Cross-modal alterations of Alpha Activity do not reflect inhibition of early sensory processing: A frequency tagging study

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Selective attention refers to the prioritization of relevant and suppression of irrelevant sensory input. Oscillatory alpha-band activity (~10 Hz) has been suggested to facilitate this process by functional inhibition of early sensory regions. The objective of the current EEG study was to compare this theory to a 'gating' function at later stages of the processing stream. Visual cues indicated whether an upcoming target required visual orientation or more demanding auditory pitch discrimination. To gauge inhibition, we probed the visual and auditory systems with frequency-tagging during the cue-to-target interval, flickering the fixation cross at 36 Hz and simultaneously playing amplitude-modulated white noise at 40 Hz. In line with previous work, we observed a post-cue increase in posterior alpha activity when anticipating auditory targets. Surprisingly, the amplitude of visual and auditory responses increased in anticipation of auditory targets, correlated with alpha activity. This indicates that responsiveness of the visual stream was not inhibited when attention was directed to auditory processing. Furthermore, anticipation of demanding auditory targets heightened the vigilance of the sensory system, independent of sensory modality. Our findings suggest that alpha modulation does not reflect 'gain control' in early sensory areas, but rather exhibits its inhibitory effects at later stages.

Introduction

In our daily life, we are often confronted with sensory information from many different sources, all at once. To operate effectively, we must reconcile the tension between environmental inputs relevant for top-down goals and sensory information that may be perceptually salient but task-irrelevant. This process of controlling the flow of information is referred to as *selective attention.* Previous research has suggested that oscillatory activity in the alpha range (~10 Hz) plays a mechanistic role in selective attention through functional inhibition of irrelevant cortices (Foxe et al., 1998; Jensen & Mazaheri, 2010; Klimesch et al., 2007). The concept of functional inhibition refers to an area of the cortex being actively hindered to process input. Functional inhibition is distinctly different from idling, where a part of the cortex is not actively involved.

Evidence supporting this functional inhibition framework of alpha modulation has arisen from studies that have revealed an increase in alpha-power over task-irrelevant sensory cortices after the onset of cues indicating the spatial location (Kelly et al., 2006; Okazaki et al., 2014; Thut et al., 2006; Worden et al., 2000; Zumer et al., 2014) or specific modality of an upcoming target (Foxe et al., 1998; Fu et al., 2001; Mazaheri et al., 2014). Moreover, previous investigations outside the domain of attentional cueing have observed 'spontaneous fluctuations' of alpha power in sensory regions, particularly in the visual cortex, to be inversely related to discrimination ability (Ergenoglu et al., 2004; van Dijk et al., 2008). It can be assumed that functional alpha inhibition is transmitted in a phasic manner, as phosphene perception as well as high-frequency and spiking activity varied in line with the alpha cycle (Dugué et al., 2011; Haegens et al., 2011; Spaak et al., 2012).

The objective of the current investigation is to use frequency-tagging of task-relevant and irrelevant cortices to investigate whether alpha modulation is connected to 'gain control' in early sensory areas through modulation of excitability (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; van Diepen et al., 2019) or whether inhibitory effects are exhibited at later stages of the processing stream (Zhigalov & Jensen, 2020; Zumer et al., 2014), gating feedforward or feedback communication between sensory areas (Bauer et al., 2020; Haegens et al., 2015; Uemura et al., 2021).

Frequency-tagging, the repetitive presentation of sensory stimuli, elicits steady-state sensory evoked potentials (SSEP), echoing the frequency of stimulation (Brickwedde et al., 2020; Colon et al., 2012; Regan, 1982; Snyder, 1992; Stapells et al., 1984; Tobimatsu et al., 1999), connected to plastic processes in the sensory system (Dinse et al., 1998; Marzoll et al., 2018). The magnitude of SSEPs is attention-dependent (Müller et al., 1998; Müller & Hillyard, 2000; Porcu

et al., 2013; Saupe et al., 2009; Toffanin et al., 2009) even for frequencies too fast to perceive consciously (Zhigalov et al., 2019). Their scalp topography reveals that SSEPs are most strongly observable over over occipital areas for visual stimuli generated in the visual cortex, and over fronto-to-central areas for auditory stimuli generated in the auditory cortex (de Jong et al., 2010; Hari et al., 1989; Pantev et al., 1996; Regan, 1982). Their distinct response, localisation and attention-dependence provide an optimal tool to study sensory signal processing over time.

Previous cross-modal research concluded that post-target SSEPs increase and decrease with respect to requisite selective attention requirements between sensory modalities, i.e., if attention is required to count targets in a visual letter stream while simultaneously ignoring auditory distractors, then visual SSEPs increase while auditory SSEPs decrease and vice versa (Saupe et al., 2009). Notably, using almost the same paradigm but manipulating the degree of attention allocated between modalities, an entirely different effect is observable. Asking participants to count targets only in one single modality while ignoring the other results in much smaller SSEPs compared to a task where targets in both the visual and auditory stream are required to be counted in parallel (de Jong et al., 2010).

The aim of the current EEG study was to directly investigate whether and at what stage of the processing stream the cue-induced modulation of alpha activity coincides with the suppression of frequency-tagging responses in task-irrelevant modalities. Based on previous studies, we utilized a cross-modal attention paradigm, in which symbolic visual cues signalled the target modality (visual or auditory) of an upcoming discrimination task (e.g., van Diepen et al., 2015). Here, we included an additional experimental manipulation in the form of frequency-tagging to assess the involvement of the auditory and visual systems in the *cue-to-target interval*. We were also interested in the relationship between alpha modulation, SSEPs, and attentional performance on a trial-by-trial basis.

In line with previous results, we hypothesized that signalling an upcoming auditory target would lead to increased alpha activity over visual occipital regions as well as increased SSEP responses to auditory and decreased SSEP to visual stimuli as indexed by frequency-tagging. In brief, while we observed the expected cue-induced alpha modulation, the amplitude of auditory as well as *visual* SSEPs increased just prior to the onset of the auditory target.

