

## Research report

# The relationship between individual alpha frequency and time perception: Testing the internal clock versus the sampling rate hypothesis



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## ABSTRACT

Perceiving the duration of events is a fundamental ability for everyday life. Traditional research has focused on the role of alpha oscillations as an endogenous pacemaker for the human internal clock, yet there is limited evidence supporting this idea. An alternative hypothesis proposes that alpha oscillations may underlie a sampling mechanism, where higher alpha frequencies correspond to increased information sampling, resulting in more accurate temporal judgments. In this study, we tested the internal clock versus sampling rate hypothesis by examining the relationship between Individual Alpha Frequency (IAF) and fine-grained time perception. Using resting Electroencephalography (EEG) and Signal Detection Theory (SDT), fifty healthy volunteers performed a time-discrimination task with 100 and 500 msec standard durations. Our results demonstrate that temporal sensitivity ( $d'$ ) but not temporal bias ( $c$ ) is influenced by IAF, with higher IAF leading to more accurate time estimates (higher  $d'$ ). The correlations were observed over frontocentral topographies consistent with previous reports of neural networks involved in time processing and were most pronounced at 100 msec relative to 500 msec, likely due to fluctuations in IAF across multiple cycles. In conclusion, our findings support the relationship between IAF and temporal sensitivity. These results challenge the pacemaker hypothesis and instead suggest a distributed mechanism where alpha oscillations enhance the precision of temporal sampling. Our study adds to the growing body of evidence highlighting the role of IAF in sensory sampling as a generative mechanism for temporal sensitivity as opposed to subjective time perception.

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## 1. Introduction

The perception of time is a key component of human cognition, yet its neural mechanisms remain only partially understood. Alpha oscillations were the first to attract attention as a potential source of temporal information (Ellingson, 1956; Legg, 1968). As spontaneous brain waves associated with the level of consciousness (Klimesch, 2012), with an average cycle period of 100 msec, they represented an ideal candidate for the “psychologically indivisible unit of time” (Anliker, 1963). However, their association with time perception has never been clearly established (Azizi et al., 2023; Kononowicz & van Wassenhove, 2016; Legg, 1968).

Recent evidence has reignited interest in the role of alpha-band activity in temporal processing (Samaha & Romei, 2024a; 2024b). For example, Samaha and Postle (2015) showed that Individual Alpha Frequency (IAF) predicts the visual sampling rate, measured as the accuracy of detecting two (*vs* one) consecutive flashes separated by a small interval (i.e., the two-flash fusion phenomenon; Ronconi et al., 2024; Deodato & Melcher, 2024). Similarly, individuals with higher IAF have been shown to be more sensitive at detecting visual contrast differences (Tarasi & Romei, 2024). Taken together, these findings suggest that alpha oscillations may serve as a visual sampling mechanism (VanRullen & Koch, 2003), where higher frequencies would lead to higher temporal resolution and more accurate perceptual experience (Cecere et al., 2015; Di Gregorio et al., 2022; Trajkovic et al., 2024).

Building on this framework, we propose that IAF could serve as a temporal unit of information processing. According to this model, time perception would emerge from the dynamic interplay between internal computational capacity, governed by IAF, and the stream of external sensory information. Specifically, greater information accumulation is expected to result in more precise temporal judgments. Accordingly, we hypothesize that higher IAF would enhance temporal sensitivity, improving the ability to discriminate fine differences between two temporal intervals.

As an alternative hypothesis, IAF has been proposed to relate to the functional unit of temporal counting, for time pacing and accumulation. From this perspective, IAF would be the individual meter of temporal subjective estimation and thus associated with temporal bias rather than accuracy. Indeed, a clock-like model has traditionally been proposed to explain the ability to perceive time, with an internal pacemaker emitting pulses at the beginning of the interval to be timed, and an accumulator summing up the pulses produced (pacemaker-accumulator model; Treisman, 1963; Treisman et al., 1994). That is, the more pulses accumulated, the longer the perceived duration. In a significant variation of this model, the pulse rate of the pacemaker is thought to be driven by alpha oscillations (range 7–13 Hz; Treisman, 1963; Treisman et al., 1994), which would represent the neural ‘ticks’ of the endogenous clock and thus serve as the source of

temporal information. However, the evidence for this relationship remains limited. Recently, a neurostimulation study, by means of transcranial alternating current stimulation (tACS) delivered over occipital areas during a time generalization task, showed that tACS delivered at off-peak alpha frequencies increased (IAF+2Hz) as well as decreased (IAF-2Hz) the perceived duration, highlighting a potential role for alpha rhythms in temporal biases (Mioni et al., 2020). Nevertheless, subsequent work did not replicate these findings (Mokhtarinejad et al., 2024), highlighting the need for further investigation.

