

Alpha-band oscillations and visual temporal resolution: An expansion and partial replication of Samaha & Postle’s 2015 study: “The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception”

Clinton S. Haarlem¹, Kevin Mitchell¹, Andrew Jackson¹, and Redmond O’Connell¹

¹Trinity College Dublin

May 06, 2024

Abstract

The study of alpha band oscillations in the brain is a popular topic in cognitive neuroscience. A fair amount of research in recent years has focused on the potential role these oscillations may play in the discrete sampling of continuous sensory information. In particular, the question of whether or not peak frequency in the alpha band is linked with the temporal resolution of visual perception is a topic of ongoing debate. Some studies have reported a correlation between the two, whereas others were unable to observe a link. It is unclear whether these conflicting findings are due to differing methodologies and/or low statistical power, or due to the absence of a true relationship. Replication studies are needed to gain better insight into this matter. In the current study, we replicated an experiment published in a 2015 paper by Samaha & Postle. Additionally, we expanded on this study by adding an extra behavioural task, the critical flicker fusion task, to investigate if any links with peak alpha frequency are generalizable across multiple measures for visual temporal resolution. We succeeded in replicating some, but not all of Samaha & Postle’s findings. Our partial replication suggests that there may be a link between visual temporal resolution and peak alpha frequency. However, this relationship may be very small and only apparent for specific stimulus parameters. The correlations found in our study did not generalize to other behavioural measures for visual temporal resolution.

INTRODUCTION

The question of whether perception is discrete, continuous or a combination of both has been a subject of ongoing debate in the fields of sensory neuroscience, psychology and philosophy for many years (VanRullen & Koch, 2003; Herzog et al., 2016; Ruzzoli et al., 2019). Many different “flash fusion” paradigms have been developed based on the notion that our sensory system may sample information in discrete time windows: if two sensory stimuli, usually visual and/or auditory, are quickly flashed within the same time window, they are fused to form a single percept. If one of the stimuli falls outside of the window, they are segregated and two separate percepts are formed.

The rhythmic nature of brain activity is often proposed as a possible mechanism to support the idea of discrete sampling and is theorized to be a driving factor behind the integration and segregation of sensory information (Schroeder & Lakatos, 2009; Keitel et al., 2022; VanRullen & Koch, 2003). More specifically, the phase and frequency of neural oscillations are thought to determine the size of the temporal sampling window.

Neural oscillations are generally grouped into five distinct bands: delta (1 – 4 Hz), theta (5 – 8 Hz), alpha (8 – 13), beta (13 – 30) and gamma (30+ Hz) (Başar et al., 2001; Ward, 2003; Keil & Senkowski, 2018). As alpha band oscillations are the dominant oscillations in the brain, they have been studied extensively and have been found to be affected by the activity of the visual system in multiple ways, with one of the most basic

findings being that alpha power is high when eyes are closed, but suppressed when eyes are open (Adrian & Matthews, 1934; Klimesch, 2012). One popular theory is that alpha-band oscillations may play a role in the modulation of visual stimulus detection (Ergenoglu et al., 2004; Hanslmayr et al., 2005; Morrow & Samaha, 2022; Mathewson et al., 2009). Some studies have found that the phase and frequency of alpha oscillations may affect whether or not a near-threshold stimulus is perceived, with higher frequency alpha oscillations being correlated with a more finely tuned capacity to segregate visual asynchronous stimuli (Busch et al., 2009; Mathewson et al., 2009; Samaha & Postle, 2015). Other studies however, failed to replicate this effect (Burgers & Noppeney, 2022; Ruzzoli et al., 2019). It is unclear whether this failure to replicate is due to the absence of a true relationship or because the previously mentioned studies all differed in their task paradigms and analysis methods. As pointed out by Keitel et al. (2022), the lack of direct replications is one of the main issues this field suffers from, along with small effect sizes and low statistical power.

To address this issue, we carried out a replication of a visual perception experiment conducted by Samaha & Postle in 2015. In this experiment, a two-flash fusion task was used to investigate how alpha-band oscillations may affect the perception of near-threshold visual stimuli. The study found that both pre-stimulus and eyes-closed peak alpha frequency correlated with flash/fusion thresholds between subjects. Moreover, the study found that within subjects, instantaneous peak alpha was correlated with perceptual accuracy.

In the current study, we employed the two-alternative-forced choice gap detection task (hereafter: flash-fusion task) used by Samaha & Postle with a larger sample size for a higher statistical power, and carried out similar EEG-data analyses to compare flash-fusion thresholds in relation with peak alpha frequency for resting-state and pre-stimulus scenarios. We also replicated within-participant analyses to investigate potential correlations between instantaneous alpha frequency and perceptual accuracy, using methods developed by Cohen (2014).

We additionally hypothesized that, if natural variation in peak alpha frequency is indeed indicative of an individual's visual temporal resolution, it should correlate with different behavioural measures of visual perception speed. We therefore expanded the original study by also including a second visual perception speed task: the critical flicker fusion threshold task (hereafter: CFF task), which utilizes a continuously flickering stimulus to estimate individual temporal resolution thresholds.