Results

To assess audio-visual excitability in anticipation of either visual or auditory targets, we applied visual cues to signal the modality of the upcoming target (auditory, visual, or unspecified). In a three-second cue-to-target interval, we frequency-tagged the fixation cross at 36 Hz and played 40Hz amplitude modulating white noise. Participants had to either discriminate between three different pitch sounds (auditory target) or three different Gabor patch orientations (visual target). If either an auditory or a visual target were signalled, 50% of the trials were accompanied by a random distractor from the target pool of the opposing sensory modality (see Fig 1)

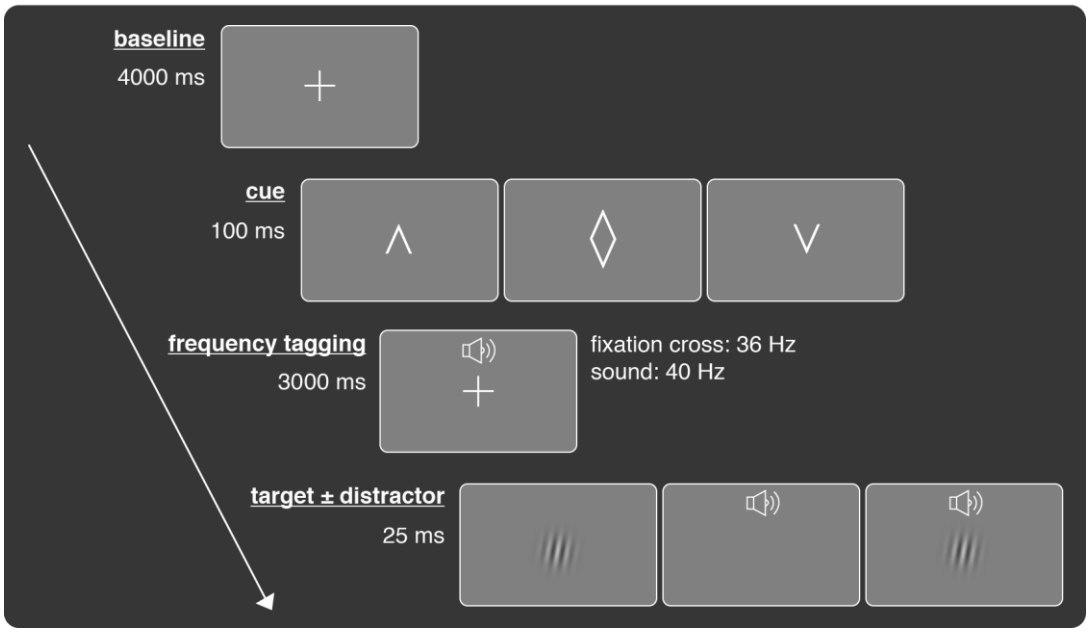


Figure 1. Cross-model discrimination task. Trials were separated by a 4 s interval, in which a fixation cross was displayed. A brief central presentation of the cue (100 ms) initiated the trial, signalizing the target modality (see figure above from left to right: auditory, unspecified, visual). In the cue-to-target interval, the fixation cross was frequency-tagged at 36 Hz. At the same time, a sound was displayed over headphones, which was frequency-tagged at 40 Hz. **B**oth tones and fixation cross contained no task-relevant information. The target consisting either of a Gabor patch or a tone was presented for 25 ms, Participants had to differentiate between 3 different Gabor rotations or tone pitches, respectively. In 50% of auditory and visually cued trials, a distractor in form of a random pitch or rotation of the un-cued modality was presented alongside the target.

Behavioural performance

We found that accuracy differed significantly between conditions (main effect over all conditions: $F_{(5,105)} = 44.16$; $p < .001$). Overall, participants were significantly less accurate in the auditory discrimination task ('overall auditory', M = 70% correct, SD = 11.7) than in the visual discrimination task ('overall visual', M = 97%, SD = 2.3; see Fig 2A), with the worst

performance occurring when auditory targets were paired with visual distractors (auditory +: M = 74% correct, SD = 13;).

A similar observation could be made with regards to reaction times, with the RTs for the auditory (overall auditory: M = 662 ms, SD = 136) discrimination task being slower than for the visual task (overall visual: M = 597 ms, SD = 130; main effect over all conditions: $F_{(5,105)} = 27.47$; $p < .001$; see Fig 2B), albeit this was mostly driven by slow responses to auditory targets paired with distractors (auditory +: M = 723 ms).

To ensure that cue presentation exerted an effect on attention, the attentional benefit was calculated (Fig. 2C). Reaction times were faster for both auditory and visual target conditions when the cue was predictive of the target condition (attentional benefit auditory: unspecifically cued auditory targets - informatively cued auditory targets = M = 81.2 ms; SD = 54.9; $p < .001$; $t_{(21)} = 6.94$; attentional benefit visual: unspecifically cued visual targets - informatively cued visual targets -; M = 54.4 ms; SD = 41.1 ; $p < .001$; $t_{(21)} = 5.19$). The magnitude of the effect on reaction time also differed between conditions ($p = .043$; $t_{(21)} = 2.16$), with stronger attentional benefit for auditory target cues. Attentional cues did not affect response accuracy (see Fig 2C), neither in auditory nor visual target conditions (auditory: p = 0.49; visual: p = 0.32).

Additionally, the effect of distractors on performance was calculated as distractor cost (i.e., the difference in accuracy and reaction time between cued targets without distractors versus cued targets with distractors) see Fig 2D). In both auditory and visual target conditions, there was a significant distractor cost for response accuracy (auditory- – auditory +: M = 10.0 %; SD = 7.3; $p < .001$; $t_{(21)} = 7.32$; visual- – visual+: M = 1.5%; SD = 3.06; $p = .02$). The effect was stronger for auditory than for visual target trials ($p < .001$; $t_{(21)} = 7.67$). Distractors also exerted strong effects on reaction times, leading to slower responses in auditory target conditions and to faster reaction times in visual target conditions (auditory- - auditory+: M = -108.1 ms; SD = 84.8; $p < .001$; $t_{(21)} = -5.98$; visual- - visual+: M = 123.6 ms; SD = 76.3; $p < .001$; $t_{(21)} = 7.60$). This difference was highly significant ($p < .001$; $t_{(21)} = -11.99$).