More generally, in the current literature it largely remains to be established how to disentangle the specific contribution of perceptual sensitivity and bias to time estimation.

In particular, the ability to discriminate durations accurately, independently of response biases (e.g., tendency to overestimate or underestimate intervals) has been largely overlooked. To date, no computational model of time perception has been empirically tested. While Signal Detection Theory (SDT; Green & Swets, 1966) was developed to identify near-threshold stimuli, parameters like the Point of Subjective Equality (PSE; i.e., the subjective perception that two stimuli have the same duration; see below) have been preferred in the classic domain of time perception (Bausenhardt et al., 2018). This is surprising, considering that it has long been established that time perception is significantly influenced by response biases. For example, a well-known finding is that the comparison of two successively presented stimuli can be influenced by the order in which the stimuli are presented (Fechner, 1966; Jamieson & Petrusic, 1975). Given these factors, we introduce here Signal Detection Theory (SDT) in the study of time perception and its relation to alpha oscillations, with the aim of disentangling its potential function in temporal processing and whether the underlying neural computations serve sensory information sampling processes rather than temporal reference frames.

According to the sampling rate hypothesis, we predict that faster IAF should lead to more precise temporal estimation (as measured through  $d'$ ), with no impact on perceptual bias (as measured through criterion). On the contrary, according to the internal clock hypothesis, faster IAF should lead to overestimation of time passing (as measured through criterion), with no impact on time sensitivity (as measured through  $d'$ ).

To this aim, we investigated whether inter-individual differences in time perception can be explained by inter-individual differences in trait alpha frequency as measured by resting EEG. Participants completed two temporal discrimination tasks (“short” and “long” stimulus durations) in which they had to judge which of two stimuli lasted longer. We hypothesized faster IAF to enhance sensitivity in discriminating temporal intervals, with a stronger effect expected in the short-duration task (standard: 100 msec; comparisons: 10–90 msec, 110–190 msec) compared to the long-duration task (standard: 500 msec; comparisons: 50–450 msec, 550–950 msec). At longer durations, which

encompass multiple alpha cycles, we anticipated a reduced influence of IAF, as additional cognitive processes as well as spontaneous fluctuations in alpha frequency likely intervene and likely contribute to IAF variations. Given the ongoing debate regarding the existence of a “gold duration” or critical interval within the subsecond range (Grondin, 2019, 2024), we selected 100 msec as the minimum duration reported in the literature, corresponding to the average alpha cycle. Additionally, we included a task with a 500 msec standard, enabling us to reach durations approaching 1 s (i.e., 950 msec) with comparison stimuli and thereby cover the entire subsecond range. This should allow us to appreciate effects in both cases with a stronger effect at the shorter duration.

## 2. Methods

### 2.1. Participants

Statistical analyses were performed on a total sample of 50 participants (19 male participants; aged 19–32 years), after excluding 2 outliers with an accuracy score more than two standard deviations ( $\pm$ ) from the group mean on both temporal discrimination tasks. The sample size of 50 participants was chosen based on the recommendations from the meta-analysis conducted by Samaha and Romei (2024b). All participants signed a written informed consent before taking part in the study, which was conducted in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna (n. 0299334, 09/11/2022). All participants had no neurocognitive or psychiatric disorders.

