witnessed for iF estimates (figure 7.2, b bottom inset), with H2 and H3 retaining the highest relative probabilities ($PMP.b = .426$, and $PMP.b = .422$, respectively) as compared to H1 ($PMP.b = .096$), and, most of all, Hu ($PMP.b = .064$). Consistently, H2 and H3 exhibited the largest Bayes Factors ($BF.u = 6.64$, and $BF.u = 6.59$, respectively) when confronted to H1 ($BF.u = 1.50$). Again, H2 and H3 are the models receiving the strongest support from our experimental evidence, indicating reliable protocol-dependent on-task IAF shifts, although with a less decisive preference for the exact ordering

7.3.1.3 Cross-Metrics Correlation

Finally, we moved on to evaluating the degree of agreement between the aforementioned metrics (i.e., *iFs* and *on-task IAFs*), using Spearman's rank correlation (ρ), to quantify how strong their association was in both IAF-1Hz and IAF+1Hz conditions (i.e., stimulation conditions in which we predicted an actual alpha frequency shift, as opposed to IAF). Results show a significant and positive monotonic relationship (Spearman's $\rho = .22$, $p < .01$), meaning that rhTMS-induced *iFs* shifts indeed tracked concurrent changes in *on-task IAFs*.

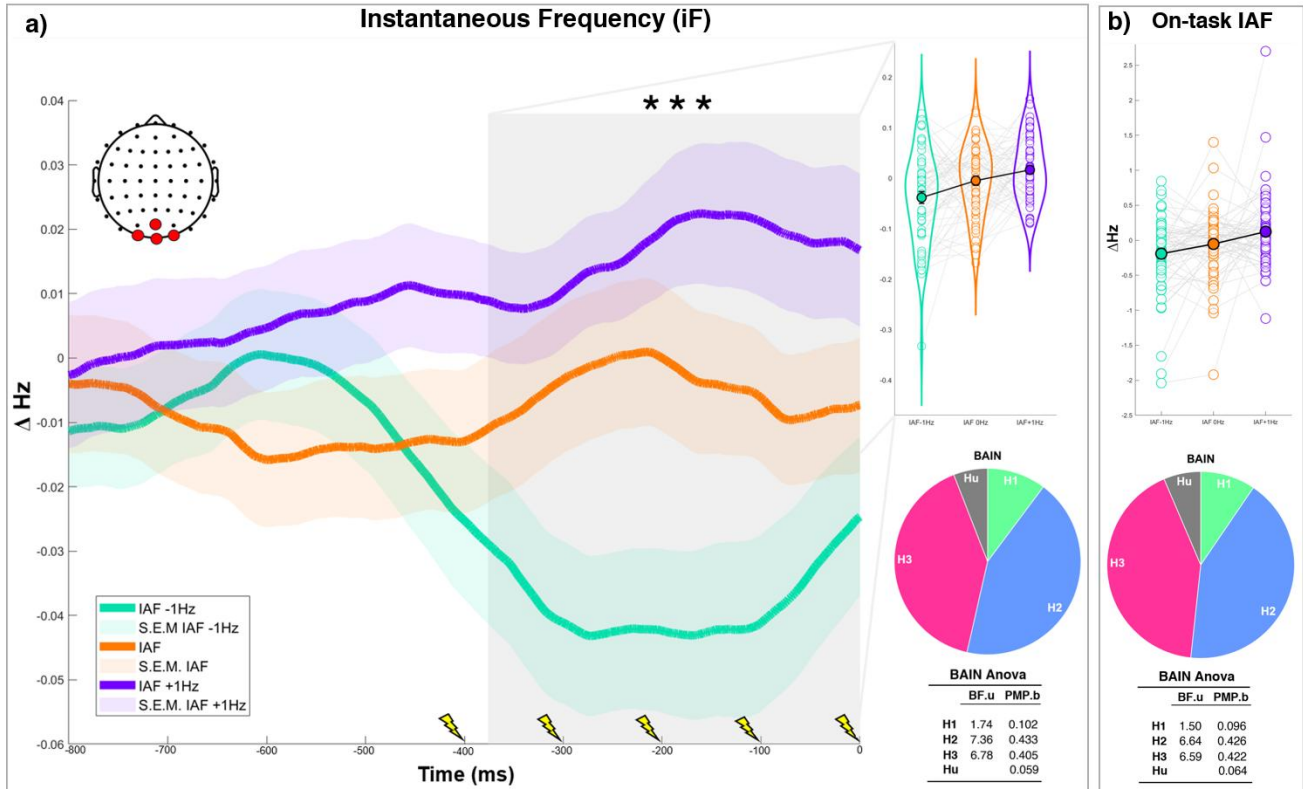


Figure 7.2 Electrophysiological results. **a)** Sham-corrected instantaneous frequency (*iF*) time course over the prestimulus window (−800 to 0 ms relative to stimuli onset; x-axis) within our occipital cluster of interest (top-left inset, red dots). Y-axis shows rhTMS-induced frequency shifts (Δ Hz); lightning icons mark the average time course of a TMS pulse train delivered at 10 Hz. Light-gray shading denotes the significant temporal cluster surviving permutation-based statistics test. **Top-right inset:** violin plots of time-collapsed *iF* within the significant window, sorted as a function of stimulation frequency (Δ Hz over the y-axis). **Bottom-right inset:** BAIN ANOVA results (H1, H2, H3, Hu shown in green, blue, magenta, and dark grey), displayed as a pie chart with accompanying table (BF.u and PMP.b). Color-filled dots and error bars represent mean and S.E.M. **b) Top inset:** raincloud plot of Sham-corrected on-task IAF (*on-task iF*) as extracted via PSD and FOOOF from a peristimulus time window (−450 ms to 150 ms), sorted as a function of the stimulation frequency, with y-axis showing rhTMS-induced frequency shifts (Δ Hz). **Bottom inset:** BAIN ANOVA results (H1, H2, H3, Hu shown in green, blue, magenta, and dark grey), displayed as a pie chart with accompanying table. Color-filled dots and error bars represent mean and S.E.M.