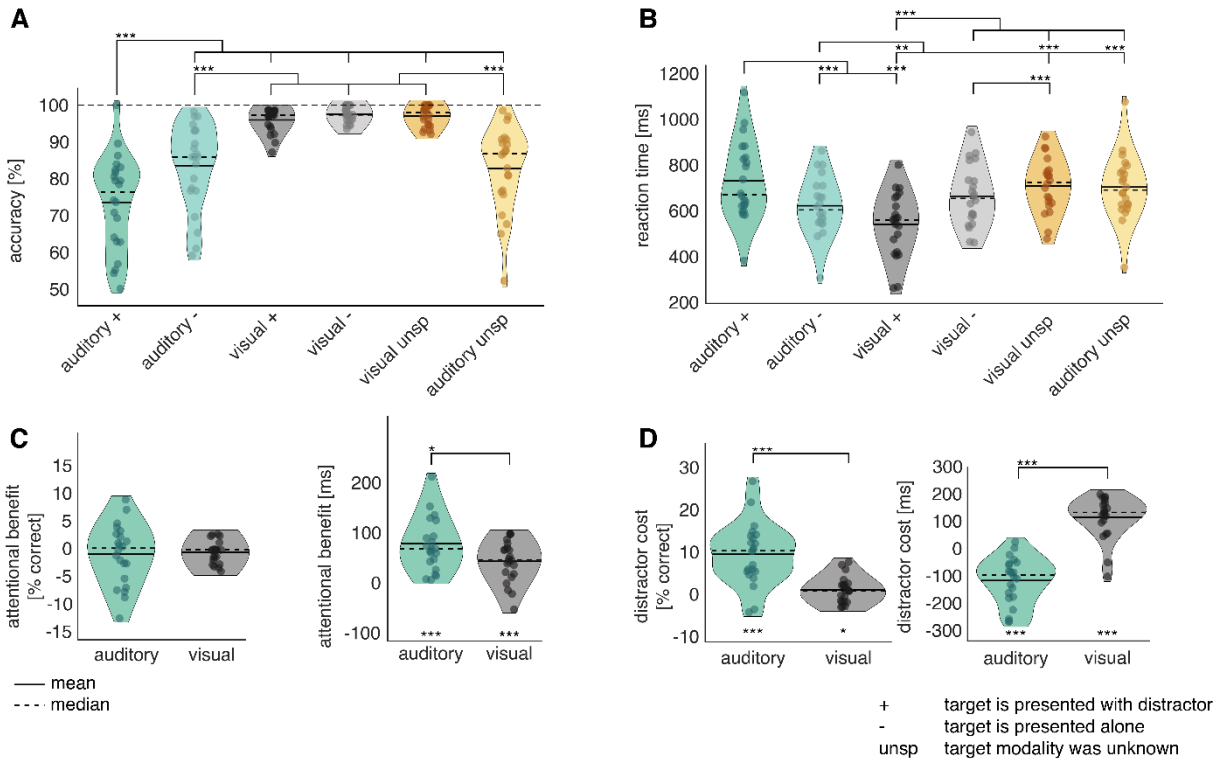


Figure 2. Analysis of task accuracy and reaction time indicates increased difficulty of auditory targets. **A-B**,) **A**, Task accuracy compared between all 6 experimental conditions reveals a drop in accuracy for responses to auditory targets. **B**, reaction times of correct trials compared between all 6 experimental conditions. The slowest reaction times are observable following auditory targets alongside visual distractors **C**, Illustration of attentional benefit: mean performance over unspecified trials was subtracted from mean performance over modality-cued trials without distractor. Attentional benefit of the cue can be observed through reaction times **D**, Illustration of distractor cost: mean performance over trials with distractors was subtracted from mean performance over trials without distractors. Distractor effects were observable for accuracy as well as reaction time; N = 22; *** sig < .001; ** sig. < .01; * sig. < .05;

Cross-modal cues differentially modulated pre-target alpha activity

We then conducted a time-frequency analysis of power in the cue-to-target interval. We found a stronger amplitude rebound from baseline for auditory compared to visual target conditions starting around 2 s before target onset (Fig 3. A-B). We also calculated the time course of alpha power changes using the Hilbert-transformation (8 – 12 Hz, Fig 3. C-D). Consistent with previous work (Mazaheri et al., 2014; van Diepen & Mazaheri, 2017), cluster permutation analysis conducted using the last two seconds before target onset revealed two clusters of difference in alpha power when expecting an auditory compared to a visual target. These effects corresponded to clusters extending from -1.84 to – 0.64 s (p = .004) and -0.62 to 0s (p = .005). The topography of these clusters replicated previous work (Mazaheri et al., 2014; van Diepen & Mazaheri, 2017), revealing a relatively unspecific topographical distribution.

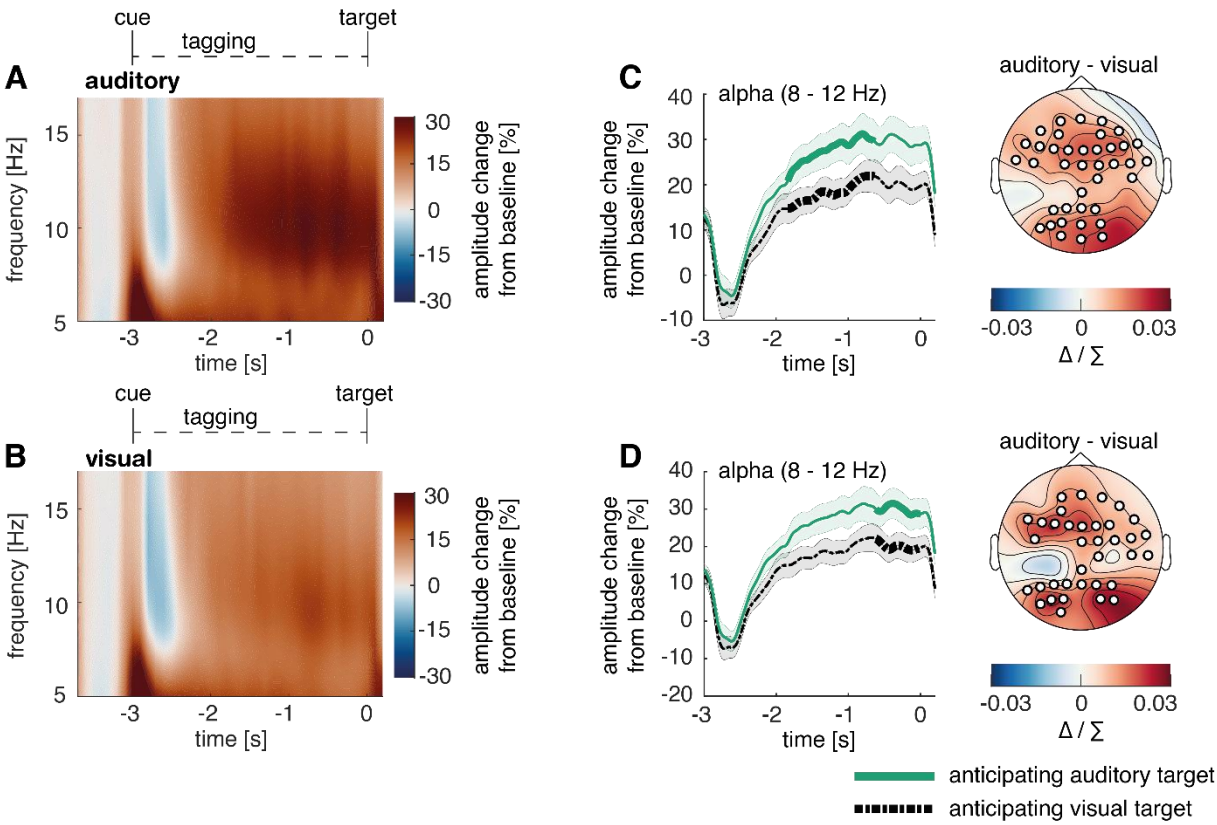


Figure 3. Post-cue modality specific modulation of alpha power in anticipation of an auditory versus a visual target A-B Time-frequency representation of power in the cue-to-target interval. A greater increase in alpha power was observed when expecting an auditory target. **C-D**. The time course of post-cue alpha power. Cluster permutation analysis resulted in two condition effects, both indicating heightened alpha activity when expecting an auditory compared to a visual target (C: $p < .01$; D: $p < .01$). Cluster electrodes are marked in white. Shading represents standard error from the mean; Δ / ∑ represents (a-b)/(a+b) normalization.

