Research report

Are alpha oscillations instrumental in multisensory synchrony perception?

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HIGHLIGHTS

- We examine the role of ongoing EEG alpha oscillations in multimodal synchrony perception.
- Individual alpha peak frequency correlates with accuracy of simultaneity judgements.
- Prestimulus alpha power was lower when simultaneity judgements were inaccurate.
- Prestimulus alpha phase did not significantly modulate simultaneity judgements.
- EEG alpha oscillations are instrumental in shaping multisensory perception.

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ABSTRACT

Different inputs from a multisensory object or event are often integrated into a coherent and unitary percept, despite differences in sensory formats, neural pathways, and processing times of the involved modalities. Presumably, multisensory integration occurs if the cross-modal inputs are presented within a certain window of temporal integration where inputs are perceived as being simultaneous. Here, we examine the role of ongoing neuronal alpha (i.e. 10-Hz) oscillations in multimodal synchrony perception.

While EEG was measured, participants performed a simultaneity judgement task with visual stimuli preceding auditory ones. At stimulus onset asynchronies (SOA’s) of 160–200 ms, simultaneity judgements were around 50%. For trials with these SOA’s, occipital alpha power was smaller preceding correct judgements, and the individual alpha frequency was correlated with the size of the temporal window of integration. In addition, simultaneity judgements were modulated as a function of oscillatory phase at 12.5 Hz, but the latter effect was only marginally significant.

These results support the notion that oscillatory neuronal activity in the alpha frequency range, which has been taken to shape perceptual cycles, is instrumental in multisensory perception.

1. Introduction

We perceive the world around us through different senses, each of which is receptive to different aspects of our environment. At the same time, these different modality inputs into our sensory organs have to be integrated into coherent and unitary percepts of objects and events, despite existing differences in sensory input formats, neural pathways, and processing times. The multisensory nature of perception suggests a sophisticated interplay between the different sensory systems. This has received much scientific attention (for reviews, see e.g. Alais et al., 2010; Calvert et al., 2004; Chen and Vroomen, 2013; Stein and Stanford, 2008; Noppeney and Lee, 2018; Vroomen and Keetels, 2010). Determining whether e.g. auditory and visual signals come from one common or from two different sources is based on prior knowledge about the environment and by bottom-up information such as by spatial proximity and temporal simultaneity (Noppeney and Lee, 2018). Temporal simultaneity refers to the fact that when two sensory inputs come from one and the same multisensory source (say the lip movements and articulated sounds from a speaker), they are perceived as being simultaneous, despite the existence of sensory modality-specific
lags. Different neural mechanisms have been demonstrated to subserve multisensory temporal binding, such as the occurrence of a temporal window of integration, and flexible adaptation or recalibration to existing or shifting time lags (for review, see Vroomen and Keetels, 2010). Using simultaneity judgements (SJ), temporal order judgements (TOJ), or related tasks, it has been established that cross-modal stimulus pairs are perceived to be simultaneous when presented within a temporal window of 20–80 ms for simple cross-modal stimuli such as auditory beeps and visual flashes (e.g. Keetels and Vroomen, 2005; Spence et al., 2001; Zampini et al., 2005a,b). This temporal window increases to a few hundred ms for more complex stimuli, such as audiovisual speech (e.g. Stekelenburg and Vroomen, 2007; Van Wassenhove et al., 2007; for review, see Vroomen and Keetels, 2010).

Although the notion of a temporal window of integration is widely accepted, its neurophysiological substrate remains unclear. Neuronal oscillations, reflecting fast periodic fluctuations in neuronal excitability, may be one candidate mechanism for implementing this window of integration. Notably, alpha oscillations, with frequencies of between 7 and 13 Hz have a periodicity of ~70 to 140 ms. This is in the same order of magnitude as the temporal windows for multisensory integration that are usually observed. Alpha oscillations are therefore considered to be a prime candidate for suberving multisensory temporal binding (Cecere et al., 2015).