7.3.2 Behavioral Data

7.3.2.1 Perceptual Sensitivity (d')

As the core proposition prompting the current study was to establish to which degree the causal tuning of prestimulus alpha oscillations shaped audiovisual sensitivity, and how positive schizotypal traits might mediate such link, we first moved on to the statistical analyses relative to perceptual acuity. Upon providing convincing evidence that our rhTMS protocol successfully shifted the cycling frequency of occipital alpha waves, we expected parallel changes in audiovisual sensitivity. To test this hypothesis, we computed d' levels per each participant and stimulation condition. We then performed Sham-correction ($d'_{IAF-1Hz} = -.041 \pm .057$; $d'_{IAF} = -.101 \pm .064$; $d'_{IAF+1Hz} = -.139 \pm .054$) and entered these data into a one-way rmANOVA, along with the associated positive sub-traits scores (PositiveSub). Opposite to our expectations, no main effect of Stimulation Frequency was found, nor of the PositiveSubs covariate (all p -values $> .05$; all $BF_{10} < 1$), except for a slightly significant Simulation Frequency*PositiveSub interaction ($F_{2,116} = 3.15$; $p < .05$; $\eta^2_p = .051$; $BF_{10} = 1.35$ [null-model = main effects], figure 7.3, a). This pattern of results was broken down using linear mixed-effects modelling, to highlight whether higher vs lower positive schizotypal sub-traits steered TMS modulation toward different behavioral responses.

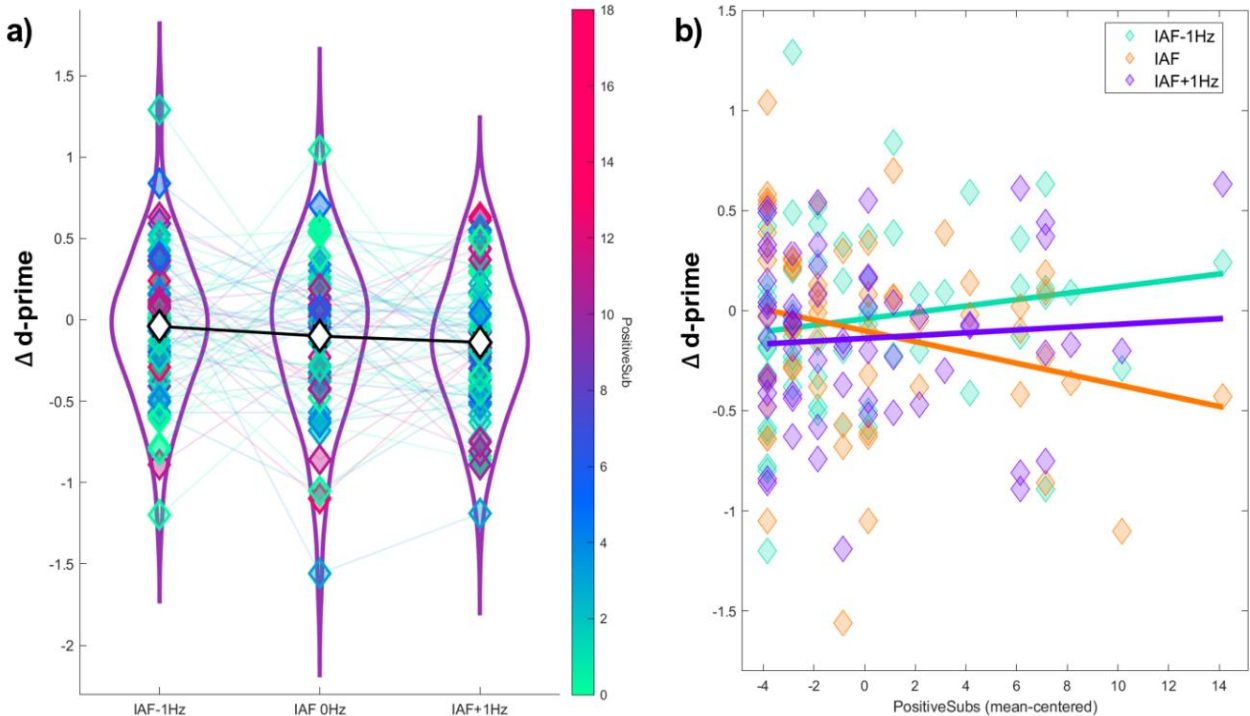


Figure 7.3 Perceptual sensitivity data (color-filled diamonds represent participants' scores). **a)** Violin plots depicting Sham-corrected d' levels (y-axis, Δd -prime) sorted as a function of the stimulation frequency (IAF-1Hz, IAF, IAF+1Hz, x-axis), and color-coded according to the degree of positive schizotypal traits (*PositiveSub* colorbar); white diamonds and error bars represent mean and S.E.M. **b)** Simple-slope scatterplot of mean-centered *PositiveSubs* (x-axis) vs. Sham-corrected d' levels (y-axis, Δd -prime), color-coded according to the stimulation frequency (IAF-1 Hz, IAF, IAF+1 Hz). Solid colored-lines represent the fixed-effect simple slopes.

Simple-slope tests showed (figure 7.3, b) that higher PositiveSub predicted lower d' levels in the IAF conditions ($\beta = -.027$, $CI [-.054, -.001]$, $p < .05$), whereas slopes at IAF-1 Hz ($\beta = .016$, $CI [-.011, .043]$, $p > .05$) and IAF+1 Hz ($\beta = .007$, $95\% CI [-.020, .033]$, $p > .05$) did not differ from zero. Further pairwise slope contrasts indicated that in the IAF condition the slope differed from IAF-1 Hz ($z = 2.38$, $p < .05$) but not from IAF+1 Hz ($z = -1.88$, $p > .05$). Overall, positive schizotypal sub-traits appear to mildly moderate perceptual acuity when rhTMS was delivered in the IAF condition: the higher, the lower d' levels.

7.3.2.2 Response Bias (c)

Beside audiovisual sensitivity, we also delved into response bias trends. In this case, we did not anticipate any frequency-dependent shift in criterion bias, although we were interested in tracking whether positive schizotypal sub-traits might play a role in shaping participants' response style. Akin to d' data, we first computed c levels per each participant and stimulation condition. Next, we performed Sham-correction ($c_{IAF-1Hz} = -.088 \pm 0.040$; $c_{IAF} = .101 \pm .043$; $c_{IAF+1Hz} = -.001 \pm .035$), and entered these data, along with the associated positive sub-traits scores (PositiveSub) into a one-way rmANOVA (figure 7.4, a).