Cross-modal cues increased the amplitude of the frequency-tagged responses across both modalities

To assess the temporal development of frequency-tagging responses, steady-state potentials were calculated using data band-pass filtered around the tagging frequency. Neuronal responses to the 40 Hz auditory tagging were strongest over central areas (Fig. 4A) and 36 Hz responses were strongest over occipital areas (Fig. 4B). To assess the differences between conditions, the Hilbert envelope of the steady-state potentials was analysed using cluster permutation analyses. When expecting an auditory target, the auditory 40 Hz frequency-tagging response was larger shortly before target onset compared to the expectation of a visual target (-0.15 to -0.08 s; $p = .041$, see Fig. 4B). Surprisingly, the visual 36 Hz frequency-tagging response was likewise increased shortly before expecting an auditory compared to a visual target (-0.16 to -0.06 s; $p = .014$). For both visual 36 Hz and auditory 40 Hz frequency-tagging responses, condition differences appeared strongest over mid-parietal regions. As such, the frequency tagging

responses might reflect effort or task difficulty affecting the vigilance of the sensory system rather than the sensory-specific allocation of attention.

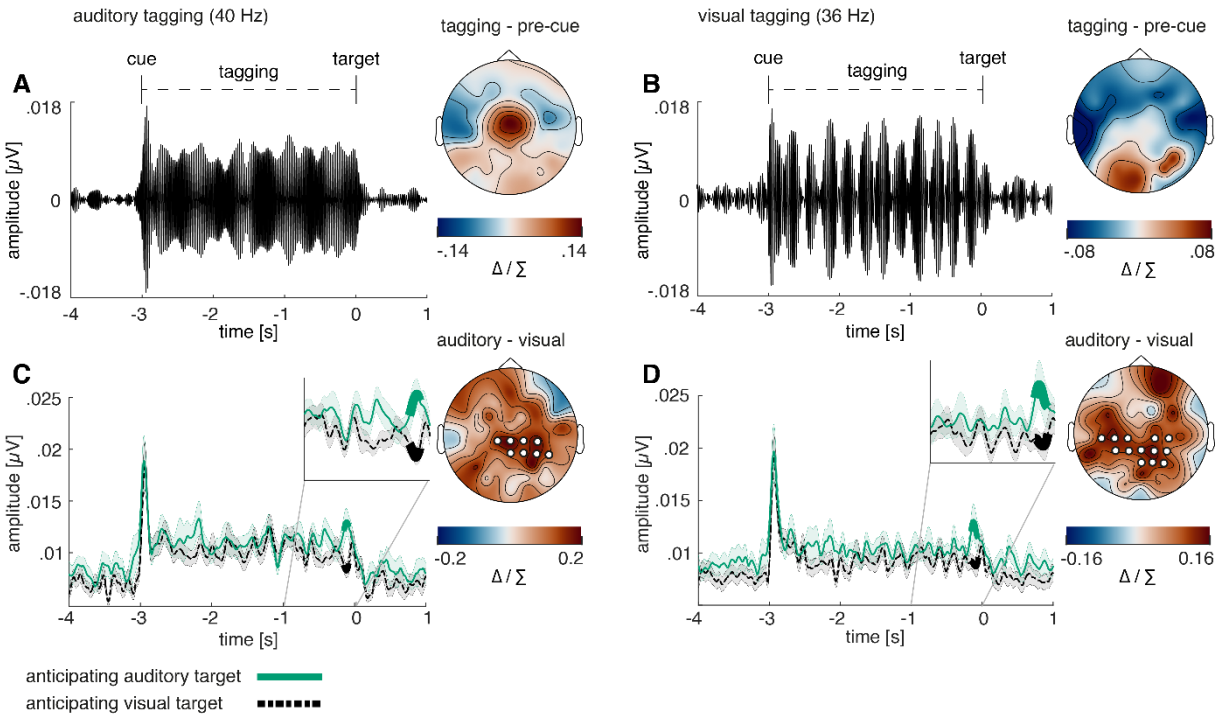


Figure 4. Increase in amplitude of both visual and auditory frequency tagged responses when anticipating auditory processing Event-related potentials and scalp topographies reveal distinct modality specific responses at the tagged frequencies. **A)** auditory steady-state evoked potential (ASSEP) averaged over 6 central electrodes displaying the highest 40 Hz power (Fz, FC1, FC2, F11, F2, FCz). **B**, visual steady-state evoked potential (VSSEP) averaged over 4 occipital electrodes displaying the highest 36 Hz power (POz, O1, O2, Oz **C**, the Hilbert-envelope of the 40 Hz ASSEP reveals an increase shortly before target onset when anticipating an auditory compared to a visual target (p = .041); **D)**, visual steady-state evoked potential (VSSEP) averaged over 4 occipital electrodes displaying the highest 36 Hz power (Poz, O1, O2, Oz). The Hilbert-envelope of the 36 Hz VSSEP likewise reveals an increase shortly before target onset when anticipating an auditory compared to a visual target (p = .014). Cluster electrodes are marked in white. Shading represents standard error from the mean. Δ / ∑ represents (a-b)/(a+b) normalization.

Alpha power was positively correlated with amplitude of frequency tagged responses

Following the observation of condition differences in alpha activity and frequency-tagging responses, we were further interested in exploring the relationship between those markers. Accordingly, we conducted trial-by-trial correlations using alpha condition differences and their electrode positions as seed, which was correlated with frequency-tagging signals over all electrodes. Multiple comparison correction was applied by testing the correlation matrix against a zero-correlation matrix with a cluster permutation approach. A positive correlation was observed over right parietal-to-occipital areas between the late alpha cluster activity and both

40 Hz (p = .009) and 36 Hz (p = .013) frequency-tagging responses when expecting a visual target (see Fig 5.A-B). This result is further illustrated by a median split analysis between trials with high and low alpha power for each participant, which is highly significant for the visual 36 Hz response (Fig 5A, middle columns, $p < .001$; $t_{(21)} = 4.23$; $BF_{(10)} = 84.60$) and marginally significant for the visual 40 Hz response (Fig 5B, middle column; $p = .052$; $t_{(21)} = 2.06$; $BF_{(10)} = 1.31$). Additionally, we averaged the correlation coefficient of each participant and calculated a one-sample t-test against 0. Both tests indicate strong correlations with alpha activity for both 40 Hz (Fig 5A, right column; $p < .001$; $t_{(21)} = 4.59$; $BF_{(10)} = 181.92$) and 36 Hz activity (Figure 5B, right column; $p < .001$; $t_{(21)} = 4.14$; $BF_{(10)} = 70.31$).