METHODS

Participants

32 participants (17 female, age range 18 – 35 years) were recruited from Trinity College Dublin. All participants provided written, informed consent and all participants had normal or corrected-to-normal visual acuity. Participants were compensated for participating with either a of their postgraduate research degree worth 1 ECTS per half hour of participation. The study was approved by the Ethics Committee of Trinity College Dublin's School of Psychology (approval ID SPREC052022-01). One participant was excluded from analysis due to near chance performance on the flash-fusion task at all stimulus levels. Two participants showed no alpha-band peak in pre-stimulus EEG recordings and were excluded only from the pre-stimulus analyses.

Computerized flash-fusion task

We modelled the flash-fusion task after the one used in Samaha & Postle and followed a similar protocol (Fig 1). Participants were seated ~60 cm away from a computer monitor with a 100 Hz refresh rate. The task consisted of white disk stimuli appearing against a black background. Each trial started with a white fixation cross in the middle of the screen, at 0.98 degrees visual angle. The fixation cross reduced in luminance before stimulus onset to prepare participants. The duration of this period was drawn from a uniform distribution between 1000 and 1500 ms. The fixation cross remained present for the duration of the trial. Disk stimuli, at 1.23 degrees visual angle, were presented either to the left or to the right side, at 2.45 degrees visual angle (0.20 cd/m²) of the fixation cross, with equal probability. Fifty percent of the trials were two-flash trials, in which a disk appeared for 40 ms, then disappeared for either 10, 20, 30, 40 or 50 ms, and then reappeared

for 40 ms. The other fifty percent were one-flash trials, in which a disk appeared for durations that varied to match the stimulus onset to stimulus offset lengths for each stimulus type of the two-flash trials. 800 ms after stimulus offset the fixation cross increased in luminance to prompt participants to make a response. Participants held a mouse in both hands during the task and responded by clicking the left button with their left thumb to indicate when they perceived a single flash trial, or by clicking the right button with their right thumb to indicate when they perceived a two-flash trial. The next trial did not start until a response had been made and participants were instructed to focus on accuracy over speed. Participants completed 20 practice trials, followed by 600 test trials divided into 6 blocks. Participants took self-paced breaks in between each block.

Our task design deviated from Samaha & Postle’s design in three minor ways: due to the physical set-up of equipment in our lab, participants were seated at ~ 60 cm away from the monitor, whereas in the original design this was ~ 70 cm. Because the original task design did not specify any specific colour values for the stimulus disks, or the amount with which fixation luminance decreased before stimulus onset, we were unable to replicate these variables exactly. We therefore opted to use white stimulus disks to optimize contrast, and we decreased the luminance of the fixation cross by 40% before stimulus onset.

Figure 1: Task set-up and stimulus conditions . Reproduced from Samaha & Postle (2015). The image presented here has been altered from the original by removing a “confidence” step at the end of each trial, which was not analysed in the original study and therefore is not included here.

A: Depiction of a trial. The start of a trial was indicated with a white fixation cross, which reduced in luminance to prompt for an upcoming stimulus. Stimulus consisted of a single flash event in half of the trials and a double flash event in the other half. Flash events were presented either to the left or to the right of the fixation cross with equal probability.

B: Double flash events consisted of a white stimulus disk appearing for 40 ms, followed by a gap of 10 – 50 ms, after which the stimulus disk reappeared for another 40 ms. Lengths of single flash events were varied to match the duration of the double flash events.

Psychometric functions

We used the results from the flash-fusion task to create a psychometric function for each participant, using the Palamedes toolbox (Prins, N. & Kingdom, F.A.A., 2018) for MATLAB (The Mathworks Inc., 2022). Following the methods used in Samaha & Postle (2015), we employed a logistic function with four parameters: “guess rate,” “threshold,” “slope” and “lapse rate” to estimate the correct response rate for the different stimulus conditions. Guess rate was fixed at 0.5. The other three parameters were estimated for each participant. Lapse rate was set to the limits of 0 – 0.06. We used goodness-of-fit testing to compare the deviance of the fit to the real data with deviance of the fit to 1,000 simulated datasets for each participant. No participant’s fit exceeded the 95th percentile, indicating that all created psychometric functions fell within the expected range for the type of data and no function was deemed an outlier.

CFF threshold measurement

We measured critical flicker fusion thresholds using a novel measuring device and custom methods, the accuracy and robustness of which were validated in a separate, parallel study (Haarlem et al., in press). The protocol for measuring CFF thresholds outlined below are reproduced from that study’s methods section. All CFF thresholds measured in the current study were also included in the dataset used in Haarlem et al.

The device consisted of an Arduino Uno R3 microprocessor and a 4500K white LED light, housed in a black container. An opaque, black viewing tube was mounted on top of the container, to standardize viewing distance at ~ 16 cm and to eliminate almost all ambient light. Flicker frequency of the LED could be adjusted with a rotary encoder dial that either increased or decreased flicker rate in 1 Hz increments. We measured luminance and colour temperature with a ColorCal Mk II. Mean luminance of the LED was ~ 255 lux. The device was powered by a personal laptop, using a USB-C cable. We measured the power input with

a Tektronix TDS 210 oscilloscope to ensure stability. The precision and stability of the LED flash timings were measured using a photometer, both before the start of, and after completion of the study.