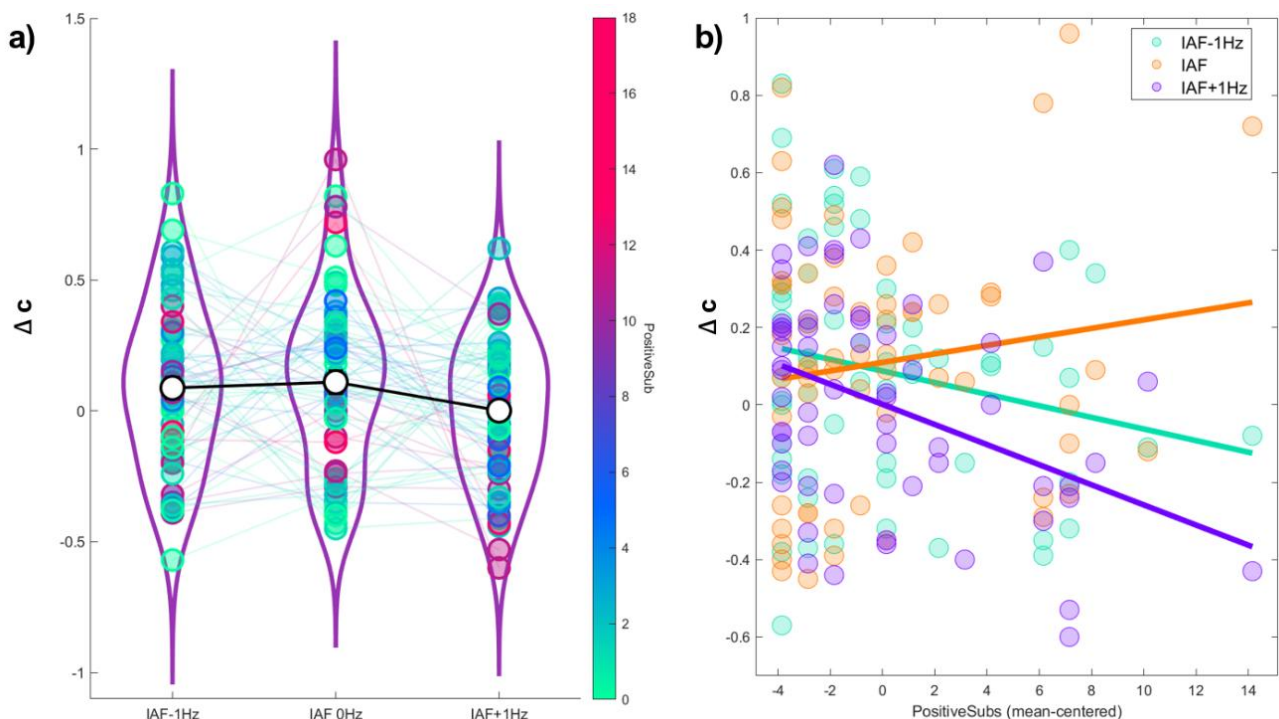


Figure 7.4 Response bias data (color-filled dots represent participants' scores). **a)** Violin plots depicting Sham-corrected c levels (y-axis, Δc) sorted as a function of the stimulation frequency (IAF-1Hz, IAF, IAF+1Hz, x-axis), and color-coded according to the degree of positive schizotypal traits (*PositiveSub* colorbar); white dots and error bars represent mean and S.E.M. **b)** Simple-slope scatterplot of mean-centered *PositiveSubs* (x-axis) vs. Sham-corrected c levels (y-axis, Δc), color-coded according to the stimulation frequency (IAF-1 Hz, IAF, IAF+1 Hz). Solid colored-lines represent the fixed-effect simple slopes.

We found no main effect of either Stimulation Frequency, nor of PositiveSub covariate (all p -values $> .05$; all $BF_{10} < 1$). However, the analysis of variance uncovered a significant Stimulation Frequency*PositiveSub interaction ($F_{2,116} = 5.97$, $p < .01$, $\eta_p^2 = .094$; $BF_{10} = 13.55$ [null-model = main effects], figure 7.4, b). Simple-slope tests showed that higher PositiveSub predicted a shift toward a more liberal criterion at IAF+1 Hz ($\beta = -.026$, $CI [-.044, -.008]$, $p < .01$) and, to a milder and non-significant extent, at IAF-1Hz ($\beta = -.015$, $95\% CI [-.033, .003]$, $p > .05$), whereas the slopes in the IAF condition ($\beta = .011$, $95\% CI [-.006, .029]$, $p > .05$) were not different from zero. Interestingly, planned slope contrasts indicated that the PositiveSub slope at IAF differed from IAF-1 Hz ($z = -2.386$, $p < .05$) and from IAF+1 Hz ($z = 3.357$, $p < .01$). To summarize, PositiveSub drove participants toward a more liberal response style when rhTMS was administered at IAF+1Hz, and to a lesser extent, at IAF-1Hz, while no significant moderation was found at IAF.

7.3.2.3 Accuracy Rates (ARs)

Lastly, we also analysed performance accuracy. ARs were thus computed per each participant and stimulation condition, Sham-corrected ($AR_{SIAF-1Hz} = -.375 \pm .855\%$; $AR_{SIAF} = -1.480 \pm .852\%$; $AR_{SIAF+1Hz} = -1.31 \pm .797\%$) prior to be fed to a one-rmANOVA, along with the associated positive sub-traits scores (PositiveSub). Results showed no significant main effects of Stimulation Frequency, PositiveSub covariate, nor their interaction (all p -values $> .05$; all $BF_{10} < 1$). In a nutshell, our stimulation protocols did not impact performance accuracy, even when accounting for positive schizotypal sub-traits.

7.4 Discussion

An intriguing issue that fuelled long-standing debates among psychophysicists concerns the supposedly cyclic nature of perception (Di Lollo & Wilson, 1978; Efron, 1970b; W. James, 1886; Shallice, 1964; Stroud, 1956). The appealing notion of some mechanism parsing an ever-flowing sensory stream into discrete samples of information, readily available to our conscious experience, invited perhaps an even more provocative question: how does our nervous system achieve such a feat? As perception operates on a sub-second timescale, brain rhythms stood out as the leading candidates within a biologically-informed account of perceptual sampling (Kristofferson, 1967; VanRullen, 2016; Varela et al., 1981). Due to their phasic bouts of excitation and inhibition, low frequency oscillations have been deemed responsible for supplying perception with the physiological apparatus that instantiate the parsing routines. Earlier and recent findings were supportive of this proposition,

particularly with regard to parieto-occipital alpha oscillations recorded during visual tasks (Coffin & Ganz, 1977; Di Gregorio, Trajkovic, et al., 2022; Dugué et al., 2011; Trajkovic et al., 2023). Cycle-to-cycle alpha transitions would thus partition the incoming visual signals into perceptual snapshots, encoded at a sampling resolution that scales with each cycle's range. Of note, the mechanistic implications of this model provide that faster- (vs slower-) oscillating rhythms should entail finer (vs coarser) parsing operations (followed by better vs worse visual performance). This maps onto the construct of perceptual windows (i.e., TBWs), which, due to their favourable temporal properties, act by aggregating (or segregating) sensory inputs into coherent representations. Convincing evidence that the speed of peristimulus alpha rhythms indeed shapes TBWs has been gathered mainly in the visual domain (Gulbinaite et al., 2017; Samaha & Postle, 2015; although see Gray & Emmanouil, 2020), or, by extension, in clinical and subclinical populations, along the schizotypal axis, in which an idiosyncratic alpha speed slow-down was witnessed (Chen et al., 2014; Giersch et al., 2009; Ramsay et al., 2021; but see Deodato et al., 2024 for a different account). However, these findings hardly translate to multisensory (audiovisual) tasks, where conflicting results have been reported as of late. Many studies unveiled a strong tie between peristimulus or prestimulus IAF, cross-modal TBWs and positive schizotypal traits (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017; Keil & Senkowski, 2017; Y. Noguchi, 2023), while others failed to replicate this association (Buergers & Noppeney, 2022; London et al., 2022; Rohe et al., 2024; Vanes et al., 2016).