Alpha oscillations have been proposed to be instrumental in unimodal sensory perception, shaping so-called perceptual cycles (VanRullen, 2016). The notion of perceptual cycles implies that sensory processing is not continuous, but rather that perceptual input is being periodically 'sampled' at a frequency of 7–13 Hz. For the visual modality, this periodicity is reflected in the observations that visual detection thresholds are lower, and visual perception is more accurate, at specific phases of the alpha oscillation than at others. For instance, the detection of visual flashes presented around perceptual threshold (Busch et al., 2009; Mathewson et al., 2009), saccadic reaction times to a peripheral target (Drewes and VanRullen, 2011), and the detection of a TMS-induced phosphene (Duguet et al., 2011) all depend on the phase of occipital alpha oscillations immediately preceding stimulus onset. Further, it has been shown that the temporal resolution of visual perception is dependent on the exact frequency of alpha oscillations (Samaha and Postle, 2015). This frequency can be modulated by task demands (Wutz et al., 2018). These findings strongly suggest that visual perception is optimal at some phases of alpha oscillations (VanRullen et al., 2014). While most of the literature on perceptual cycles has focused on the visual modality, evidence has been reported for perceptual cycles in the somatosensory modality as well (Ai and Ro, 2014; Baumgarten et al., 2015). In the auditory modality, results have been less clear. Obleser and colleagues (Strauß et al., 2015) observed phase differences in ongoing alpha power between correct and incorrect lexical decisions (word vs. non-word) immediately preceding stimulus presentation in a lexical decision task. However, other attempts at demonstrating the existence of auditory perceptual cycles have been unsuccessful (see VanRullen et al., 2014 for review). Only when auditory cortex is being entrained by rhythmic stimuli, clear effects of the phase of the entrained rhythm on auditory perception have been reported (e.g. Henry and Obleser, 2012; Kayser et al., 2016; Schroeder and Lakatos, 2009; for review, see Thorne and Debener, 2014).

The above work on perceptual cycles deals exclusively with unimodal sensory perception. A small number of studies have demonstrated that alpha oscillations influence cross-modal perception as well. For instance, a sound can reset the phase of rhythmic activity in visual cortex (Lakatos et al., 2009; Romei et al., 2012) and as a result influence subsequent visual perception (Diéderich et al., 2014; Fiebelkorn et al., 2011). Conversely, visual stimuli can reset auditory cortex rhythms (Kayser et al., 2008; Pererodin et al., 2015; for review, see Thorne and Debener, 2014).

More pertinent to our proposal that alpha oscillations are instrumental in the temporal binding of auditory and visual stimuli, are two recent studies that have examined different aspects of alpha oscillations during multisensory tasks. One of these studies (Cecere et al., 2015) has demonstrated a significant correlation between individual alpha peak frequency (IAF) and the temporal window of integration in the sound-induced double-flash illusion task. Most convincingly, this study additionally showed that when IAF was either slowed down or sped up through transcranial alternating current stimulation, the size of the temporal window of integration changed accordingly. In another study (Grabot et al., 2017), however, a temporal order judgement task did not yield any correlation between IAF and temporal window of integration. This suggests that the observed correlation may be dependent on the experimental paradigm employed (e.g. illusion-induction vs. temporal order detection). Note that in the latter study, correct order judgements around the point of subjective simultaneity were associated with lower prestimulus alpha power.