The protocol consisted of a measurement of 3 different quantifications of a participant’s ability to perceive flashes and was based on a combination of two commonly used psychophysical experimental techniques: the method of limits and the method of constant stimuli. The protocol started with the method of limits: participants observed a constantly lit LED light through the viewing tube and were then instructed to turn the rotary encoder clockwise, to make the light source start flashing. Participants were then asked to keep rotating the dial to increase the flash frequency in 1 Hz increments until flashes could no longer be perceived and the light appeared steady. The frequency at which this occurred was recorded. The LED light source was then set to a flash frequency of 65 Hz, which is above the threshold at which humans are able to perceive light flashes at the described intensity. For the second measurement, participants were instructed to observe the light source again, but this time they were asked to turn the dial counter-clockwise to decrease flash frequency, until they first observed flashing. The frequency at which this happened was again recorded.

The third step consisted of the method of constant stimuli: for each participant, we took the highest value measured with the method of limits, and created a series of 10 flash frequencies in 1 Hertz steps: 5 frequencies below the recorded threshold, and 4 frequencies above it. Each of the frequencies in the series was then multiplied by 5 to produce a set of 50 stimuli. We then randomized the entire set and presented it to the participant. Participants were then instructed to cycle through all of the 50 frequencies in the series, one by one, using the rotary encoder dial to instantiate the next stimulus in the set. Participants were asked to inform the experimenter for each stimulus whether they observed a steady light or not. The final critical flicker fusion threshold for the individual was determined by calculating the highest frequency in the series at which the user was able to perceive flashing 80% of the time.

Participants completed the CFF task roughly 30 minutes prior to the first eyes-closed EEG recording.

EEG-recording and processing

We recorded EEG from 128 scalp electrodes, using the Active Two Biosemi system, arranged according to the 10-5 system (Oostenveld & Praamstra, 2001). We recorded electrooculogram vertically, with one electrode just above the eyebrow and one approximately 3 cm below the eye. EEG was recorded with a sampling rate of 512 Hz.

We recorded eyes-closed resting state EEG for two minutes both prior to starting, and after completion of the computerized perceptual task. Participants were asked to relax and sit still during this period. The EEG recordings were then cut into 1-second, non-overlapping epochs. Pre-stimulus-EEG data was epoched from -700 – 0 ms relative to stimulus onset. Epoches data was then detrended and we spherically interpolated an average of 2.9% of electrodes for eyes-closed data and an average of 3.4% of electrodes for pre-stimulus data.

We used Matlab (Mathworks, 2022) for the pre-processing of all EEG-recordings, using custom Matlab scripts. Current source density (CSD) transformation is used in many EEG studies in order to reduce volume conduction effects and signal mixing (Kayser & Tenke, 2006; 2015). This step was not carried out in Samaha & Postle’s original study. We therefore opted to analyse the data both with- and without applying CSD transformation in order to determine its impact.

For the CSD-transformed eyes-closed EEG data, we rejected epochs when voltages exceeded a CSD-transformed amplitude threshold of $500 \mu\text{V m}^2$ for both scalp and eye electrodes. An average of 47 (standard deviation (SD) 53.5) epochs were rejected per participant. For CSD-transformed pre-stimulus EEG data, we rejected epochs when voltages exceeded a threshold of $500 \mu\text{V m}^2$ for scalp electrodes or $100 \mu\text{V}$ for eye electrodes (eye electrodes were not included in the CSD-transformation and therefore required a lower threshold). We rejected an average of 125 (SD 108.2) epochs per participant.

For the non-CSD-transformed eyes-closed EEG-data, we rejected epochs when voltages exceeded a threshold of $100 \mu\text{V}$ for scalp electrodes and $500 \mu\text{V}$ for eye electrodes. We rejected an average of 32 (SD 28) eyes-closed EEG-data epochs per participant. For non-CSD-transformed pre-stimulus EEG-data, we rejected

epochs when voltages exceeded 100 μ V for all electrodes. We rejected an average of 52 (SD 58.8) epochs of pre-stimulus EEG-data per participant.

Epochs were then multiplied by a hamming window and fast Fourier transformed with a frequency resolution of 0.1 Hz. Individual alpha peak frequency was defined as in Samaha & Postle and was extracted from the highest amplitude in the power spectrum within the frequency range 8 – 13 Hz. All participants showed a clear peak within this range at all scalp electrodes for eyes-closed data. Similar to the original study, not all electrodes showed a peak in the 8 – 13 Hz frequency range and no electrode showed a peak for all participants for pre-stimulus data. We therefore followed the original methodology and chose whichever electrode had the highest power amplitude within the alpha band range for each participant.

Because it has been shown that peak alpha frequency can change over time within an individual (Cohen, 2014), we computed instantaneous alpha to assess if pre-stimulus alpha frequency is higher prior to correct task responses compared to incorrect responses. Instantaneous alpha corresponds to the first temporal derivative of the phase angle time series. To calculate instantaneous alpha, we replicated Samaha & Postle’s method, and chose the electrode that had the highest amplitude in the alpha band range for the pre-stimulus recordings at the group level, which we interpreted as the electrode that had the highest alpha amplitude for most participants: electrode C16. Following our same reasoning as with the previous analysis, we again also computed instantaneous alpha frequency for electrode B7. We epoched the pre-stimulus EEG-recordings from -700 to 0 ms relative to stimulus onset, and then copied, flipped and appended each epoch to avoid edge artifacts. Using code developed by Cohen (2014), we then defined frequency boundaries of 8 – 13 Hertz, and applied a zero-phase bandpass filter with 15% transition zones. We extracted the analytic signal with a Hilbert transform and median filtered using default parameters set by Cohen: we applied the median filter ten times with different window sizes ranging from 10 to 400 ms, in steps of 10 ms. As Samaha & Postle only reported instantaneous frequency for the 500 ms prior to stimulus onset, we followed their method and only calculated instantaneous alpha for the timepoints ranging from -500 – 0 ms.