In the current work, we planned to shed further light onto the spectral signatures of audiovisual perception. To do so, we causally attuned the oscillating frequency of prestimulus occipital alpha rhythms to a faster vs slower cycling pace, prompting finer vs coarser perceptual sampling rates in participants asked to perform a modified version of the well-known SIFI task. This was achieved by leveraging entrainment-inducing TMS protocols (Thut, Veniero, et al., 2011) administered during a paradigm designed to pull apart perceptual sensitivity (d') vs response bias (c) in multisensory performance, while accounting for the degree of positive schizotypal traits at the individual level. In line with the discrete sampling hypothesis of perception (VanRullen & Koch, 2003), we predicted greater audiovisual acuity when rhTMS entrained endogenous occipital alpha rhythms to a faster (as compared to a slower) frequency rate, and no significant change to response bias as a function of the stimulation protocol. Our results, however, run counter this account.

On the one hand, electrophysiological analyses substantiate a foundational assumption which our study was built upon. Namely, TMS trains delivered in a rhythmic fashion differentially entrained oscillatory dynamics to the machine frequency output. Our spectral metrics, though derived using distinct methodological pipelines, underscored a robust TMS-dependent frequency shift within the peristimulus time window targeted by our stimulation protocol. This aligns with a growing body of

literature suggesting TMS is a viable tool, not only for boosting the amplitude of cortical rhythms (Albouy et al., 2017; Riddle et al., 2024; Thut, Veniero, et al., 2011), but also to etch entrainment signatures into the speed of ongoing brain oscillations (Di Gregorio, Trajkovic, et al., 2022; Trajkovic, Di Gregorio, et al., 2024; Trajkovic, Sack, et al., 2024). Further, we provided sound evidence for the reliability of instantaneous frequency estimates (M. X. Cohen, 2014; Samaha & Postle, 2015) as an analytical approach to delve into oscillatory speed dynamics in TMS-denoised EEG signals. To our knowledge, this is the first time ever such an attempt has successfully been made, offering cognitive electrophysiologists a principled alternative to standard peak-detection workflows. This even more so applies if the fair quantitative agreement between instantaneous frequency estimates and state-of-the-art PSD-based control methods (i.e., peak extraction via FOOOF) is factored in.

On the other hand, though, our pattern of behavioral results fails to align with what would have been anticipated, had entrainment been effective. Up- or down-shifting prestimulus alpha frequency peaks did not result in significant changes to audiovisual sensitivity, nor performance accuracy, consistent with recent lines of research struggling to establish a causal link between multisensory binding windows and alpha rhythms (Buergers & Noppeney, 2022; Haarlem et al., 2024; London et al., 2022). Methodological nuances embedded into the aforementioned experimental designs have been invoked as the key drivers of null-findings (Samaha & Romei, 2024). When borrowing such perspective, it could be argued that, in the current work, TMS targeted ongoing brain rhythms in a task whose accuracy threshold was set to float around 70%, as compared to prior investigations providing compelling evidence in this regard. So far, causal tuning of occipital alpha speed, either achieved via rhTMS or transcranial alternating-current stimulation (i.e., tACS) has been found to significantly shape visual and audiovisual performance, as long as threshold accuracy rates were set around 50% (Di Gregorio, Trajkovic, et al., 2022), or a shift in the perceptual inflection point was the main metric under scrutiny (Cecere et al., 2015). In our case, anchoring performance to a fixed SOA perhaps stabilized interindividual variability in behavioral terms, but at the price of dampening d' sensitivity to manipulations devised to prompt horizontal shifts in the TBW, rather than a local change in signal-to-noise ratio. More on this, setting accuracy to around 70% could have placed the operating point well away from TBW's inflection ($\approx 50\%$), in which the slope (and thus sensitivity to horizontal shifts) is maximal, further degrading the detectability of rhTMS-evoked audiovisual effects. It might then be that our null-findings were mostly due to a sub-optimal psychophysical set-up, which blunted an otherwise robust TMS-based frequency entrainment. Were such an interpretation correct, it would set apart the notion of perceptual sampling rate (VanRullen & Koch, 2003) from the construct of TBWs (Wallace & Stevenson, 2014), with critical mechanistic implications, both at the behavioral and neurocomputational level.

Additional constraints may have also arisen due to the TMS-EEG pipeline. More specifically, the frequency range here adopted (i.e., $\pm 1\text{Hz}$), although aligned with prior work (Di Gregorio, Trajkovic, et al, 2022), might have produced too weak a magnitude modulation to induce measurable changes in d' . Consistent with interpretation, several entrainment-based studies leveraging tACS have reported robust behavioral outcomes when set at a wider $\pm 2\text{Hz}$ range (Bender et al., 2019; Mioni et al., 2020; Ronconi et al., 2022; Wolinski et al., 2018; Zhang et al., 2019), including a SIFI-based paradigm in which marked shifts in cross-modal perception were reported (Cecere et al, 2015). Therefore, it cannot be ruled out that the peak-shifting range we used instantiated entrainment-like phenomena detectable at the EEG level, yet too mild to elicit the expected behavioral changes.

Another point that could be made with respect to the neurostimulation protocol concerns the actual viability of TMS in audiovisual tasks. Each magnetic pulse the machine emits comes with a loud clicking noise, which might have turned into a massive experimental confound due to the contingency of our paradigm on auditory inputs. Although the SIFI was shown to be immune from TMS sensory by-products (Bertaccini et al., 2023), we cannot entirely rule out this scenario. In addition, TMS is known to be endowed with a rather high degree of topographical specificity (Thut, Veniero, et al., 2011). That is, entrainment-induction occurs at a local scale (i.e., focal over the stimulated site). This convenient feature might have turned out to be an unexpected drawback, as audiovisual interplay requires distributed computations that could recruit a wider set of sensory and associative areas (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Y. Li & Noguchi, 2025; Noesselt et al., 2007). In this case, the need of a broader target for entrainment protocols to yield behavioral changes should reconcile our data with significant results obtained using tACS (Cecere et al., 2015; Herrmann et al., 2013).