However, if we consider that unimodal perception is sensitive to the phase of ongoing alpha oscillations (as expressed in the perceptual cycles hypothesis; VanRullen, 2016), this notion may extend to multisensory temporal binding. One may argue that, rather than individual alpha peak frequency and prestimulus alpha power, it is the phase of prestimulus alpha oscillations that should be most instrumental in determining whether or not multisensory temporal binding takes place. In this view, under difficult discrimination conditions, one would expect perceived simultaneity of multimodal stimuli to be dependent on the stage of the perceptual cycle (as indexed by the phase of the alpha cycle). This is commensurate with claims that alpha phase is related to prioritizing information in time (for review, see Jensen et al., 2012). One direct test of the hypothesis that alpha phase is instrumental in multisensory temporal binding comes from the study of Van Wassenhove and colleagues (Grabot et al., 2017). However, these authors did not observe systematic differences in prestimulus alpha phase as a function of participants’ temporal order judgements. Another study used simultaneity judgements, with stimulus onset asynchronies (SOAs) chosen such that they induced maximal perceptual uncertainty (Ikumi et al., 2019). In a task in which auditory stimuli preceded visual stimuli (AV condition), the authors found that the phase of prestimulus oscillations at around 13 Hz correlated with subjective simultaneity. This occurred in the absence of concurrent changes in EEG amplitude. Remarkably, when visual stimuli preceded the auditory ones (VA condition), which is the more natural situation because light travels faster than sound, the authors did not observe any correlation between prestimulus alpha phase and perceived simultaneity. Although the results from Ikumi et al. (2019) suggest that alpha oscillations are instrumental in shaping temporal judgements, the fact that a relationship between prestimulus alpha phase and perceived simultaneity was only observed in the AV condition challenges the generalizability of their findings.

To summarize, the existing literature on the role of alpha oscillations in the temporal binding of auditory and visual stimuli is at best inconclusive. We aim to elucidate this role by addressing three open empirical questions. We performed an EEG experiment in which participants performed SJ of visual and auditory stimuli presented with different stimulus onset asynchronies (SOAs), focusing specifically on visual-first (VA) stimulus pairs. SOAs of 160–200 ms were associated with maximal perceptual uncertainty, as indexed by roughly equal numbers of ‘simultaneous’ and ‘not simultaneous’ judgements from the participants. One question we address is whether the phase of occipital alpha oscillations (as a proxy of the stage of the perceptual cycle) is instrumental in determining (or at least influencing) participants’ SJ for VA stimulus pairs (as opposed to Ikumi et al. (2019), who only observed this effect for AV stimulus pairs)? A second question is whether the observed relationship between IAF and temporal window of integration is specific to illusion-induction tasks (as in Cecere et al., 2015), or whether it can also be observed in a task that involves temporal judgements (as opposed to Grabot et al., 2017). And third, does the observed difference in prestimulus alpha power between correct and
incorrect temporal order judgements (as in Grabot et al., 2017) replicate in a SJ task?

2. Results

2.1. Behavioural data

We were mainly interested in the cognitive and perceptual processes around the PSS, because SJ around the PSS are most difficult, and therefore most likely to be influenced by the state of the sensory cortices at the time the first stimulus is presented. Therefore, for each participant we selected the SOA for which trials that yielded a ‘simultaneous’ judgement (S trials) and trials with a ‘not simultaneous’ judgement (NS trials) were most evenly distributed. Additionally, we then verified whether the proportion of S and NS trials for this SOA was in between 0.3 and 0.7 (or 0.7 and 0.3). For 22 out of the 33 initial participants, these criteria were met. The EEG data from all other participants and all other SOAs were excluded from further analysis. Table 1 presents the selected SOA, and the distribution of S and NS judgements for the selected SOA for each participant.

Table 1
Selected SOA, proportion of S and NS trials for this SOA, and inclusion or exclusion of participants based on behavioural selection criteria.