### 2.2. Experimental procedure

The experiment consisted of two discrimination tasks in a two-alternative forced-choice (2AFC) paradigm (Fig. 1): a temporal task with short durations (“Short/100 msec”) and another with long durations (“Long/500 msec”). We selected these two durations (100 msec and 500 msec) to capture different temporal dynamics: 100 msec aligns with the average alpha cycle, allowing us to test its direct influence on time perception, while 500 msec extends the range to

encompass longer intervals where additional cognitive processes, such as working memory, but also fluctuations in IAF may contribute, offering a broader view of temporal sensitivity across the subsecond range.

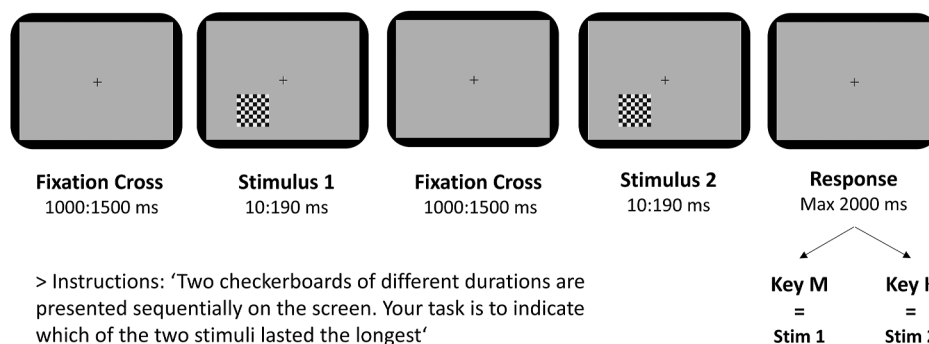
Each participant performed both tasks, and the order of tasks was counterbalanced across subjects.

Two checkerboards were presented sequentially on the screen. Participants were instructed to use the keyboard to indicate whether the first (“m” key) or the second (“k” key) stimulus was the one lasting longer. A fixed contrast level (RGB 35/220; Tarasi & Romei, 2024) was used, while the duration of the stimulus presentation was varied.

Within each task, the “standard” stimulus remained constant in duration across trials, while the “comparison” stimulus varied (‘method of comparison’; Grondin, 2010). Importantly, standard and comparison stimuli were never identical in duration, thereby preventing ambiguous responses and ensuring that all trials contributed meaningfully to the estimation of temporal discrimination sensitivity. Specifically, the comparison differed from the standard by a “% ratio difference” (or delta) ranging from  $\pm 10\%$  to  $\pm 90\%$ . As a result, comparison durations in the short task ranged from 10 to 90 and 110 to 190 msec, while in the long task they ranged from 50 to 450 msec and 550 to 950 msec.

The order of presentation of the standard and comparison intervals was randomized and counterbalanced across trials (‘roving method’; Macmillan & Creelman, 1991; Bausenhardt et al., 2018). In half of the trials, the standard was presented first; in the other half, it was presented second. Although participants were not informed about the standard explicitly, its fixed value across trials is known to promote the formation of an internal standard (Dyjas, Bausenhardt & Ulrich, 2012), which serves as a reference even under randomized presentation order. Each trial started with a Fixation Cross (jittered duration: 1000–1500 msec) followed by the presentation of the first stimulus, and after a variable inter-stimulus interval (ISI; jittered: 1000–1500 msec), the second stimulus was presented. Participants were then prompted to respond (max 2000 msec) (Fig. 1).

Each participant completed 360 trials per task, for a total of 720 trials across the experiment. In half of the trials (180), the standard stimulus was presented first, while in the remaining



**Fig. 1 – Experimental paradigm.** The figure illustrates the structure of the experimental paradigm for the Short Temporal Task (100 msec). Participants were presented with two checkerboards separated by a fixation cross and were asked to judge which of the two lasted longer. They had 2 sec to respond by pressing the “m” key for the first stimulus or the “k” key for the second stimulus. The procedure for the Long Temporal Task (500 msec) was identical, with the only difference being the duration of stimulus presentation.