In brief, under the present methodological constraints, the current results do not provide conclusive evidence concerning the causal role played by the speed of occipital alpha rhythms in orchestrating audiovisual perception. Linear mixed-effects modelling nevertheless revealed a trait-dependent moderation on TMS-driven behavioral responses. Positive schizotypal sub-traits were associated with reduced audiovisual sensitivity when rhTMS at IAF was delivered (i.e., the most neutral stimulation condition), such that individuals with higher positive traits displayed poorer d' levels. This aligns with prior reports of demeaned perceptual acuity and wider TBWs in participants lying on the upper end of the schizotypal continuum (Haß et al., 2017; Mussgay & Hertwig, 1990; Partos et al., 2016; H. Zhou et al., 2022), and with evidence that severity of positive-like traits (e.g., Odd Belief and Magical Thinking) often couples with disrupted multisensory temporal processing (Ferri et al., 2018; Marsicano et al., 2022). With respect to response bias, the drift toward a more liberal decision style observed in the IAF+1Hz condition, contingent on the degree of positive traits, reflects an increased amount of 2-

flashes reports, likely associated with a greater number of false alarms (i.e., illusory 2-flashes reports in 1F2S trials). Given the fixed near-threshold operating regime and the consequent limitation on d' variability, such criterion effects may represent the behavioral dimension most likely to remain detectable in the current paradigm, and should therefore be interpreted cautiously. Accordingly, rather than motivating strong mechanistic claims, these findings point to an interaction between alpha-state perturbation and interindividual variability in schizotypal traits that is worth future scrutiny, including whether rhTMS-driven changes might relate to altered gating of sensory evidence (Jensen & Mazaheri, 2010) or to phase-resetting dynamics and feedback channelling (Fries, 2005), under psychophysical set-ups better suited to track sensitivity shifts.

To conclude, although rhTMS entrained occipital alpha rhythms to faster vs slower oscillating rates, SDT-informed analyses, under the present psychophysical set-up, cannot be taken as conclusive evidence against a causal involvement of this spectral signature in dictating audiovisual TBWs. In this context, how positive schizotypal traits and alpha entrainment jointly act on cross-modal sensitivity vs response bias remains an intriguing experimental question, best addressed in future studies adopting operating points closer to TBW's inflection ($\approx 50\%$) and/or mapping performance across SOA ranges.

Chapter 8: General Discussion and Conclusions

Over the past two decades, the field of mental health research has undergone a methodological renaissance, promoting a gradual shift toward a more mechanistic and pathophysiological understanding of psychiatric disorders (Insel et al., 2010). At the intersection of neurobiology, behavioral sciences and clinical practice, this multidisciplinary orientation has been reframing psychopathology as a syndromal endpoint on a seamless, dimensionally-arrayed spectrum (Krueger & Eaton, 2010), wherein symptoms are to be treated as graded variations from adaptive to dysfunctional behavior, rather than discrete nosographic categories (Cuthbert, 2014; Krueger & Eaton, 2010). Such theoretical reappraisal invoked a thorough scrutiny of the biobehavioral features co-occurring and covarying, respectively, with (sub)clinical manifestations along a given psychopathological continuum and their degree of severity (Insel et al., 2010). The translational implications are twofold. First, and straightforwardly so, neurobiological or behavioral markers are informative about the underlying pathomechanisms, and can be leveraged to devise novel therapeutic strategies, or fine-tune existing ones. Second, biobehavioral markers may provide a reliable compass for clinicians to navigate often ill-defined diagnostic landscapes, and pre-emptively flag healthy individuals likely en-route to high-risk clinical outcomes (Insel et al., 2010). More recently, psychosis-like phenomena have furnished an intriguing testbed for this novel approach, given the substantial overlap between SCZ spectrum disorders and schizotypal personality traits in the general population across clinimetric, genomic, neurofunctional and cognitive-perceptual domains (Claridge, 1997; Cochrane et al., 2012; Ettinger et al., 2014; Nelson et al., 2013).

The psychosis (or SCZ) continuum has indeed challenged both psychiatrists and translational scientists as to whether any behavioral or neurobiological marker predictive of an individual's clinical trajectory could be identified. At the perceptual and symptomatic level, hallucinatory-like manifestations typifying the psychotic dimension have been proposed to branch off from the same endophenotype in which low-level audiovisual alterations so often documented along the psychosis continuum are rooted (Javitt, 2009b; Stevenson et al., 2017). The SIFI has been sitting mid-way across these key stances: illusory in nature, therefore capturing hallucinatory features (Shams et al., 2000), and frequently probed, though with conflicting outcomes and mechanistic accounts, in psychosis-prone individuals (Balz et al., 2016; Ferri et al., 2018; Haß et al., 2017; Paredes et al., 2025; Rohe et al., 2024; Vanes et al., 2016). Even more appealing, in a translational sense, is the question of the latent endophenotype purportedly governing such a complex trait-behavior interplay. Under the assumption that individuals high on the psychotic dimension should be more susceptible to the SIFI due to a disruption of bottom-

up audiovisual computations, does the speed of posterior alpha rhythms, a stable neurophysiological index (Gasser et al., 1985) posited to both dictate the temporal resolution of visual perception (Coffin & Ganz, 1977; Kristofferson, 1967; VanRullen, 2016; Varela et al., 1981) and track the severity of positive-like symptoms along the SCZ continuum (Ramsay et al., 2021; Trajkovic et al., 2021), orchestrate these interactions?

Across four studies, this set of hypotheses has been tested by putting together clinimetrics, psychophysics, electrophysiology and neurostimulation. We first asked (Chapter 4) whether participants high in schizotypy (as compared to low) displayed worse audiovisual performance (in a revised version of the SIFI task) due to poorer perceptual sensitivity, rather than a more liberal response bias, and detailed the extent to which this could be predicted by the severity of positive schizotypal sub-traits. In line with our expectations, we found dilated audiovisual binding windows in participants with high schizotypal traits, with degraded visuo-temporal precision being the most likely mechanistic explanation, and the degree of positive-like sub-traits as the underlying driver. Bearing in mind the role of alpha oscillations in conscious perception, we then reviewed the EEG literature (Chapter 5) accrued over recent years within the clinical domain to identify which alterations in the alpha band are most reliably observed in SCZ spectrum disorders. Amid many controversial findings, the sole consistent result across multiple reports was a significant slowing of occipital alpha rhythms in patients with SCZ, positioning this trait-like index among the most plausible candidate biomarkers along the SCZ continuum. As such, prior to the causal manipulation of occipital alpha speed, we conducted a feasibility study (Chapter 6) to assess whether alpha-tuned rhTMS, known to entrain brain oscillations, did interfere with audiovisual processing. Results showed that rhTMS-induced acoustic and somatosensory sensations had no significant impact on SIFI occurrence, demonstrating this protocol could serve as a viable tool to probe the electrocortical dynamics underpinning multisensory integration. This paved the way to the last study (Chapter 7), in which we leveraged rhTMS paired with online EEG recordings to causally up- and down-shift the cycling frequency of posterior alpha rhythms in participants screened for their schizotypal traits and asked to complete a SIFI task at a threshold SOA. Contrary to our predictions, successfully increasing or decreasing alpha oscillatory speed did not result in corresponding shifts in perceptual sensitivity, although a substantial mediation by schizotypal sub-traits on TMS-driven changes in response bias was revealed.