Statistical analysis

We used R (v4.2.1; R Core Team 2021) and RStudio (version 2023.3.0.386; Posit Team 2023) to carry out the statistical analysis. All data was checked for the presence of significant outliers and we used linear models to assess linearity, distribution of residuals and homogeneity of variance. Unless otherwise stated, no statistically significant outliers were detected and all data met assumptions of linearity, homogeneity of variance and normal distribution of residuals, and two-tailed correlations were tested with Pearson’s correlation coefficient. We used cluster-based permutation testing, using the “permutes” (Voeten, 2022) and “permuco” (Frossard, 2021) packages, to analyse instantaneous alpha. 5000 permutations of randomly shuffled data were used to create a distribution of cluster sizes expected under the null- hypothesis. Clusters of real data that exceeded the 95th percentile of this null distribution were deemed statistically significant.

Statistical power analysis

To compare statistical power and effect size between our replication and the original study, we calculated these parameters using the “pwr” package (Champely, 2020). With a sample size $n = 20$ and $\alpha = 0.05$, Samaha & Postle’s reported correlation coefficients of $r = -0.503$ (for eyes-closed data) and $r = -0.605$ (for pre-stimulus data) resulted in a statistical power of 0.644 and 0.84, respectively. With our sample size of $n = 31$ and $\alpha = 0.05$, correlations in our replication would need to be $r = 0.41$ or greater for eyes-closed data, and $r = 0.5$ or greater for pre-stimulus data, to match or exceed the statistical power of Samaha & Postle’s original study.

RESULTS

For all participants, alpha power was highest at occipital and parietal electrodes, both for the eyes-closed and pre-stimulus EEG data. Alpha power for pre-stimulus EEG-recording was substantially reduced compared to eyes-closed EEG recording (Fig 2).

Figure 2: Topography of resting state alpha band (8 – 13 Hz) power, recorded from 128-

electrode EEG. The topographies display data averaged over all participants. Alpha band power was highest in the occipital region for both eyes-closed EEG recording (left) and pre-stimulus EEG recording (right).

Effect of Current Source Density (CSD)-transforming on peak alpha frequency

We extracted peak alpha frequencies from the dataset both after applying CSD-transformation during EEG pre-processing and without applying CSD-transformation (see Methods). For resting state data, the two versions of the dataset were highly correlated ($r = 0.96$, $P < 0.001$) and the mean difference between the two was 0.07 Hz ($t = 1.9$, $P > 0.05$). Pre-stimulus CSD transformed data was also highly correlated with its non-CSD transformed counterpart ($r = 0.62$, $P < 0.001$). The mean difference between these versions was 0.27 Hz. Though the two datasets did not differ from each other significantly ($t = 1.96$, $P > 0.05$), a difference of 0.27 Hz in the alpha band range could potentially be meaningful. We therefore conducted all further correlation tests with both the CSD transformed and the non-CSD transformed versions of the data. Unless otherwise stated, we found no difference between the two versions of the data and only reported results from the non-CSD transformed dataset.

Flash fusion task

Eyes-closed EEG analysis

Eyes-closed EEG data consisted of a 2-minute pre-task and a 2-minute post-task recording, which were highly correlated with each other ($r = 0.91$, $P < 0.001$). Pre- and post-task recordings were therefore analysed as one dataset for each participant. We detected a moderate correlation in the expected direction ($r = -0.43$, $P < 0.05$) between eyes-closed peak alpha frequency and flash-fusion thresholds (Fig 3, left). We found no correlation between eyes-closed alpha power and flash-fusion thresholds ($r = 0.14$, $P > 0.05$).

Pre-stimulus EEG analysis

Following the original study's protocol for pre-stimulus data, we calculated peak alpha frequency from the electrode that showed the highest amplitude in the alpha band range for each participant. We detected no significant correlations between peak alpha frequency and flash-fusion thresholds ($r = -0.29$, $P > 0.05$) (Fig 3, middle), or between pre-stimulus peak alpha power and flash-fusion thresholds (Pearson's $r = 0.18$, $P > 0.05$).

Having initially failed to replicate Samaha & Postle's original result with the pre-stimulus dataset, we included a second analysis, post-hoc. Previous findings (Pfurtscheller et al., 1996; Busch et al., 2009; Ruzzoli et al., 2019) have indicated that high alpha power may be indicative of suboptimal performance or the absence of sensory processing, and a suppressed alpha power may be indicative of focused attention. Therefore, selecting the electrodes with highest amplitudes during task performance to extract peak alpha frequency may not be the most informative for pre-stimulus data. We therefore selected the electrode that had the highest power amplitude in the alpha band range in the *eyes-closed* data and used this same electrode to measure alpha levels in the pre-stimulus data: electrode B7, located in the occipital region. Two participants did not show a peak in the alpha band in pre-stimulus recordings for electrode B7 and we therefore excluded these participants from the respective analyses. This time, we found a moderate correlation between flash-fusion thresholds and pre-stimulus peak alpha frequency ($n = 29$, $r = -0.42$, $P < 0.01$) (Fig 3, right).