half, the comparison stimulus was presented first. For each level of % ratio difference between the standard and comparison stimuli (i.e.,  $\pm 10\%$ ,  $\pm 20\%$ , ...,  $\pm 90\%$ ), participants performed 20 trials. The entire experiment was conducted in a single experimental session, which included three short breaks: one halfway through each task, and one between the two tasks. Stimuli were presented on an 18-inch CRT display (display resolution  $1280 \times 1024$  pixels, refresh rate 100 Hz) at a distance of  $\sim 57$  cm in a dimly lit room. The 100 Hz refresh rate corresponds to frame durations of 10 msec, allowing for precise timing of the standard stimuli at 100 msec and 500 msec (i.e., 10 and 50 frames, respectively). This refresh rate was used consistently across all participants and sessions to ensure accurate temporal presentation. The luminance of the CRT display was gamma-corrected. Participants were seated in a comfortable chair in front of the monitor. Stimuli were generated and presented using MATLAB (version 2016, The MathWorks Inc.) and the Psychophysics Toolbox. The visual stimuli were  $8 \times 8$  black and white checkerboards that appeared in the lower left visual field (Tarasi & Romei, 2024). The checkerboards presented contained iso-luminant gray circles within each of the cells.

### 2.3. EEG acquisition and data analysis

Participants comfortably sat in a room with dimmed lights. EEG was recorded at rest for 2 min, while participants kept their eyes closed. A set of 64 electrodes was mounted according to the International 10–10 system. EEG was referenced to FCz electrode, and all impedances were kept below 10 k  $\Omega$ . EEG signals were acquired at a rate of 1000 Hz. EEG was preprocessed offline with custom MATLAB scripts (Version R2020b) and with the EEGLAB toolbox (Delorme 2004). The EEG recording was filtered offline in the .5-to-70 Hz band. The signals were visually inspected. Noisy channels were spherically interpolated, and recording segments corrupted by artifacts were eliminated. The recording was then re-referenced to the average of all electrodes.

We conducted the analyses considering all the 64 electrodes.

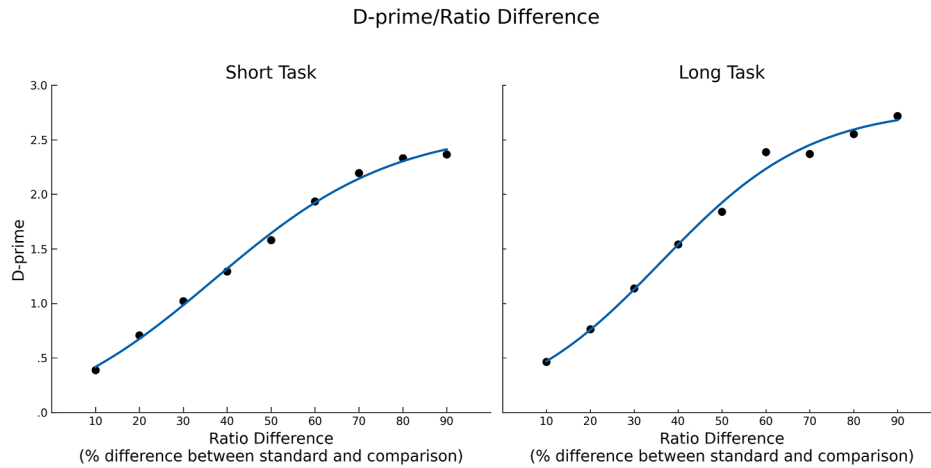
Using the pwelch function in MATLAB (2-sec Hanning window with 25% of overlap), we computed the power spectral density and defined the trait IAF as the local maximum of the spectrum within the frequency range 7–13 Hz. We repeated the same procedure for each electrode separately. The average peak of alpha was centered at  $10.30 \pm .08$  Hz.

Akin to the mechanism described in visual processing (Di Gregorio et al., 2022; Tarasi & Romei, 2024; Trajkovic et al., 2024), we hypothesized that faster alpha oscillations, measured as Individual Alpha Frequency (IAF), would correspond to a more precise/sensitive temporal judgment. Specifically, this precision would manifest as greater sensitivity to differences between two temporal intervals. To test this hypothesis, we adopted a Signal Detection Theory (SDT) approach (Green & Swets, 1966), a robust psychophysical method that isolates sensitivity ( $d'$ ) from perceptual bias (criterion,  $c$ ). Trials were categorized based on the physical relationship between the comparison and standard intervals, independently of presentation order. Comparisons longer than the standard (e.g., 110 msec vs 100 msec) were