The same positive correlation with alpha activity was found when expecting an auditory target only for 36 Hz activity (p = .010), but not for 40 Hz activity (see Fig 5.C). A median split between high and low alpha activity (p = .008; $t_{(21)} = 2.94$; $BF_{(10)} = 6.09$) and correlation coefficients (p = .001; $t_{(21)} = 3.67$; $BF_{(10)} = 26.07$) provided moderate to strong evidence for this effect.

Additionally, we compared how correlation coefficients between alpha activity and frequency-tagging differed when anticipating an auditory versus a visual target. Multiple comparison correction was applied with cluster permutation analysis. Aa psychophysical interaction between the strength of the correlation associating alpha and 36 Hz activity and condition became apparent (p = .037; *see* Fig. 5D) and was observed most strongly over right-central electrodes. Comparing the correlation coefficients of participants over this cluster revealed a strong effect and even a change of direction in the correlation ($p < .001$; $t_{(21)} = -3.96$; $BF_{(10)} = 47.91$). Particularly, when expecting a visual target, there was a negative correlation between 36 Hz and alpha activity, which turned positive when expecting an auditory target. Both correlations also differed significantly from 0 (expecting a visual target: p = .048; $t_{(21)} = -2.11$; $BF_{(10)} = 1.41$; expecting an auditory target: p = .012; $t_{(21)} = 2.76$; $BF_{(10)} = 4.33$).

It is further noteworthy that the correlation between alpha activity and 36 Hz frequency-tagging response when expecting a visual target, was also present when using the early alpha cluster as seed (~ 1200 to 400 ms before target onset, see Fig. 5F), in which case alpha activity preceded the 36 Hz activity (p = .016*)*. For this correlation, the median split between high and low alpha trials only reached marginal significance (p = .075; $t_{(21)} = 1.87$; $BF_{(10)} = 0.98$). Testing correlation coefficients against 0 again revealed a significant effect (p = .001; $t_{(21)} = 3.78$; $BF_{(10)} = 32.66$).

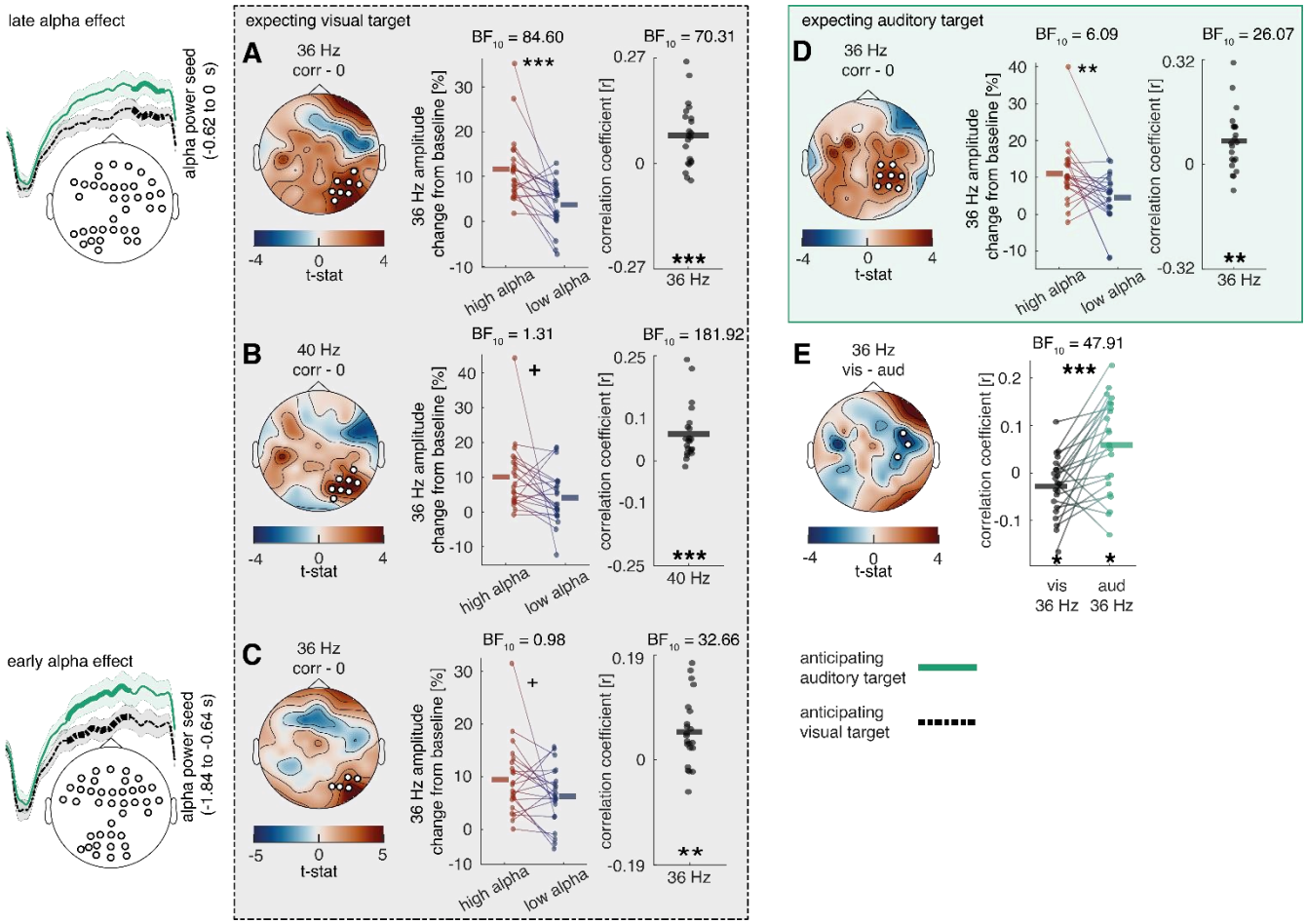
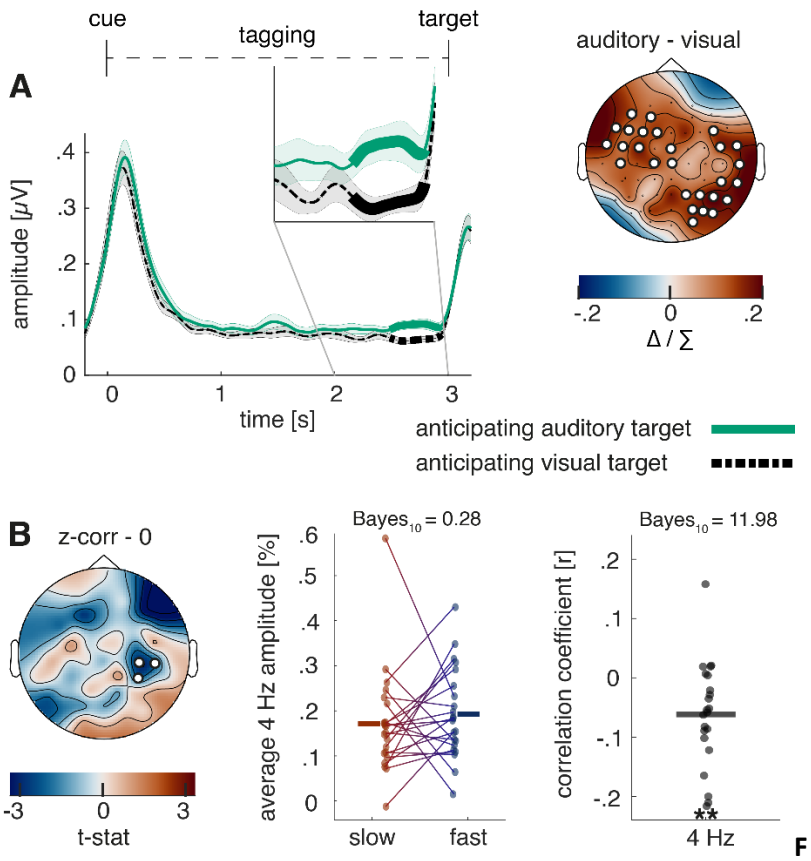