| SOA with the most equally distributed responses | proportion of S/NS judgements at this SOA | Participant included in the final set? |
|-----------------------------------------------|------------------------------------------|---------------------------------------|
| 160                                           | 47/53                                    | yes                                   |
| 160                                           | 41/59                                    | yes                                   |
| 160                                           | 50/50                                    | yes                                   |
| 160                                           | 53/47                                    | yes                                   |
| 160                                           | 50/50                                    | yes                                   |
| 160                                           | 58/42                                    | yes                                   |
| 160                                           | 40/60                                    | yes                                   |
| 160                                           | 43/57                                    | yes                                   |
| 160                                           | 51/49                                    | yes                                   |
| 160                                           | 51/49                                    | yes                                   |
| 160                                           | 61/39                                    | yes                                   |
| 160                                           | 48/52                                    | yes                                   |
| 160                                           | 49/51                                    | yes                                   |
| 200                                           | 47/53                                    | yes                                   |
| 200                                           | 57/43                                    | yes                                   |
| 200                                           | 60/40                                    | yes                                   |
| 200                                           | 50/50                                    | yes                                   |
| 200                                           | 54/46                                    | yes                                   |
| 200                                           | 49/51                                    | yes                                   |
| 200                                           | 67/33                                    | yes                                   |
| 200                                           | 63/37                                    | yes                                   |
| 180                                           | 78/22                                    | no                                    |
| 160                                           | 28/72                                    | no                                    |
| 160                                           | 9/91                                     | no                                    |
| 180                                           | 77/23                                    | no                                    |
| 200                                           | 73/27                                    | no                                    |
| 200                                           | 89/11                                    | no                                    |
| 200                                           | 86/14                                    | no                                    |
| 200                                           | 89/11                                    | no                                    |
| 200                                           | 70/30                                    | no                                    |
| 200                                           | 71/29                                    | no                                    |
| 180, 200                                      | 73/27                                    | no                                    |

2.2. Phase modulation of perceived simultaneity

The results of the phase binning analysis (Section 4.7.1) are summarized in Fig. 2. For frequency bins outside of the alpha range (here 7.5 Hz and 17.5 Hz), we did not observe any clear relationships between (binned) prestimulus phase and perceived simultaneity. At 10 Hz and at 15 Hz there are faint hints at clustering of simultaneity judgements around certain phase bins, but the effects are far from reaching significance. At 12.5 Hz however we did observe a clear sinusoidal pattern in the simultaneity judgements as a function of phase bin. Although this effect falls into the tail of the null distribution and borders on significance, the p-value is above the alpha level of 5% (p = 0.077).

2.3. Analysis of individual alpha frequency

Mean IAF across participants was 10.34 (SD 0.83, range = 9.3 Hz–11.8 Hz). The correlation between IAF and b1 (the parameter modelling the width of the temporal window of integration, cf. Section 4.7.2) was 0.44, p = 0.038 (Fig. 3). Since higher values for b1 represent more narrow temporal windows of integration, the correlation indicates that a higher IAF is associated with a higher sensitivity to detect AV asynchrony.

2.4. Time-frequency analysis of power

Fig. 4 shows the time-frequency representation of power for S and NS trials (Fig. 4A) and their difference (Fig. 4B), respectively. Occipital alpha power was larger preceding the visual stimulus for S trials than for NS trials (cluster p-value = 0.039).

3. Discussion

In order to further elucidate the role of alpha oscillations (7–13 Hz) in the temporal binding of auditory and visual stimuli, participants performed a visual-auditory simultaneity judgement task. The point of subjective simultaneity occurred at SOAs of 160 to 200 ms. There, simultaneity judgements were at chance level. For these SOAs, alpha power was lower for trials with ‘not simultaneous’ judgements (NS trials) than for trials with ‘simultaneous’ judgements (S trials) preceding the onset of the first (i.e., the visual) stimulus. In addition, we found a significant positive relationship between individual alpha peak frequency (IAF) and the sensitivity to detect AV temporal differences. Finally, we observed a sinusoidal modulation of the proportion of S judgements as a function of phase bin around 12.5 Hz only. However, this effect failed to reach significance (p = 0.077). At other frequencies than 12.5 Hz there were no indications of a phase-dependency of simultaneity judgements.
3.1. Does prestimulus alpha phase modulate simultaneity perception?