considered signal-present (target trials), while shorter comparisons (e.g., 90 msec vs 100 msec) were treated as signal-absent (non-target trials). A “longer” response to a target was coded as a hit, and a “shorter” response as a miss. Conversely, a “longer” response to a non-target was classified as a false alarm, and a “shorter” response as a correct rejection. For example, judging a 90 msec comparison as longer than a 100 msec standard constituted a false alarm. This method allowed us to operationalize the criterion not in terms of positional bias (first vs second interval), but rather as a measure of temporal under- or overestimation bias. This conceptualization follows the established use of SDT criterion as a continuous measure of perceptual bias in visual perception research (e.g., Di Gregorio et al., 2022), which we adapt here to examine temporal estimation biases. For the sensitivity analysis,  $d'$  values (where higher values indicate higher sensitivity) were calculated as a function of the % ratio difference for each task (Fig. 2). A psychometric sigmoid function was fitted for each participant on the extracted  $d'$  values [ $y = a + b / (1 + \exp(-(x - c) / d))$ ; Cecere, 2015], where  $a$  is the upper asymptote,  $b$  the lower asymptote,  $c$  the inflection point, and  $d$  the slope. The inflection point parameter  $c$  provides an objective index of the stimulus value at which the response function changes most rapidly, corresponding to the point of maximal sensitivity gain. Lower inflection points indicate better performance at smaller interval differences, while steeper slopes reflect greater sensitivity to small changes in temporal duration. Participants were excluded if the sigmoid model showed poor fit quality (adjusted  $R^2 < .5$ ), in line with prior studies (Deister et al., 2024). This criterion ensured robust estimation of sensitivity parameters and was independent of behavioral accuracy or EEG features. Importantly, all excluded participants exhibited IAF values within the canonical alpha range (7–13 Hz), and there were no signs of abnormal EEG patterns. The exclusion reflects insufficient model fit rather than poor task engagement or deviant physiology.

We conducted Spearman correlation analyses to investigate the relationship between IAF values (extracted from each EEG channel) and the individual inflection point and slope parameters. To explore the spatial specificity of the IAF effect on performance, we performed a cluster-based permutation analysis. This involved calculating the correlation between IAF and behavioral performance (inflection point and slope) for each electrode and assessed the number of neighboring electrodes with a significant relationship ( $p < .05$ ). To evaluate the significance of the spatial clusters, we ran a permutation test ( $n = 2000$ ), shuffling the relationship between IAF and behavioral performance separately for the inflection point and slope. The number of neighboring electrodes in the real data was then compared with the permuted data. Clusters in the real data were deemed statistically significant at  $\alpha = .05$  if their size exceeded the 95th percentile of the null distribution.

We also investigated whether time overestimation or underestimation correlates with IAF, consistent with the pace-maker hypothesis. Temporal bias was quantified using two measures: response bias (criterion,  $c$ ) and Point-of-Subjective Equality (PSE). For response bias, we conducted a series of one-sample  $t$ -tests on individual  $c$  values to assess the presence of temporal bias. Values of  $c$  significantly different from