Figure 3: Correlations between flash fusion thresholds and peak alpha frequency. Left: we found a moderate correlation between flash fusion threshold and peak alpha frequency extracted from resting state EEG-recording. Middle: Peak alpha frequency extracted from the electrode that has the highest amplitude in the alpha band for pre-stimulus EEG-recording was not correlated with flash fusion thresholds. We found a moderate correlation between flash fusion threshold and peak alpha frequency extracted from electrode B7 for pre-stimulus EEG-recording.

Intermediate stimulus comparisons

To ensure that the found correlation was not an artifact of the extracted thresholds, Samaha & Postle also conducted tests with the proportion of correct responses on the intermediate stimulus onset asynchrony (30

ms gap). We replicated this analysis, and found a moderate correlation between the proportion correct and peak alpha frequency from eyes-closed EEG-recording ($r = 0.33$, $P < 0.05$, one-tailed). We found no statistically significant correlation for peak alpha frequency extracted from electrode B7 for pre-stimulus EEG-recording ($r = 0.28$, $P = 0.07$, one-tailed).

Instantaneous alpha

We extracted instantaneous alpha, according to Cohen’s method, as a within-participant measure for time resolved changes in peak alpha frequency between trials. We computed instantaneous alpha for the electrode used in the previous analysis, B7 and, following the protocol of the original study, also for electrode C16, which had the highest amplitude in the alpha band for most participants in the pre-stimulus EEG data. We then compared pre-stimulus instantaneous alpha frequency between correct and incorrect responses. The mean instantaneous alpha extracted from electrode B7 was 10.361 Hz (SD = 0.023) for correct responses and 10.363 Hz (SD = 0.025) for incorrect responses. For electrode C16, mean instantaneous alpha frequency for correct answers was 10.318 Hz (SD = 0.039). For incorrect answers it was 10.326 Hz (SD = 0.026). Cluster-based permutation testing revealed no time clusters with a statistically significant difference in instantaneous alpha between correct and incorrect answers for either electrode (Fig 4).

Figure 4: Within subject analysis of instantaneous alpha for correct (blue) versus incorrect (orange) responses. Left: instantaneous alpha extracted from electrode C16. Right: instantaneous alpha extracted from electrode B7. Shaded regions indicate $\pm$ standard error of the mean.

CFF task

Eyes-closed EEG analysis

Participants completed the CFF task prior to EEG recording. Mean CFF was 50.01 Hz (SD = 6.32). We found no correlation between the task and eyes-closed peak alpha frequency (Pearson’s $r = 0.01$, $P = 0.95$) or peak alpha power (Pearson’s $r = 0.14$, $P = 0.35$). QQ-plots showed a slight deviation from normality for the CFF task data. We therefore also conducted our correlation test using Spearman’s rank correlation, but this did not significantly alter analysis results: Spearman’s $r = 0.04$, $P = 0.83$.

Comparison of the two behavioural tasks

We compared the thresholds obtained with the CFF task with those obtained with Samaha & Postle’s flash fusion paradigm. We found no correlation between the two ($r = -0.13$, $P = 0.49$).

A summary of all main results is outlined in Table 1.

Table 1: Overview of main results. This table lists the main results for this study, and indicates which analyses were carried out as replications of Samaha & Postle’s original study, and which were additional, original methods. Significant correlations shown in bold.

Correlation analysis (Pearson’s r)	Correlation analysis (Pearson’s r)
Replicated from Samaha & Postle 2015	Flash fusion task and eyes-closed peak alpha frequency
	Flash fusion task and eyes-closed peak alpha power
	Flash fusion task and pre-stimulus peak alpha frequency
	Flash fusion task and pre-stimulus peak alpha power
	Proportion of correct responses on intermediate stimulus and eyes-closed peak alpha frequency
	Proportion of correct responses on intermediate stimulus and pre-stimulus peak alpha frequency
Original methods	Pre-stimulus peak alpha frequency and perceptual accuracy
	Flash fusion task and pre-stimulus peak alpha frequency extracted from electrode C16
	Critical flicker fusion threshold and eyes-closed peak alpha frequency
	Critical flicker fusion threshold and eyes-closed peak alpha power
	Critical flicker fusion threshold and flash fusion task

DISCUSSION

Though the study of alpha band oscillations in the brain and their potential effect on sensory perception is a popular area of research, conflicting results illustrate a need for more replication studies. Our results add more insight into the possible role of peak frequency and amplitude of rhythmic brain patterns in sensory perception. Our study replicated some of the findings of Samaha & Postle, but not all.

Flash fusion task

Similar to the original study, we found a moderate correlation between peak alpha frequency from eyes-closed EEG data and flash-fusion thresholds. Following the original paper’s methods for pre-stimulus EEG recording analysis, we analysed the electrode that showed the highest amplitude in the alpha band range for pre-stimulus EEG recording for each participant, and found no correlation between peak alpha frequency and flash fusion thresholds for pre-stimulus EEG recordings. However, regions with high alpha power during visual task performance might not be indicative of the areas where focused, fast temporal processing might be taking place. We therefore also analysed electrode B7, which had the highest alpha band amplitude for most participants during eyes-closed EEG recording. For electrode B7, we found a moderate correlation between pre-stimulus peak alpha frequency and flash fusion thresholds. Consistent with Samaha & Postle’s findings, flash-fusion thresholds were not correlated with either eyes-closed or pre-stimulus peak alpha power.