8.1 Revising Multisensory-Sampling Accounts in the Psychosis Continuum

Together, these findings do not provide conclusive causal support for an alpha-mediated sensory sampling account, at least in the context of audiovisual integration. Rather, they are consistent with a

two-component framework in which positive-like sub-traits robustly index reduced multisensory temporal precision (Chapter 4), whereas any behavioral consequences of alpha-speed modulation (under these parameters) appear limited, and better captured through the lens of decisional styles (Chapter 7). On the one hand, positive-like schizotypal traits, in and of themselves, appear robustly entwined with interindividual differences in visuo-temporal precision. This supports recent bottom-up interpretations of SCZ symptoms (Javitt, 2009b; Javitt et al., 1999) that ground hallucinatory-like experiences in early disruptions to the computational machinery that channels low-level signals to high-order regions: sensory inputs encoded with reduced fidelity propagate upstream as noisy perceptual traces, which interact with sub-optimal monitoring strategies, inflating misperceptions and hallucinatory reports (Javitt, 2009b). These mechanistic implications may apply even more strongly to multimodal processing. When cross-modal stimuli are to be integrated or segregated, the computational challenge is greater, and poorly-tuned perceptual systems placed under more strain (Javitt et al., 1999). Our results are supportive of this view, given the patterns of reduced temporal sensitivity in high-schizotypy individuals (Chapter 4), and, to a milder extent, in individuals with pronounced positive sub-traits (as seen in the IAF condition, the most neutral one assumed to induce little changes to the ongoing speed of alpha rhythms; Chapter 7). Paired with the tight association between visuo-temporal precision and cross-modal binding window width (i.e., CW in Chapter 4), this confirms how the psychometric construct of multisensory TBW is heavily reliant on the sensory precision of a given system, and therefore shaped by the severity of positive-like traits along the SCZ continuum (Stevenson et al., 2012, 2017; Wallace & Stevenson, 2014). From here, it becomes reasonable to assume that susceptibility to the SIFI can be framed as a particular instance of impoverished audiovisual sensitivity dilating an observer's integration window (Haß et al., 2017), and that a greater propensity for illusory extra-flash reports corresponds to a reliable behavioral phenotype capturing subclinical profiles more liable to psychosis (Ferri et al., 2018).

On the other hand, these pieces of evidence raised the question of whether any latent biological marker could similarly track psychosis-prone individuals along the SCZ continuum, while at the same time shaping visuo-temporal precision. Building on the broader clinical literature, the relatively consistent observation of slower resting IAF in psychosis-prone patients positioned posterior alpha rhythms as a neurophysiologically plausible candidate mechanism. This is consistent with the notion of a parsing process that rhythmically samples sensory information at the timescales matching the temporal span of audiovisual binding windows (Cecere et al., 2015; Shams et al., 2000; VanRullen & Koch, 2003; Varela et al., 1981), which appear enlarged both in patients diagnosed with SCZ and high-schizotypy individuals (Ferri et al., 2018; Haß et al., 2017).

However, our causal findings downplay this account, and recast the functional meaning of occipital alpha rhythms within a more nuanced framework, with positive schizotypal sub-traits playing a key role. The observation that entraining spontaneous alpha oscillations to a faster frequency rate primarily altered response bias in a trait-dependent manner is suggestive of a complex interplay between perception, clinimetrics and neurophysiology. Instead of pacing an observer's sampling rate, our data indicate that increasing alpha oscillatory speed may produce trait-gated shifts toward a more liberal response criterion and greater illusory reports (extra-flash perceived in 1F2S trials). The current evidence for a trait-mediated tie between IAF and decisional styles might reflect an endophenotypic predisposition (i.e., indexed by the severity of positive schizotypal traits) tilting a system toward an integration-oriented decision-making regime (i.e., two flashes, rather than one, are more likely to co-occur with two beeps, and perceived as such), magnified when alpha frequency is upshifted.

All in all, the present research project has therefore met our predictions only in part. Whereas high schizotypy individuals displayed broader TBWs, most plausibly due to degraded audiovisual precision associated with positive-like sub-trait severity (Ferri et al., 2018; Javitt, 2009b; Stevenson et al., 2017), our causal data suggest that up- or down-shifting occipital alpha cycling rate does not elicit corresponding changes in cross-modal sensitivity. In line with discrete theories of perception, in which each alpha cycle is assumed to correspond to a sampling event, we expected that faster alpha oscillatory rates, as compared to slower ones, would entail finer (vs coarser) perceptual acuity (VanRullen, 2016; Varela et al., 1981). In this regard, evidence from our TMS-EEG study is less a falsification of the aforementioned hypothesis than a boundary-setting result showing how IAF modulation does not uniformly translate into audiovisual sensitivity changes, at least given the present experimental conditions.

These observations lend weight to distinct, non-mutually exclusive mechanistic accounts of the interplay between positive-like schizotypal traits and alpha oscillatory speed during audiovisual integration. To begin with, the role of occipital IAF in shaping perceptual sensitivity has been widely documented, either through causal or correlational designs, within the visual domain (Di Gregorio, Trajkovic, et al., 2022; Samaha & Postle, 2015), whereas in audiovisual tasks evidence is more mixed and sparser (Burgers & Noppeney, 2022; Cecere et al., 2015; Keil & Senkowski, 2017; London et al., 2022; Y. Noguchi, 2023). Taken together with clinical evidence showing slower resting-state alpha rhythms in psychosis-prone individuals (Ramsay et al., 2021; Trajkovic et al., 2021), this pattern implies that IAF may index fine-grained visual circuit properties only partially captured by transient frequency shifts during tasks involving additional sensory modalities, supporting its role as a broader biomarker of altered temporal organization rather than as a direct cross-modal sensitivity phenotype. This view also resonates with accounts that conceptualize oscillatory anomalies in SCZ as emergent

signatures of disrupted E/I balance in cortical microcircuits, whereby aberrant alpha dynamics may signal broader failures in temporal integration and large-scale coordination of heteromodal inputs (Uhlhaas & Singer, 2010).