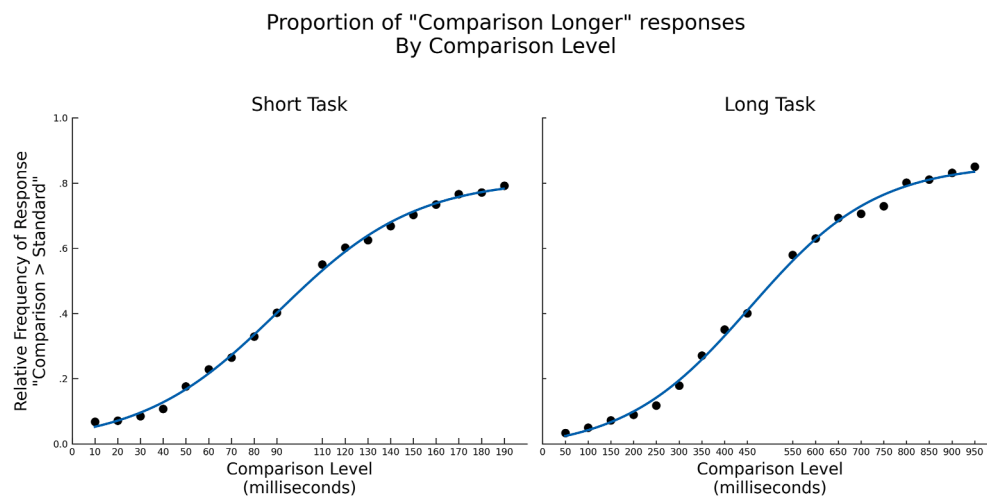


**Fig. 2 – Sensitivity ( $d'$ ) as a function of the percentage difference between the standard stimulus and the comparison. The points represent the average  $d'$  value calculated across participants for each level of ratio difference in the Short Temporal Task (standard: 100 msec; on the left) and in the Long Temporal Task (standard: 500 msec; on the right).**

0 indicate bias: positive  $c$  values correspond to a conservative criterion (temporal underestimation), where even large differences between standard and comparison are judged cautiously; conversely, negative  $c$  values correspond to a liberal criterion (temporal overestimation), where participants are more likely to judge the comparison as longer than the standard, regardless of the actual difference between intervals. Given that we did not expect a strong relationship between criterion and IAF, we complemented traditional correlation analyses with Bayesian correlation analyses to provide evidence supporting the absence of such a relationship. Specifically, Bayesian correlations were conducted on IAF averaged across a cluster of central electrodes (Cz, C2, C4) separately for each temporal task, allowing us to quantify the

strength of evidence in favor of the null hypothesis (no correlation).

As a second measure, we calculated the PSE, which reflects the perceived equivalence between standard and comparison intervals (Block et al., 2018). This can be interpreted as an index of perceived duration. A PSE value shorter than the standard interval indicates that the comparison interval is more often perceived as longer than the standard, reflecting an overestimation bias. Conversely, a PSE value longer than the standard suggests a tendency to underestimate the comparison interval (Grondin, 2024). To measure the PSE, we plotted the probability of responding "comparison > standard" as a function of comparison duration for each task (Fig. 3). A psychometric sigmoid function was fitted for each participant



**Fig. 3 – Proportion of responses in which the comparison stimulus was judged to have a longer duration than the standard, as a function of the comparison duration (in milliseconds). Black dots represent the mean proportion across participants for each comparison duration level in the Short Temporal Task (standard 100 msec; comparison durations: 10–90 msec and 110–190 msec; on the left) and in the Long Temporal Task (standard 500 msec; comparison durations: 50–450 msec and 550–950 msec; on the right).**

$[y = a+b/(1 + \exp(-(x-c)/d))]$ ; Cecere et al., 2015], and PSE was defined as the comparison level (x-axis) corresponding to the 0,5 on the y-axis (Block et al., 2018).

To further validate our interpretation of the criterion as a measure of temporal bias (rather than positional bias), we examined its relationship with the PSE. Although derived from different modeling frameworks, both indices are sensitive to systematic distortions in perceived duration. We therefore conducted a correlation analysis between individual  $c$  values and PSEs, testing the hypothesis that participants with a conservative response bias (i.e., temporal underestimation) would also require longer comparison intervals to perceive them as equal to the standard. This approach allowed us to assess whether these two independent measures converge in capturing a common underlying temporal bias.

Then, we performed Spearman correlation analyses to examine the relationship between IAF values extracted from each EEG channel and individual measures of criterion and PSE.

To assess potential time-order effects on our measures, we conducted supplementary analyses comparing PSE values between trials where the standard interval was presented first versus second. This analysis was performed to evaluate whether systematic biases related to presentation order could account for the observed temporal underestimation patterns or their relationship with alpha frequency. PSE values were calculated separately for each presentation order condition using the same sigmoid fitting procedure described above.

### 3. Results

We investigated the role of alpha pace on time perception using a Signal Detection Theory (SDT) approach.  $d'$  was computed for each time ratio and a sigmoid function  $[y = a+b/(1 + \exp(-(x-c)/d))]$ ; Cecere et al., 2015] was fitted on  $d'$  values (Fig. 1). Sensitivity was assessed through two measures: inflection point and slope index. We hypothesized that participants with higher IAF would demonstrate greater sensitivity in discriminating between temporal intervals, as reflected by an earlier inflection point and a steeper slope.