Although the phase dependence of simultaneity judgements in visual-first (VA) stimulus pairs is clearly observable in the data (Fig. 2), the effect was not significant. Thus our results are largely in line with those from Ikumi et al. (2019), who observed a similar phase dependence for auditory-first (AV) stimulus pairs, but failed to find an effect for VA pairs. It is interesting to note that the present effect is observed at 12.5 Hz. This closely corresponds with the frequency of 13 Hz at which Ikumi et al. (2019) observed their phase dependence in AV pairs. Taken together, the results of the two studies suggest that the phase of alpha oscillations is instrumental in multisensory simultaneity perception, although this has been clearly demonstrated only for AV stimulus pairs. It is unclear why this asymmetry in the results for different modality orders occurs. It may be related to the more generally established finding that simultaneity judgements are poorer for VA stimulus pairs (e.g., Cecere et al., 2017; Stevenson and Wallace, 2013). These poorer judgements may partly obscure the delicate relationship between those judgements on the one hand, and alpha phase on the other hand. Another reason underlying this asymmetry may be that VA is the most naturally occurring temporal asynchrony in real life (as light travels faster than sound). Therefore the brain may be better adapted to slight temporal differences in VA synchrony than in AV synchrony, resulting in a smaller influence of alpha phase on simultaneity judgements in VA stimulus pairs. In any case, taken together, the study by Ikumi et al. (2019) and the present one are compatible with the notion that oscillatory perceptual cycles at alpha frequencies may constitute the neurophysiological mechanism underlying a window of temporal integration in multimodal perception, although convincing evidence for this phenomenon for VA stimulus pairs is still lacking.

3.2. Individual alpha frequency correlates with the size of the temporal window of integration.

Cecere et al. (2015) employed a double-flash illusion task and demonstrated that individual alpha peak frequency (IAF) correlates with the individually-determined size of the temporal window of integration. We replicate the findings from Cecere et al. (2015), as we observed a positive correlation between IAF and a measure that reflects the temporal window of integration. Our results thus extend the findings of Cecere et al. (2015) to the perception of temporal simultaneity. At the
same time, our results are in contrast with those of Van Wassenhove and colleagues (Grabot et al., 2017). In the latter study, the authors failed to find a correlation between perception accuracy and IAF in a temporal order judgement task. It is unclear at present what may have caused this discrepancy in the results between two very similar tasks (simultaneity judgement in the present study, temporal order judgement in Grabot et al., 2017). More data points are needed before any firm conclusions can be drawn with regards to this discrepancy. However, combined with those of Cecere et al. (2015) our results indicate that the relationship between IAF and temporal window of integration is a phenomenon that extends beyond illusion-induction tasks.

3.3. Simultaneity judgements coincide with spontaneous fluctuations in readiness of the visual cortex.

We observed alpha power in the time interval immediately preceding the visual stimulus to be smaller on trials with NS judgements. These findings extend those of a previous study which reported similar results in a temporal order judgement task (Grabot et al., 2017). Together these studies indicate that the relationship between prestimulus alpha power and a task involving temporal judgements are robust across these two different tasks. These findings are embedded in a larger context of studies that demonstrate a relationship between alpha power and (visual) perception, as occipital alpha power has been related to cortical idling (Pfurtscheller et al., 1996), inhibition (Foxe and Snyder, 2011; Klimesch et al., 2007) and gating (Jensen and Mazaheri, 2010).

3.4. Alpha oscillations are instrumental in multisensory synchrony perception

It is of interest to note that the observed effects, although all within the alpha frequency range (7–13 Hz), have slightly different peak frequencies: The prestimulus alpha power differences are largest between 9 and 11 Hz. Similarly, the IAF ranges between 9.3 Hz and 11.8 Hz across participants. However, the phase dependency effects are observed at 12.5 Hz, which is clearly higher than the two other effects. They therefore occur on the descending flank of the alpha peak for individual participants. It is unclear to us at present whether these small frequency differences are a technical issue resulting from differences in the underlying analysis techniques (e.g. frequency smoothing for time-frequency analysis of alpha power, peak-picking for determining IAF, and frequency binning in the phase analysis), or whether there is a more functionally related explanation for it.