Such considerations foreground the key conflicting finding of the current research project. Entraining ongoing prestimulus alpha rhythms at faster frequency rates mainly modulated audiovisual response criterion (the behavioral dimension most likely to remain free to vary once sensitivity is constrained by a fixed near-threshold regime) in a trait-gated manner. Although prior work on visual perception has revealed a tight link between decisional styles and fluctuations in posterior alpha power (Iemi et al., 2017; Limbach & Corballis, 2016), we here observed similar behavioral correlates as a function of both IAF manipulation and personality traits. One plausible, overarching interpretation is that positive-like schizotypal traits might reflect latent network frailties encompassing low-level cognitive and perceptual processing, which, in our TMS-EEG study, are not further expressed as coarser cross-modal precision, but instead map onto a greater predisposition for integration (over segregation) and a more liberal decision-making style, when ongoing alpha speed increases. Within this context, two explanatory accounts could be cautiously sketched. The first builds on the notion of alpha rhythms as a sequence of duty cycles regulating cortical excitability (Jensen & Mazaheri, 2010). In this view, increasing occipital alpha frequency under temporal ambiguity may concurrently increase the temporal density of excitability bouts in the visual system reduce the amount of available visual evidence within the critical time window, thereby favouring greater reliance on auditory inputs. A complementary model invokes alpha phase resetting and feedback channelling instead (Fries, 2005): faster prestimulus alpha oscillations may strengthen cross-areal phase alignment between auditory and visual regions following sound onset, amplifying the impact of auditory information channelled in a feedback manner to the visual cortex, promoting a liberal response bias in individuals with high schizotypy.

Importantly, the extent to which these patterns of results genuinely reflect electrocortical dynamics is anchored in both our feasibility study (Chapter 6) and the causal design of the TMS-EEG protocol (Chapter 7). The former provided robust evidence against any artifactual influence of acoustic and somatosensory by-products of alpha-tuned rhTMS on the occurrence of SIFI, thereby validating this toolchain for probing audiovisual mechanics in a causal fashion. The latter combined TMS and EEG not only to differentially entrain brain rhythms at faster or slower IAF, but to also verify through spectral analyses to what degree this manipulation succeeded, confirming that the intended oscillatory target was effectively engaged.

To summarize, the current data highlight that positive schizotypal sub-traits in healthy individuals are strongly associated with poorer audiovisual sensitivity, enlarged TBWs and, most plausibly, increased SIFI susceptibility (Ferri et al., 2018; Haß et al., 2017). However, within the present task parameters,

the causal evidence hereby presented does not provide conclusive support for IAF as a single lever controlling these operations, and instead suggests a context-dependent influence of occipital alpha timescales that, under a fixed near-threshold operating regime, is more readily expressed in multisensory decisional strategies in a trait-gated manner.

Some cross-project limitations should be acknowledged though. The most evident concerns the recruitment of healthy individuals, screened for their schizotypal traits using a personality questionnaire, as opposed to a clinical sample of patients diagnosed with SCZ. From a translational standpoint, these considerations constrain both how far our findings can be interpreted and how broadly they can be applied. Although the project was built upon the notion of a seamless continuum of overlapping features across the psychosis dimension (Cochrane et al., 2012; Ettinger et al., 2014; Nelson et al., 2013), the symptomatic profiles and functional impairments observed in patients far exceed those seen in high schizotypy participants, and likely involve additional layers of neurocomputational disruption that the present work cannot capture. This limitation is perhaps compounded by the non-nested design across studies (i.e., Chapter 4 and Chapter 7), which prevents strong claims about within-subject coupling between positive-like sub-traits, visuo-temporal precision scaffolding multisensory binding windows, and alpha-band oscillatory dynamics. Moreover, the present data probed audiovisual integration in the illusion-inducing context of the SIFI, a paradigm devised to bias multisensory perception toward one sensory modality (audition) over another. It remains to be established whether the associations hereby observed between personality traits, temporal sensitivity, decisional strategies and alpha rhythms generalise to other audiovisual tasks or more ecological settings.

Additional constraints arise from the TMS-EEG pipeline. A first, and perhaps most straightforward, consideration concerns the magnitude of the frequency modulation achieved through our TMS protocol. Although aligned with prior rhTMS work (Di Gregorio, Trajkovic, et al., 2022), the peak-shifting range we adopted ($\pm 1\text{Hz}$) might have been too narrow to induce detectable changes in d' . Consistent with such an interpretation, several studies using tACS-based modulation of ongoing brain rhythms pace have reported behavioral effects when set at a wider $\pm 2\text{Hz}$ range (Bender et al., 2019; Mioni et al., 2020; Ronconi et al., 2022; Wolinski et al., 2018; Zhang et al., 2019). This same approach has also been applied with respect to the SIFI, yielding marked shifts in cross-modal perception (Cecere et al., 2015). Accordingly, we cannot rule out that our parameter settings produced entrainment-like phenomena robust at the electrophysiological, level yet too mild to elicit reliable behavioural changes. To these remarks, it may be also added that the effectiveness of entrainment responses likely varied on an interindividual basis given the same stimulation intensity (60% MSO) and the very same scalp site undergoing the stimulation (Oz) were used across participants.

A second line of reasoning pertains to the cortical site targeted by our stimulation protocol, and the possibility that V1, in and of itself, may not be the only region supporting temporal perception dynamics within the occipital lobe. For instance, recent findings point to MT/V5 as an alternative key node along the dorsal stream: alpha oscillatory phase over this region has been shown to predict subjective perception at a double-flash visual task (Ronconi et al., 2024). These correlational results were further strengthened by a follow-up work leveraging bifocal tACS administered to causally up- or down-shift IAF (i.e., $\pm 2\text{Hz}$) over right and left MT/V5, which significantly reshaped sensitivity to temporal proximity of visual cues (Santoni et al., 2025). While the aforementioned studies primarily quantified performance through accuracy rates rather than a signal detection framework, they are nonetheless dovetail with both neuroanatomical evidence, as MT/V5 lies in close proximity to STS (a functional hotspot for audiovisual integration), and earlier TMS and fMRI pieces of research implicating MT/V5 in time perception (Battelli et al., 2007; Bueti, Bahrami, et al., 2008; Bueti, Walsh, et al., 2008; Salvioni et al., 2013). From this perspective, the absence of IAF-mediated changes in perceptual sensitivity following rhTMS could be interpreted as the result of targeting a cortical locus that was not optimally localized to effectively modulate the neural computations most relevant to the SIFI.