For the sensitivity analysis, a total of 39 participants were retained for the Short Temporal Task (Standard 100) and 43 participants for the Long Temporal Task (Standard 500). The others were discarded because the curves did not fit or the Adjusted R2 was less than .5 (Deister et al., 2024). This ensured that key parameters (inflection point and slope) were derived from meaningful psychometric data. Exclusions were unrelated to behavioral accuracy or EEG profiles; all participants showed typical alpha IAFs (7–13 Hz) and no abnormal spectral features. Poor fits likely reflected intra-individual variability rather than atypical perception. This conservative criterion prioritized psychometric robustness over sample size.

We conducted a Spearman correlation analysis between the inflection point and slope measures and estimated IAF for each channel. A frontocentral effect emerged in the Short Temporal Task (Fig. 4A). Specifically, permutation-based statistical analysis revealed a significant negative correlation between the inflection point and the IAF in a cluster of

frontocentral electrodes (AF3, AF7, AF8, AFz, C1, C2, C4, C5, CP6, Cz, F1, F3, F5, F6, F7, F8, FC5, FC6, Fp1, Fp2, FT7, FT9; Fig. 4A). This finding suggests that faster alpha oscillations are associated with an earlier inflection point. In other words, participants with higher IAF values appear to achieve optimal performance with smaller differences between temporal intervals.

A similar pattern was found for the slope index in the Short Temporal Task (AF3, AF4, AF7, AF8, AFz, C1, C2, CP2, CPz, Cz, F2, F4, F6, F7, F8, FC1, FC2, FC4, FC6, Fp1, Fp2, FT10, FT8, FT9; Fig. 4A). This indicates that faster alpha oscillations are linked to a steeper slope, meaning that small changes in temporal interval differences lead to more pronounced improvements in discrimination performance.

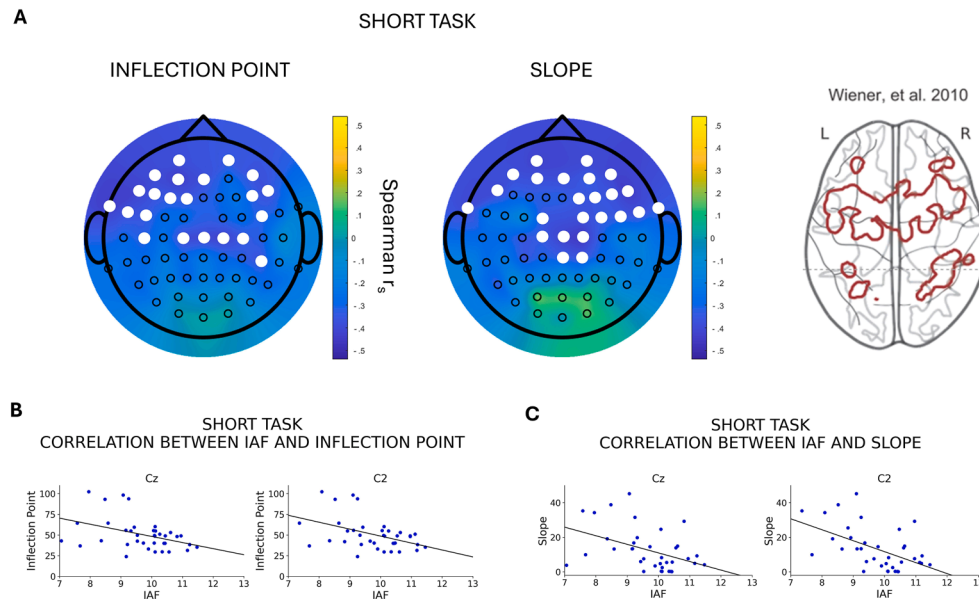
Furthermore, a similar but weaker effect was observed in the Long Temporal Task regarding the inflection point (C1, C2, C4, C6, CP1, CP4, CP6, Cz; Fig. 5A), while no significant effect emerged for the slope index. This suggests that the relationship between IAF and temporal sensitivity extends across different interval durations, albeit with diminished strength for longer intervals, in line with our hypothesis.