Figure 5. Relationship between cue induced alpha modulation and amplitude of frequency tagged responses A-C, previously obtained alpha clusters (see Fig. 3) were correlated over trials with 40 Hz and 36 Hz clusters (see Fig. 4). The analysis was performed using a cluster-permutation approach, testing a correlation model against a 0-correlation model. Clusters diverging from the 0-correlation model are presented topographically. Additionally, median splits between high and low alpha trials as well as correlation coefficients of these clusters are displayed for all participants **A**-**B,** a positive correlation is visible between alpha activity in the last 400 ms and steady state potentials shortly before target onset when expecting a visual target (36 HZ: p = .013; 40 Hz: p = .009). **C**, when expecting an auditory target, there is a positive correlation is visible between alpha activity in the last 400 ms and 36 Hz activity shortly before target onset (p = .010). **D,** the correlation between alpha activity 400 ms and 36 Hz activity shortly before target onset changes its direction depending on whether an auditory or a visual target is expected (*p* = .037). **F**, a positive correlation is also visible between alpha activity as early as ~1200 ms to 400 ms and 36 Hz activity shortly before target onset when expecting a visual target (p = .016). N = 22; *** sig < .001; ** sig. < .01; * sig. < .05. + sig. < .1;

Intermodulation frequency

Lastly, we analysed the steady-state response of the intermodulation frequency at 4 Hz. Increased intermodulation shortly before target onset could be observed when expecting an auditory compared to a visual target (-0.51 to -0.0620 s; $p < .001$). This effect was strongest over left fronto-to-central electrodes and right central-to-occipital electrodes (see Fig 6. A).

With the goal to examine whether there are any behaviourally effects of the condition difference, trial by trial correlations with reaction times of each of the 2 auditory and visual conditions were performed. Only in the easiest condition, when expecting a visual target that was not accompanied by a distractor, a negative correlation with reaction time could be found, strongest over right central electrodes (see Fig 6. B; p = .046). While a median split between slow and fast trials did not reach significance (p = .50; $t_{(21)}$ = -0.69; $BF_{(10)}$ = .28), testing the correlation coefficients against 0 revealed strong evidence for a correlation (p = .004; $t_{(21)}$ = -3.28; $BF_{(10)}$ = 11.98).



igure 6. Steady-state response in the intermodulation frequency and its behavioural relevance. A, the Hilbert-envelope of the 4 Hz steady-state response reveals an increase shortly before target onset when anticipating an auditory compared to a visual target (p < .01). **B,** there is a trial-by-trial correlation between 4 Hz activity and reaction time when a visual target without distractor was presented. The correlation is further illustrated by a median split between fast and slow reaction time trials as well as by correlation coefficients for each participant. N = 22; ** sig. < .01;

Discussion

The neuropsychological account of attention defines it as the selective facilitation (i.e., prioritization) of relevant sensory input and suppression of irrelevant sensory input. Oscillatory activity in the alpha range (~10 Hz) has been suggested to play a mechanistic role in attention through inhibition of irrelevant cortices, commonly referred to as the 'alpha inhibition hypothesis' (Foxe et al., 1998; Jensen & Mazaheri, 2010; Klimesch et al., 2007). In the current cross-modal attention study we directly tested this hypothesis by using frequency-tagging to specifically examine how cues signalling the modality of an upcoming target (either the auditory or visual modality) affected the responsiveness of the relevant and irrelevant sensory cortices prior to target onset. In-line with previous work, we observed a post-cue increase in posterior alpha power in anticipation of processing auditory targets. However, contrary to prevalent theories proposing visual gain suppression when focusing on the auditory modality,

we observed that the amplitude of visual frequency-tagging responses increased just prior to the onset of the auditory target. This suggests that responsiveness of the visual stream was not inhibited when attention was directed to auditory processing and was not inhibited by occipital alpha activity. Our results reconcile previously paradoxical results on audio-visual attention and support the view that alpha activity gates downstream communication pathways.

Frequency-tagging

In the current experiment, we specifically chose to analyse the cue-to-target interval, where both visual and auditory SSEPs present preparatory states for the upcoming task, independent of task-related processing or performance. The magnitude of auditory SSEPs was increased shortly before target onset when expecting a demanding auditory target compared to a visual target, very much in line with previous reports (e.g., Saupe et al., 2009). In contrast to the results reported in Saupe et a., (2009), where visual SSEPs decreased when attending the auditory modality, visual SSEPs increased shortly before target onset when expecting an *auditory* target in our data. This is especially surprising as auditory targets were frequently accompanied by visual distractors, rendering it optimal for task success to completely ignore any visual input. As auditory targets were significantly more difficult than visual targets, these results strongly speak to a a vigilance increase of sensory processing independent of modality and an inability to selectively disengage one sensory modality in anticipation of a demanding task. This view is consistent with previous work which visual SSEPs elicited by irrelevant background stimulation increased with task load in an auditory discrimination task (Jacoby et al., 2012). Furthermore, our results indicate that task demand is a strong candidate to reconcile previously

seemingly paradox results, as splitting attention between the auditory and visual system seemed possible in simpler tasks (Driver & Spence, 1998; Saupe et al., 2009) and impossible under high demand (de Jong et al., 2010; Driver, 1996; Driver & Spence, 1998; Spence & Driver, 1996). An alternative account for our findings stems from the evidence, that participants are more likely to only perceive and react to the visual modality, when confronted with audio-visual stimuli (Colavita, 1974; Spence, 2009). However, this effect was mostly limited to speeded modality discrimination/target detection tasks (Sinnett et al., 2008; Spence, 2009). Furthermore, the increased difficulty of the here-used auditory stimuli was confirmed in a previous block-design study (van Diepen & Mazaheri, 2017). Nevertheless, visual dominance could play a role for auditory target difficulty as well as predictions over the reciprocity of the audio-visual relationship.