A final consideration in regard to which aspects of our paradigm may have driven the null behavioral effects in our TMS–EEG study revolves around task geometry. That is, SIFI performance was probed at a single, near-threshold SOA, individually titrated to ensure accuracy rates around 70%. Such a design is well suited to capturing decision policy shifts under uncertainty, but may be relatively insensitive to subtle changes in sampling rate or temporal precision that would manifest as alterations in the shape or position of the full psychometric function. This even more so apply when factoring in the sub-optimal operating point, which could have been placed closer to TBW’s inflection point (i.e., 50% accuracy rate). Constraining performance to a narrow SOA band might have compressed variance in d' , whereas criterion remained free to absorb trait- and state-dependent biases. It therefore remains possible that alpha-speed modulation would produce detectable effects on multisensory sensitivity when assessed across the entire temporal binding window or, alternatively, at near chance-level SOAs, as done in prior work (Cecere et al., 2015; Di Gregorio, Trajkovic, et al., 2022; Keil & Senkowski, 2017)

8.2 Translational Implications and Future Directions

The aforementioned findings carry several translational implications. At the behavioral level, reduced visuo-temporal acuity appears to be a perceptual fingerprint of psychosis-prone individuals,

manifesting as an increased susceptibility to the SIFI that is also observed in healthy individuals located toward the schizotypal end of the psychosis continuum (Ferri et al., 2018). In clinical terms, this pattern may represent a sensitive marker of heightened risk to develop SCZ, which could, in principle, be incorporated into diagnostic routines to better inform clinicians' decision-making. Such an approach would be beneficial in multiple respects. First, the translational potential of SIFI-based measures has already been demonstrated in other subclinical samples, most notably older adults. Here, multisensory abilities indexed by SIFI performance predict age-related functional outcomes and fall-proneness (McGovern et al., 2014; Setti et al., 2011), prompting the deployment of SIFI paradigms at scale in longitudinal cohorts (e.g., TILDA in Ireland) as proxies of multisensory temporal precision with predictive value for gait, fall trajectory, functional ageing and cognitive status (Hirst et al., 2019, 2022; O' Dowd et al., 2023; Setti et al., 2023). Beyond stratification and early risk detection, SIFI-related temporal binding metrics have been shown to be liable to changes through targeted audiovisual training, although generalisation of such improvements to everyday-life outcomes remains to be clearly established (O'Brien et al., 2020; Setti et al., 2014). Reframed within the present results, this suggests the SIFI could similarly serve as a viable additional strategy to pre-emptively identify illusion-prone individuals along the psychosis continuum who may be at higher risk of SCZ onset. Second, the clinical version of the SIFI task could be readily shortened to approximately 10 minutes with minimal loss of information, making it particularly time-efficient. Third, implementation is highly cost-effective, as it requires standard audiovisual equipment (i.e., personal computer, monitor and loudspeakers). Fourth, a recent study indicates that the web-based version of the task can be as informative and efficient as laboratory implementations, enabling deployment in large-scale samples and thereby increasing its potential screening reach (Flanagan et al., 2025).

Moving to the neurophysiological level, results from the TMS-EEG study, while not offering clinic-ready insights, shed some light on entrainment-induced oscillatory perturbations and the extent to which they modulate illusion-proneness in a trait-dependent manner, within the methodological constraints of the present design. Tuning prestimulus alpha states to faster frequency rates, in the current audiovisual paradigm, tilted decision policies toward sub-optimal integration of auditory signals into visual responses, in observers with positive-like sub-traits. As such, our findings have more cautionary than therapeutic in their significance, implying that alpha-targeted neuromodulation is unlikely to be benefit-neutral and should not be regarded as a direct lever to ameliorate temporal precision. Rather, they suggest any forthcoming entrainment-based protocol set to restore neurophysiological imbalances in clinical settings should carefully contemplate alternative parameter spaces (e.g., slowing rather than speeding) and titration strategies.

These considerations point to several promising avenues for future research. A straightforward next step is to extend this SIFI paradigm to patients with SCZ, carefully stratifying the sample by illness stage (chronic vs post-acute). Provided that similar patterns of behavioral and computational results emerge, this would pave the way for large-scale screening interventions in which web-based versions of the task are first deployed in the general population, alongside positive SPQ items. Individuals high in positive schizotypal sub-traits, and displaying broadened TBW could then be enrolled in longitudinal studies designed to test the extent to which these phenotypes prospectively track transition risk or symptoms trajectories, thereby consolidating the continuum hypothesis from both clinical and translational perspectives. At the mechanistic level, an appealing addendum would be integrating explicit BCI models to expand on the current findings and confirm at a finer-grained level whether poorer visuo-temporal acuity patterns hereby observed map onto specific parameter changes, such as reduced visual precision, altered priors over a common cause, or their joint modulation. Germane to this proposition, including confidence ratings at the end of each SIFI trial could yield valuable information about the metacognitive machinery supporting illusion-proneness, and how it interplays with low-level sensory computations. These extensions also apply to future TMS-EEG implementations of the SIFI. In such designs, condition-wise or trial-by-trial changes in IAF or other oscillatory metrics (power, long-range connectivity, phase) could be related to BCI parameters or metacognitive indices, going beyond SDT metrics alone. Lastly, and perhaps most intuitively, these instances of TMS-driven entrainment and online EEG recording could be implemented under a single chance-level SOA regime (50% accuracy) or, alternatively, across a wide range of temporal delays, to probe whether and how alpha-speed (or power) modulation primarily reshapes decision policies in a trait-gated fashion, or whether it can induce genuine shifts in individuals' TBWs and the underlying nuances of temporal sensitivity.

8.3 Conclusions

To conclude, this research project indicates that the severity of positive-like sub-traits along the SCZ continuum is entwined with poorer visuo-temporal acuity and, most plausibly, greater susceptibility to a modified version of the SIFI. Using the same paradigm, we further demonstrated that entrainment-induced shifts of occipital IAF, a putative biomarker of psychosis, were accompanied by changes in decisional strategies in a trait-gated manner: the higher the positive sub-traits, the more liberal the response criterion (i.e., more extra-flash illusory reports) when IAF was entrained at a faster frequency. Importantly, however, the present TMS-EEG design likely imposed a systematic constraint on detecting sensitivity modulation, as transcranial stimulation was delivered at a too narrow frequency

range, and performance was probed at a fixed, near-threshold operating regime, potentially limiting the emergence of more subtle entrainment-related changes in perceptual sensitivity. In this sense, the current findings should be read less as causal evidence against an alpha-mediated sensory sampling account than as a boundary-setting outcome highlighting how sub-optimal operating-point selection can bias behavioral readouts toward criterion rather than d' . The aforementioned results, however, remain broadly consistent with bottom-up accounts of hallucinatory-like phenomena and models implicating early sensory alterations, plausibly linked to E/I imbalances, as key contributors to subclinical symptoms along the SCZ continuum. Within this framework, occipital IAF, while originally proposed as an index of temporal sampling resolution, may be better captured as an electrophysiological handle on multisensory decision policies under uncertainty, particularly in individuals high in positive schizotypal traits. Together, these pieces of evidence may inform translational research and, in the longer term, contribute to the refinement of diagnostic and screening routines aimed at identifying individuals at elevated risk of psychosis, supporting pre-emptive policies in clinical settings.

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