Intermediate stimulus

Similar to the original study, we found a correlation between the proportion of correct responses on the intermediate stimulus and peak alpha frequency from eyes-closed EEG data. We did not replicate the correlation of $r = 0.4$ found in the original study for pre-stimulus EEG data. With $n = 20$ and $\alpha = 0.05$, the original finding yielded a statistical power of 0.56. With our sample size, the effect size needed to match this power is 0.32. Our level of correlation, $r = 0.28$, came close to that of the original study, but it did not reach statistical significance. The low power and effect size of both the original and current results make it difficult to draw conclusions about any true relationships regarding peak alpha frequency and the proportion of correct responses on the intermediate stimulus. The lack of stronger correlations could suggest that a potential relationship between peak alpha frequency and temporal perception may be small and only apparent for near threshold stimuli. As the intermediate stimulus onset asynchrony is designed to be observable for most participants in more than 50% of the trials, it makes sense that correlations with a potential indicator for finely tuned temporal perception may be weak or even absent, as observing this stimulus would not require extremely fast visual processing. As such, there is a higher chance for incorrect responses to be due to other factors than slower temporal processing, such as lack of attention or blinking.

Instantaneous alpha

Samaha & Postle reported a correlation between instantaneous alpha and response on the flash fusion task, with correct responses being linked with a higher instantaneous alpha. Such an effect was not observed in the present study. We analysed electrodes that had the highest alpha amplitudes at the group level for both eyes-closed (B7) and pre-stimulus (C16) EEG-recording, and neither showed any time clusters within the -700 – 0 ms pre-stimulus window where instantaneous alpha frequency was significantly different for correct versus incorrect responses. Data from several other recent studies have also failed to support this link (Buergers & Noppeney, 2022, Ruzzoli et al., 2019). Though we have attempted to model our task as closely to Samaha & Postle’s as possible, there were some differences in our methodology which could potentially account for the discrepant results. For instance, from Samaha & Postle’s methods, it is not reported by how much the fixation cross decreased in luminance to prompt the participant of the upcoming stimulus. If this luminance shift was more drastic in our study, it could have caused a stronger phase reset effect, possibly nullifying any natural phase differences between trials (Harris, 2023).

CFF task and peak alpha frequency

We found no correlation between thresholds obtained with the CFF task and peak alpha frequency from eyes-closed EEG recording. This result illustrates how the choice of behavioural task may influence the

results obtained in brain rhythmicity studies. As already touched upon by Buegers & Noppeney (2022), the effect alpha frequency may have on temporal perception may be very small and brittle, and may only be apparent for very specific stimulus parameters. A lack of correlation between the CFF task and peak alpha frequency may also be due to the continuous nature of the task stimulus, which may force alpha oscillations out of their natural rhythms; a phenomenon that is often intentionally induced in Steady State Visually Evoked Potential (SSVEP) research (Regan, 1966; Norcia et al., 2015). Alpha power is also expected to reduce greatly during perception of a continuous stimulus, which in turn might affect alpha frequency as well, as the two are found to be intrinsically linked (Nelli et al., 2017). Additionally, previous literature has suggested that peak alpha frequency may only be indicative of perceptual sensitivity when the stimulus last for less than one alpha cycle (Keitel et al., 2022, Michail et al., 2022).

CFF and flash fusion task comparison

We also found no correlations between the thresholds obtained with the two different tasks. Though this may initially seem surprising, the flash fusion task fundamentally differs from the CFF task in several ways. For example, the former is essentially a two-alternative-forced-choice task, in which participants need to choose between two possible responses in each trial. This introduces a guess rate which may skew “true” flash-fusion thresholds. The responses may also be influenced by a pre-existing bias for one of the two options (Buegers & Noppeney; 2022). The flash fusion task also requires 600 trials for the proper fitting of a psychometric curve. This causes fatigue to become a significant factor and, though computationally corrected for during psychometric function fitting, introduces a certain lapse rate. The two tasks also differ in the number of different stimuli: the flash fusion task has five different fixed gap lengths, whereas no practical upper bound for flicker-fusion threshold exists in the CFF task, making the latter perhaps more suitable to assess inter-individual differences in the absolute maximum threshold, but less so for employing standardized tests to investigate brain activity correlates. Thresholds obtained with the CFF task may also not be directly comparable to those obtained with the flash fusion task due to a steady increase of mean luminance over time as flicker frequency increases in the former, which effectively increases flicker fusion thresholds up to a certain point. It is also important to note that Samaha & Postle’s flash fusion task was designed to assess possible correlates with alpha oscillations; which are a specific measure for visual attention and focus (Clayton et al., 2018, Pfurtscheller et al., 1996). The gap detection style task is very suitable to investigate the level of attention a participant pays to each stimulus. Any moment of inattention may mean that the gap in the stimulus is missed and a trial is considered incorrect. This is not the case for the critical flicker fusion task, in which the stimulus is always present, giving participants the opportunity to refocus and reconsider what they are perceiving throughout the whole task. The latter reason would not only explain the lack of correlation between the two behavioural task responses, but also between the CFF task and peak alpha frequency.