A revision of the Alpha inhibition hypothesis

Top-down cued changes in alpha power have now been widely viewed to play functional route in directing attention: the processing of irrelevant information is attenuated by increasing alpha power in cortices involved with processing this information (Foxe, Simpson, & Ahlfors, 1998; Hanslmayr et al., 2007; Jensen & Mazaheri, 2010). However, recent evidence suggests that alpha activity does not inhibit gain in early sensory processing stages (Antonov et al., 2020; Gundlach et al., 2020; Gutteling et al., n.d.; Zhigalov & Jensen, 2020). To date there has been no direct investigation into the effect of alpha increases on later stages in the processing stream. In the current study, as expected, we observed a post-cue increase in occipital alpha activity in anticipation of an auditory target. However, we also observed an increase in the amplitude of visual SSEPs during the cue-target interval, which directly contradicts the widespread view of alpha activity exerting ‘gain control’ in early sensory areas by regulating excitability (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; van Diepen et al., 2019). Here we propose that alpha activity, rather than modulating early primary sensory processing, exhibits its inhibitory effects at later stages of the processing stream (Antonov et al., 2020; Gundlach et al., 2020; Zhigalov & Jensen, 2020; Zumer et al., 2014), gating feedforward or feedback communication between sensory areas (Bauer et al., 2020; Haegens et al., 2015; Uemura et al., 2021). Our data provides hints in favour this view, as we can show that alpha activity covaries over trials with SSEP magnitude in adjacent areas. If alpha activity exerted gain control in early visual regions, increased alpha activity would have to lead to a decrease in SSEP responses. In contrast, we observe that increased alpha activity likely originating from early visual cortex is related to *enhanced* visual processing at later stages of the processing stream. It seems plausible to assume

that inhibition of other unrelated communication pathways leads to prioritised and thereby enhanced processing over relevant pathways. In line with previous literature, we therefore suggest that alpha activity limits task-irrelevant feedforward communication, thereby enhancing processing capabilities in relevant downstream areas. Furthermore, we could show that the magnitude of the correlation between alpha power and visual information processing varied between conditions, suggesting a dynamic and adaptive network.

It is known that the localisation of alpha activity reflects the retinotopic organisation of visual spatial attention topographically over the parietooccipital cortex (Kelly et al., 2006; Popov et al., 2019). Notably, recent studies provided evidence, that the same organisation can be observed for auditory attention. Specifically, the localisation of visual alpha activity in the parietooccipital cortex reflects the spatial direction of auditory attention (Klatt et al., 2021; Popov et al., 2021). This observation can be explained through micro-saccades towards the spatial location of sounds, which are irrevocably connected to alpha oscillations (Popov et al., 2021). While we did not manipulate spatial attention, our results fit well to the notion of visual alpha activity serving as a sensory orientation system, relaying visual information to task-relevant downstream processing areas, and blocking communication to irrelevant pathways.

The intermodulation frequency

Previous research showed that simultaneous frequency-tagging in multiple frequencies evokes a response in the intermodulation frequency (f1 – f2). In multimodal settings, this frequency is thought to reflect cross-modal integration (Drijvers et al., 2021). This is very well in line with our findings, where increased vigilance of the sensory system arising from anticipation of a difficult auditory target resulted in an increase in the intermodulatory frequency. Furthermore, we could show that this frequency covaries over trials with reaction time in the easiest condition, where visual targets were presented without any distractors. A lack of this connection in other conditions might reflect increasing interferences from higher task difficulty, rather than a lack of the effect itself, but this remains to be tested. We cannot exclude an alternative explanation, as theta oscillations are known to be involved in movement preparation, it is possible that phase-resets could lead to time-locked appearance of these oscillations (Tomassini et al., 2017).

Conclusion

Our results taken together suggest that under high task difficulty, audio-visual excitability is enhanced, reflecting an increase in vigilance for the sensory system, even if this increases

processing of distracting information. We showed that this vigilance shift, as reflected by SSEP responses, can be affected by alpha activity, presumably through relaying of sensory information over communication pathways, thereby controlling the downstream flow of sensory information.

Materials and Methods

Participants

In total, 24 healthy volunteers participated in this study (mean age: 19.1 ± 1.8 SD; 17 women). Due to technical difficulties, one participant could not finish the experiment and one participant did not exceed chance level in the behavioural task (~33 %). Both were therefore removed from any further analysis. All remaining participants reported normal or corrected-to-normal vision, no history of psychiatric or neurological illness and provided written informed consent. After completion of the experiment, participants received either monetary compensation or certification of their participation for their university course program. The study protocol was approved by the Ethics Committee of the School of Psychology at the University of Birmingham and is in accordance with the Declaration of Helsinki.

Cross-modal attention paradigm

Each trial was initiated by a brief presentation of a cue (100 ms) signalling the modality of the upcoming discrimination task (v-shape: visual modality; inversed v-shape: auditory modality; diamond-shape: unspecified). During the following cue-to-target interval, the fixation cross was frequency-tagged at 36 Hz. At the same time, a 40 Hz frequency-tagged sound (amplitude modulated white noise) was played over headphones (see Fig. 1). No task was connected to this interval and participants did not need to pay attention to either the sound or the fixation cross. After three seconds, the frequency-tagging stopped, and the target was presented for a very brief moment (25 ms). It consisted either of a Gabor patch (visual modality) or a sound (auditory modality). If the target modality was visual, participants had to use the three arrow buttons on the keyboard to indicate whether the Gabor patch was tilted to the left (-10°), vertical (0°), or tilted to the right (10°). Additionally, in 50% of the trials, a random distractor from the pool of auditory targets was presented simultaneously to the visual target over headphones. Similarly, if the target modality was auditory, participants used the same buttons to indicate whether the pitch of the tone was low (500 Hz), medium (1000 Hz) or high (2000 Hz). Again, in 50% of the trials, a random distractor from the pool of visual targets was also presented. If the cue was unspecified (diamond shape), either a visual (50% of unspecified trials) or an auditory target was presented, never accompanied by any distractors. Experimental trials were separated by an inter-trial interval of 4 seconds, to avoid carry-over effects from previous trials. The resulting 6 conditions were randomly ordered and balanced out over the experiment.