Regardless of these small differences in peak frequency, the different results from the present study clearly converge onto an instrumental role for alpha oscillations in multisensory synchrony perception: simultaneity judgements are preceded by lower alpha power, are correlated with individual alpha peak frequency, and are dependent on prestimulus phase (at least for AV stimulus pairs, with a hint that the
same may be true for VA pairs). Taken together with previous studies (Cecere et al., 2015; Grabot et al., 2017; Ikumi et al., 2019), the available evidence suggests that irrespective of specific experimental paradigms, alpha oscillations are functionally related to multisensory binding, and constitute (part of) the neural architecture that underlies the temporal window of integration in multimodal perception. This fits well with the broader notion that oscillatory neuronal activity at around 10 Hz shapes perceptual cycles in unimodal sensory perception (VanRullen, 2016).

4. Experimental procedure

4.1. Participants

Thirty-three healthy students of Tilburg University participated in the experiment (age range: 18–25; 24 females). The participants were fully informed about all the procedures regarding the experiment (which was approved by the Ethics Committee of Tilburg University) and gave their written informed consent. All participants had normal hearing and normal/ corrected to normal vision, had no neurological disorders, and did not use psycho-active drugs or medication. Based on behavioural performance criteria (see the section on EEG data selection and processing for a detailed explanation), the results of 11 participants were excluded from the final analyses. Thus, the final set comprised 22 participants (age range: 18–25, 17 females).

4.2. Stimulus materials

The stimulus materials consisted of a visual and an auditory stimulus. The visual stimulus was a centrally aligned white circle (Wingdings 2 font, size 50), presented for 50 ms on a black background, on a monitor with a resolution of 1024 by 768 pixels, and 60 Hz refresh rate, positioned at a distance of approximately 70 cm from the participant’s head. The auditory stimulus was a pure tone (1000 Hz, 60 dB SPL), presented for 50 ms via two loudspeakers placed to the right and the left of the monitor.

4.3. Experimental design

During the experiment, participants performed a simultaneity judgement. To this end, stimuli were either presented simultaneously (SOA = 0 ms) or consecutively, the visual stimulus always being the first to occur. SOAs were, on average, symmetrically distributed around the point of subjective simultaneity (PSS). In pilot studies, the PSS was determined to be at an SOA of 180 ms on average. Therefore, SOAs of 0, 40, 80, 120, 160, 180, 200, 240, 280, 320 and 360 ms were used in the experiment. Each SOA was repeated 30 times during the experiment, except for the three SOAs closest to the PSS (160, 180 and 200 ms), which were repeated 100 times. Thus, in total the experiment consisted of 540 trials. Order of SOAs was randomized for each participant separately.

Each trial started with a black screen, presented for 1500 ms. Then, the visual and auditory stimuli were presented for 50 ms each, followed by a response delay interval (black screen) of 1900 ms. The response delay was included in order to minimize motor anticipatory processes in the peri-stimulus time interval, which are visible in the EEG from approximately 1500 ms prior to movement execution (e.g. Pfurtscheller and Lopes da Silva, 1999). At the end of the response delay, a response was prompted by presenting the words ‘synchronous = left button, asynchronous = right button’ on the screen. Participants were instructed to press one of two buttons on a button box situated on the table in front of them, with the index finger of their right hand. Upon the button press, an asterisk was presented at the center of the screen for a random time interval of between 850 and 1150 ms, indicating the inter-trial interval.

4.4. Procedure

Participants were instructed about the EEG recordings and about the simultaneity judgement task. They then gave their informed consent. Participants were prepared for the EEG recordings, and were seated in a dimly lit, sound-attenuating cabin. They performed a short practice block of 14 trials, in order to familiarize them with the EEG recordings and with the task.