In conclusion, we have replicated some, but not all of the results from a previous study investigating the possible relationship between peak alpha frequency and visual temporal resolution. Our work adds to the ever-expanding body of research data aiming to tease apart the link between brainwave oscillations and visual perception. We have additionally shown that the choice of behavioural task is key in exploring these possible relationships.

ACKNOWLEDGMENTS

We would like to thank Dr. Jason Samaha and Dr. Bradley Postle for their original research, Dr. Mike X. Cohen for EEG analysis scripts and interpretation, Dr. Kevin Walsh for task script creation, Dr. John Grogan for assistance with EEG analysis and Pat McKeown, Dasha Monakhovych and Hannah McDermott for assistance with data collection and participant recruitment. Funding for the project was provided by funding from Trinity College Dublin under the Provost’s Postgraduate Award 2019 scheme to ALJ, KJM and ROC.

REFERENCES

Adrian, E. D., & Matthews, B. H. C. (1934). The berger rhythm: potential changes from the occipital lobes

in man. *Brain* ,57 , 355–385.

Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *International Journal of Psychophysiology* , 39 (2–3), 241–248. [https://doi.org/10.1016/S0167-8760\(00\)00145-8](https://doi.org/10.1016/S0167-8760(00)00145-8)

Buergers, S., & Noppeney, U. (2022). The role of alpha oscillations in temporal binding within and across the senses. *Nature Human Behaviour* , 6 (5), 732–742. <https://doi.org/10.1038/s41562-022-01294-x>

Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience* , 29 (24), 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>

Champely, S. (2020). pwr: Basic Functions for Power Analysis (Version 1.3-0) [R package]. <https://CRAN.R-project.org/package=pwr>

Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2018). The many characters of visual alpha oscillations. *European Journal of Neuroscience* , 48 (7), 2498–2508. <https://doi.org/10.1111/ejn.13747>

Cohen, M. X. (2014). Fluctuations in oscillation frequency control spike timing and coordinate neural networks. *Journal of Neuroscience* ,34 (27), 8988–8998. <https://doi.org/10.1523/JNEUROSCI.0261-14.2014>

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research* , 20 (3), 376–383. <https://doi.org/10.1016/j.cogbrainres.2004.03.009>

Frossard J. & Renaud, O. (2021). Permutation Tests for Regression, ANOVA, and Comparison of Signals: The permuco Package. *Journal of Statistical Software*, 99(15), 1–32. <https://doi.org/10.18637/jss.v099.i15>

Haarlem, C. S., O’Connell, R. G., Mitchell, K. J. & Jackson, A. L. (in press). The speed of sight: individual variation in critical flicker fusion thresholds. *PLoS One* .

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters* , 375 (1), 64–68. <https://doi.org/10.1016/j.neulet.2004.10.092>

Harris, A. M. (2023). Phase resets undermine measures of phase-dependent perception. *Trends in Cognitive Sciences* , 27 (3), 224–226. <https://doi.org/10.1016/j.tics.2022.12.008>

Herzog, M. H., Kammer, T., & Scharnowski, F. (2016). Time Slices: What Is the Duration of a Percept? *PLoS Biology* , 14 (4). <https://doi.org/10.1371/journal.pbio.1002433>

Kayser, J., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. Evaluation with auditory oddball tasks. *Clinical Neurophysiology* , 117 (2), 348–368. <https://doi.org/10.1016/j.clinph.2005.08.034>

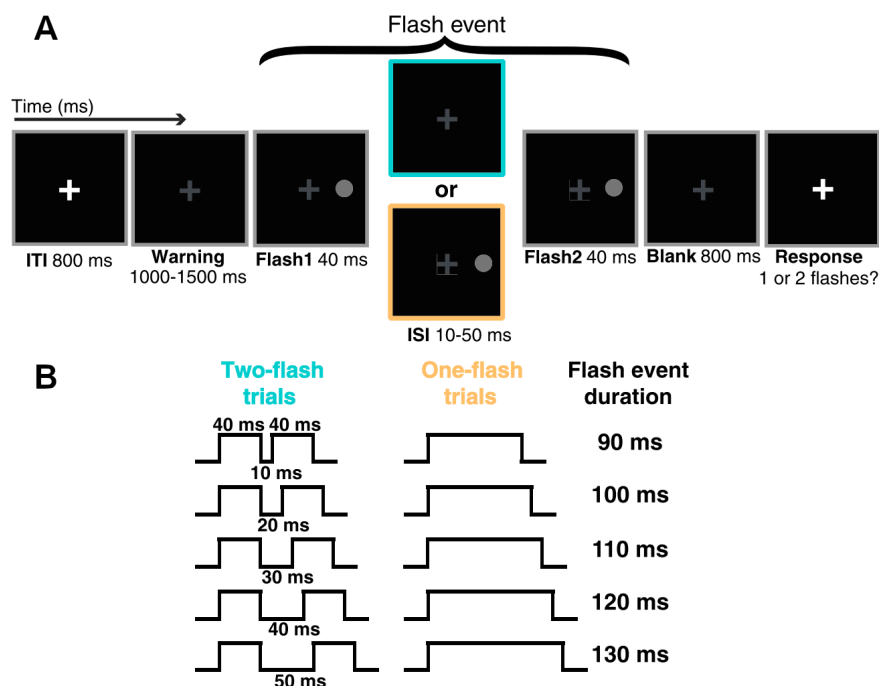
Kayser, J., & Tenke, C. E. (2015). On the benefits of using surface Laplacian (Current Source Density) methodology in electrophysiology. *International Journal of Psychophysiology* , 97 (3), 171–173. <https://doi.org/10.1016/j.ijpsycho.2015.06.001>