During the experiment, participants were instructed to keep their gaze locked to a fixation cross presented at the centre of the screen. Preceding data collection, participants performed 36 practice trials to get accustomed to the task and the target stimuli. The ensuing experiment was split into 26 trial sequences, separated by self-chosen breaks, which together resulted in 468 trials and lasted between 80 and 90 minutes. The discrimination task was programmed and presented with MATLAB® R2020b and Psychtoolbox-3 on an LCD-monitor featuring a 140 Hz refresh rate. The onset of the visual and auditory tagging frequencies (i.e stead state stimuli) were tracked using the Cedrus Stimtracker (https://cedrus.com/stimtracker/index.htm).

Behavioral analysis

We were interested in accuracy in the discrimination of visual targets and auditory targets, as well as reaction times. Furthermore, we examined the distraction cost of having a target presented with a distractor of a different modality as well as the reaction time to make the target discrimination. The distraction cost was calculated as the reaction time difference between cued targets with distractors (i.e visual and auditory stimuli presented together) and cued targets without distractors (either a visual or auditory stimulus presented alone). All incorrect trials as well as trials with reaction times faster than 100 ms or exceeding 1500 ms were removed from analysis (0.5 % too fast, 9.2% too slow).

EEG data acquisition

All EEG recordings were conducted using a WaveGuard Cap (ANTneuro), featuring 64 Ag/AgCL electrodes (10-10 system; ground: Fz; reference: Cpz; EOG: left canthus). Electrodes positions were prepared with OneStep cleargel conductive paste and impedances were kept below 100 kΩ. The measured signal was transmitted using an ANTneuro EEGosports amplifier (low-pass filter: 150 Hz; high-pass filter: 0.5 Hz; sampling rate: 500 Hz).

EEG Preprocessing

Offline analyses were performed in MATLAB ® R2020b. The data was pruned from artifacts by visual inspection using the EEGLAB toolbox (Delorme & Makeig, 2004). Additionally, blinks and ocular artefacts were removed from the data using independent component analysis (ICA). EEG channels were re-referenced to an average of all channels (excluding EOG).

Amplitude of the evoked frequency-tagging response

To investigate the temporal dynamics of amplitude of the frequency tagged responses after the onset of the attentional cues (also the precise onset of the frequency tagged stimuli) the data

was epoched into 6-second segments starting 1.5 seconds prior to cue onset. Next the data were narrow-band filtered around the 36 Hz activity to capture the visual frequency-tagging, 40 Hz activity in to capture the auditory frequency-tagging, and the intermodulation frequency at 4 Hz, which can be derived by subtracting both frequency-tagging responses ($f_i = f_{auditory} - f_{visual;}$ see Drijvers, Spaak & Jensen, 2020). Here we used a Blackmann-windowed sync filters adapted to a suitable ratio of temporal and frequency resolution for the specific frequency of each of the tagged signals: filter order 116 for 35.5 to 36.5 Hz and 39.5 to 40.5, filter order 344 for 3.5 to 4.5 Hz. The filtered data at each of the tagged frequencies as well the intermodulated frequency were baseline corrected (interval between 700 and 200 ms preceding cue onset) before calculating the average over trials to obtain steady-state evoked potentials). The power envelope of the SSEPs of tagged frequencies was estimated using Hilbert transformation.

Temporal dynamics of the induced EEG changes

In addition to looking at the cue evoked changes in the amplitude of the frequency tagged signals, we investigated the induced changes in the EEG signal at the frequencies of the tagged auditory and visual stimuli, alpha activity (9-11 Hz, filter order 276 for 7.5 to 12.5 Hz), as well as the intermodulation frequency (4 Hz; filter order 344 for 3.5 to 4.5 Hz). Here rather than averaging the epoched data filtered at the specific frequency ranges, we performed the Hilbert transform, and averaged the power-envelope of the specific frequencies across trials. This approach is very much analogous to the standard time-frequency analysis using convolutions (van Diepen & Mazaheri, 2017; Zhigalov et al., 2019), but affords more control to examine the temporal dynamics of the specific frequencies of interest.

Time-frequency representations of power

In addition to the estimating frequency power envelopes, Time–frequency representations (TFRs) of power of the EEG signal were estimated using the Fieldtrip toolbox (Oostenveld et al., 2011). The power or frequencies between 5 and 20 Hz were calculated for each trial, using a sliding time window (frequency steps: 0.5; time steps: 10 ms). The length of the window was adjusted to a length of 3 cycles per frequency and tapered with a Hanning window. For each trial, both datasets were normalised to display relative percent change from baseline using the following formula: [(activity – baseline) / baseline], where baseline refers to the interval between 700 and 200 ms before cue onset. To estimate the topographical distribution of voltage differences between conditions, uncorrected power values were normalised applying the following formula: [$\Delta/\sum = (a - b) / (a + b)$], where a and b reflect the different conditions.

Statistical analysis

Condition differences in the behavioural task were estimated with paired t-tests and repeated measures ANOVAS, utilizing Tukey-Kramer Post-Hoc test. Power differences between conditions were analysed using cluster permutation analysis (Maris & Oostenveld, 2007). In this procedure, condition labels were randomly shuffled 1000 times, creating pairs of surrogate conditions. To test for significance, paired t-tests were conducted for each data point and each channel, resulting in one t- matrix for real conditions and 1000 t-matrices for surrogate conditions. Significant t-values ($p < .05$) were defined as clusters if there was at least one significant data point present at the same time and frequency in at least two neighbouring channels. To correct for multiple comparisons, a condition difference was only assumed, if the maximum sum of t-values in a real cluster exceeded the same sum of 95% of the clusters found in the surrogate data.

The relationship between induced changes in alpha activity and frequency tagged responses was assessed using trial by trial Spearman correlations. For each participant and each electrode, a correlation coefficient was calculated between the average activity in a previously identified cluster, which was used as seed (e.g., condition differences in alpha activity), and the average activity of the electrophysiological correlate of interest (e.g., 36 Hz activity over the previously identified time window). The resulting channel by participant matrix was tested against null-correlation model using the cluster permutation approach described above. Derived clusters were additionally tested and visualised by comparing median split trials of high vs low activity. Furthermore, the average correlation coefficient of the cluster was tested against a 0-correlation model for each participant using t-statistics. Lastly, a psychophysical interaction between electrophysiological correlations and conditions was performed using correlation coefficients for each participant and electrode, testing them between conditions using the cluster permutation approach. Perceptually uniform and universally readable colormaps were applied to all visualisations (Crameri et al., 2020). All data are presented as mean ± standard error of the mean (SEM).

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