The 540 experimental trials were presented in 11 blocks (10 blocks of 50 trials each, and a last block consisting of 40 trials), each lasting approximately 5 min. After each block, participants were allowed a short break, and continued with the next block by pressing one of the buttons. The entire session, including participant preparation and debriefing, lasted approximately 2 h.

4.5. EEG recordings

The EEG was analog filtered in a frequency range between DC and 102 Hz, and digitized and recorded with a sampling rate of 512 Hz from 64 locations using active Ag–AgCl electrodes (BioSemi, Amsterdam, the Netherlands) mounted in an elastic cap and including two mastoid electrodes. Electrodes were placed according to the extended International 10–20 system (see Fig. 5). Two additional electrodes served as reference (Common Mode Sense active electrode, placed halfway between P03 and P02) and ground (Driven Right Leg passive electrode, placed halfway between P0z and P04). Vertical and horizontal EOG signals were measured with electrodes above and below the left eye, and on the outer canthi of each eye, respectively.

4.6. EEG data preprocessing

The selected EEG data (see Section 2.1) were analyzed using Vision Analyzer (Brainproducts, DE), and the Matlab-based open source toolbox FieldTrip (http://www.fieldtriptoolbox.org; Oostenveld et al., 2011). Data were re-referenced to the average of left and right mastoids. In a few cases, bad channels were reconstructed using a spherical spline interpolation. The raw data was then segmented into 100 epochs ranging from 1200 ms before to 2200 ms after the onset of the visual stimulus. Eye-movement and obvious muscle artifacts were removed from the data using Vision Analyzer’s built-in ICA procedure. Trials with remaining artifacts on the EOG channels exceeding ± 100 μV were

Fig. 5. electrode layout. The electrodes marked with a + (P1, P2, P3, P4, P5, P6, Pz, PO3, PO4, PO7, PO8, POz, O1, Oz and O2) were used in the statistical analysis of the time-frequency data.
discarded from further analysis. Subsequently, EEG channels with artifacts exceeding ±220 μV were automatically detected, visually inspected, and discarded from further analysis when judged appropriate. In total, 9% of trials were rejected due to artifacts.

4.7. EEG data analysis

For each of the research questions formulated in the introduction, we performed different analyses on the preprocessed EEG data. First, in order to address the question of whether the phase of occipital alpha oscillations modulates perceived simultaneity, we created phase bins based on prestimulus phase, and looked for periodicity in the proportion of S and NS judgements across phase bins. Second, to address the relationship between IAF and temporal window of integration, we computed IAFs for all participants and correlated it with model-based estimates of the individual temporal window of integration. And third, we computed differences in prestimulus alpha power between S trials and NS trials. The details of the different analysis procedures are given below.

4.7.1. Phase modulation of perceived simultaneity

In order to determine a possible phase modulation of the perceived simultaneity, for each participant we divided trials into phase bins based on the phase estimate at channel Oz 100 ms prior to the onset of the first (i.e. visual) stimulus, as follows: we defined 10 phase bins on the unit circle, with their centers equally spaced between -π and π. To each bin, we assigned the 21 trials in which the prestimulus phases were closest to the center phase of the bin, resulting in partially overlapping phase bins (see van Elswijk et al., 2010 for a similar procedure). Next, we computed the proportion of NS responses within each phase bin, across trials pertaining to that phase bin, and across participants. In order to determine whether phase (or rather, phase bin) periodically modulates simultaneity perception, we then fitted a 1-cycle cosine to these proportions. The amplitude of the cosine fit is indicative for the extent to which prestimulus phase modulates simultaneity perception. Note that, in the binning procedure, a single data epoch was typically assigned to more than one bin (twice on average), resulting in overlapping phase bins, and a partial dependency between consecutive bins. For this reason, in order to determine the statistical significance of the cosine amplitude (reflecting the depth of the phase modulation) we opted for a statistical procedure that is not affected by this partial dependence: Phase bins were randomly shifted around for each participant (while preserving bin order, using MATLAB’s built-in circshift function), and grand average proportions of NS responses were computed. 10,000 such randomizations created a null distribution of cosine amplitude values. We then verified whether the actually observed cosine amplitude fell within the upper 5% percentile of this null distribution. In order to be able to test for the frequency-specificity of a potential phase-dependency of simultaneity perception, we performed this analysis for a set of frequencies from 7.5 Hz to 17.5 Hz, in steps of 2.5 Hz.