Keil, J., & Senkowski, D. (2018). Neural Oscillations Orchestrate Multisensory Processing. *Neuroscientist* , 24 (6), 609–626. <https://doi.org/10.1177/1073858418755352>

Keitel, C., Ruzzoli, M., Dugué, L., Busch, N. A., & Benwell, C. S. Y. (2022). Rhythms in cognition: The evidence revisited. *European Journal of Neuroscience* , 55 (11–12), 2991–3009. <https://doi.org/10.1111/ejn.15740>

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences* ,16 (12), 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>

- Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus α phase predicts visual awareness. *Journal of Neuroscience* , 29 (9), 2725–2732. <https://doi.org/10.1523/JNEUROSCI.3963-08.2009>
- Michail, G., Toran Jenner, L., & Keil, J. (2022). Prestimulus alpha power but not phase influences visual discrimination of long-duration visual stimuli. *European Journal of Neuroscience* ,55 (11–12), 3141–3153. <https://doi.org/10.1111/ejn.15169>
- Morrow, A., & Samaha, J. (2022). No evidence for a single oscillator underlying discrete visual percepts. *European Journal of Neuroscience* , 55 (11–12), 3054–3066. <https://doi.org/10.1111/ejn.15362>
- Nelli, S., Itthipuripat, S., Srinivasan, R., & Serences, J. T. (2017). Fluctuations in instantaneous frequency predict alpha amplitude during visual perception. *Nature Communications* , 8 (1). <https://doi.org/10.1038/s41467-017-02176-x>
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottetereaur, B. R., & Rossion, B. (2015). The steady state VEP in research. *Journal of Vision* , 15 (6), 1–46. <https://doi.org/10.1167/15.6.4>.doi
- Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology* , 112 (4), 713–719. [https://doi.org/10.1016/S1388-2457\(00\)00527-7](https://doi.org/10.1016/S1388-2457(00)00527-7)
- Pfurtscheller, G., Stancák, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band - An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology* , 24 (1–2), 39–46. [https://doi.org/10.1016/S0167-8760\(96\)00066-9](https://doi.org/10.1016/S0167-8760(96)00066-9)
- Posit team (2023). *RStudio: Integrated Development Environment for R* (Version 2023.3.0.386). Posit Software, PBC, Boston, MA. <http://www.posit.co/>
- Prins, N. & Kingdom, F. A. A. (2018). Applying the Model-Comparison Approach to Test Specific Research Hypotheses in Psychophysical Research Using the Palamedes Toolbox. *Frontiers in psychology*, 9:1250 . <https://doi.org/10.3389/fpsyg.2018.01250>
- R Core Team (2022). *R: A language and environment for statistical computing* (Version 4.2.1). R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by modulated light. *Electroencephalography and Clinical Neurophysiology* ,20 (3), 238–248. [https://doi.org/10.1016/0013-4694\(66\)90088-5](https://doi.org/10.1016/0013-4694(66)90088-5)
- Ruzzoli, M., Torralba, M., Morís Fernández, L., & Soto-Faraco, S. (2019). The relevance of alpha phase in human perception. *Cortex* ,120 , 249–268. <https://doi.org/10.1016/j.cortex.2019.05.012>
- Samaha, J., & Postle, B. R. (2015). The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception. *Current Biology* , 25 (22), 1–6. <https://doi.org/10.1016/j.cub.2015.10.007>
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences* , 32 (1), 9–18. <https://doi.org/10.1016/j.tins.2008.09.012>
- The MathWorks Inc. (2022). Statistics and Machine Learning Toolbox Documentation, Natick, Massachusetts: The MathWorks Inc. <https://www.mathworks.com/help/stats/index.html>
- VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognitive Sciences* , 7 (5), 207–213. [https://doi.org/10.1016/S1364-6613\(03\)00095-0](https://doi.org/10.1016/S1364-6613(03)00095-0)
- Voeten, C. C. (2022). *permutes: Permutation Tests for Time Series Data* (Version 2.6) [R package]. <https://CRAN.R-project.org/package=permutes>
- Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences* , 7 (12), 553–559. <https://doi.org/10.1016/j.tics.2003.10.012>



Hosted file

Fig2.tiff available at <https://authorea.com/users/778989/articles/914545-alpha-band-oscillations-and-visual-temporal-resolution-an-expansion-and-partial-replication-of-samaha-postle-s-2015-study-the-speed-of-alpha-band-oscillations-predicts-the-temporal-resolution-of-visual-perception>

Hosted file

Fig3.tiff available at <https://authorea.com/users/778989/articles/914545-alpha-band-oscillations-and-visual-temporal-resolution-an-expansion-and-partial-replication-of-samaha-postle-s-2015-study-the-speed-of-alpha-band-oscillations-predicts-the-temporal-resolution-of-visual-perception>

Hosted file

Fig4.tiff available at <https://authorea.com/users/778989/articles/914545-alpha-band-oscillations-and-visual-temporal-resolution-an-expansion-and-partial-replication-of-samaha-postle-s-2015-study-the-speed-of-alpha-band-oscillations-predicts-the-temporal-resolution-of-visual-perception>