4.7.2. Analysis of individual alpha frequency

First, in order to determine IAF for each participant, the EEG data recorded during the entire SJ task were filtered with a 1-Hz high pass filter, down-sampled to 100 Hz, and segmented in epochs of 10 s each. After EOG correction (ICA) and artifact rejection (± 150 μV), Fast Fourier Transformation (FFT) was used to estimate spectral power in each epoch, yielding a frequency resolution of 0.1 Hz. Power spectra were averaged across epochs, and subsequently averaged across channels at which alpha power tends to be most prominent (PO7, PO3, POz, PO4, PO8, O1, Oz, O2). IAF was then determined as the peak in power in a frequency range from 7 to 13 Hz. For each participant there was one clearly identifiable peak in the 7–13 Hz frequency band.

Next, a logistic function was fitted on the individual participants' response profiles, so as to model the proportion of ‘simultaneous’ responses, where SOA stands for the stimulus onset asynchrony:

\[
\text{proportion of simultaneous responses} = \frac{1}{1 + e^{-b_1 \cdot b_{1\text{SOA}}}}
\]

Across participants this function fitted the individual response profiles reasonably well (mean R² = 0.67, SD = 0.29). The parameter b₁ in the logistic function mainly represents the steepness of the function, with higher values of b₁ reflecting a steeper function. This parameter was taken as a measure of the sensitivity to detect temporal asynchrony between the two modalities. Finally, we computed the correlation between IAF and parameter b₁.

4.7.3. Time-frequency analysis of power

Time-frequency representations of power were obtained by spectral decomposition with fast Fourier transforms in a time range of 800 ms prestimulus to 1000 ms poststimulus, using an asymmetric taper that emphasizes the contribution of the time points closer to the rightmost edge of the data window to the spectral estimates (as defined in equation 3 from Mitchell et al., 2007), with a time window of 400 ms, in 10-ms time steps. We evaluated the frequency range from 2 to 30 Hz, in 1-Hz steps. Because we were mainly interested in the differences in power before stimulus onset, power was expressed as the absolute change in power relative to a baseline interval ranging from 800 to 600 ms prior to the onset of the visual stimulus. Trials were then averaged separately for S and NS judgements, and differences between the two types of trials were tested using a cluster-based random permutation analysis (Maris and Oostenveld, 2007) as implemented in the Matlab toolbox Fieldtrip (Oostenveld et al., 2011). As we were specifically interested in differences in occipital alpha power we performed a cluster-based random permutation test in which the frequency range was restricted to 7–13 Hz. The latency range for the analysis was −200 ms to 0 ms prior to visual stimulus onset. The following parietal and occipital EEG channels were entered into the analysis (P1, P2, P3, P4, P5, P6, Pz, PO3, PO4, PO7, PO8, POz, O1, Oz and O2, see Fig. 5). All three dimensions (time, frequency and channels) were used for clustering, and the sum of the t-statistics within each cluster was used as a cluster-level statistic. The null distribution was based on 5000 random permutations. Finally, grand-average time–frequency representations were computed for display purposes.

CRediT authorship contribution statement

Marcel Bastiaansen: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. Hermine Berberyan: Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. Jeroen J. Stekelenburg: Conceptualization, Methodology, Formal analysis, Writing - review & editing. Jan Mathijs Schoffelen: Methodology, Formal analysis, Software, Writing - review & editing. Jean Vroomen: Conceptualization, Writing - review & editing.

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