In order to test the pacemaker hypothesis, we evaluated temporal bias using criterion ( $c$ ) and PSE measures, and we did not expect a correlation with alpha frequency. These measures were calculated for 50 participants in each task.

We observed a positive criterion in both tasks, indicating that participants tended to underestimate the comparison interval (Short Temporal Task:  $c = .20$ ; Long Temporal Task  $c = .15$ ;  $p < .001$ , one-sample  $t$ -test). This conservative bias suggests that participants remained cautious in their judgments, even when the difference between the standard and comparison intervals was large. Crucially, there was no correlation between the criterion and IAF (Fig. 6). This null result was further supported by Bayesian correlation analyses conducted on IAF averaged across central electrodes (Cz, C2, C4), which yielded Bayes Factors indicating moderate evidence in favor of the absence of a relationship (Short Temporal Task:  $BF_{10} = .196$ ; Long Temporal Task:  $BF_{10} = .238$ ).

Regarding the Point-of-Subjective Equality (PSE), participants consistently exhibited an underestimation bias in both tasks (with intervals of 105.6 msec and 515.2 msec perceived, on average, as 100 msec and 500 msec, respectively;  $p < .001$ , one-sample  $t$ -test). Interpreting the PSE as an index of perceived duration, these results suggest that in both temporal tasks, participants typically perceived the comparison interval as shorter than the standard. However, as with the criterion, no correlation was observed between PSE and IAF (Fig. 7). Interestingly, these shifts in criterion and PSE do not correlate with IAF, once again confirming the independence of IAF in accounting for precision estimation rather than perceptual bias in time estimation.

However, we found a significant positive correlation between criterion and PSE in both tasks (Spearman's Correlation: Short Temporal Task:  $r_s = .55$ ,  $p < .0001$ ; Long Temporal Task:  $r_s = .71$ ,  $p < .0001$ ; Fig. 8). That is, participants with a more conservative criterion (i.e., a tendency to judge comparison intervals as shorter than the standard) also exhibited higher PSEs (i.e., required longer comparisons to perceive equality). This convergence supports our interpretation of the criterion not as a positional bias, but as an index of temporal



**Fig. 4** – Results of the sensitivity analysis for the Short Temporal Task. **A.** Topographical maps show significant negative correlations between individual alpha frequency (IAF) and two sensitivity measures: inflection point (left) and slope (center). White markers indicate electrodes where permutation-based cluster analysis identified significant effects ( $p < .05$ , cluster corrected). A faster IAF was associated with an earlier inflection point and a steeper slope (note: lower slope values indicate greater steepness), suggesting enhanced temporal sensitivity. The right panel shows a meta-analytic timing network, as presented in Wiener (2024), originally based on data from Wiener et al. (2010). The network is projected onto a glass brain, illustrating overlap between the observed frontocentral effects and regions typically implicated in timing. **B.** Scatterplots showing the relationship between IAF and inflection point in two representative electrodes: Cz (left) and C2 (right). Each blue dot represents an individual participant's data point, with IAF on the x-axis and inflection point on the y-axis. The black line represents the best-fitting linear trend. Higher IAF values are associated with lower inflection points, supporting the hypothesis that faster alpha rhythms enhance temporal discrimination (Spearman correlations: Cz:  $r_s = -.42$ ,  $p < .05$ ; C2:  $r_s = -.43$ ,  $p < .01$ ). **C.** Scatterplots showing the correlation between IAF and slope index in Cz (left) and C2 (right). A higher IAF is associated with steeper slopes (i.e., lower slope values indicate greater steepness), meaning smaller differences between comparison and standard intervals produced sharper transitions in decision performance [Spearman correlations: Cz:  $r_s = -.43$ ,  $p < .01$ ; C2:  $r_s = -.47$ ,  $p < .005$ ].

underestimation—and more broadly, demonstrates that both measures reflect a common underlying bias in time perception. Interestingly, these shifts in criterion and PSE do not correlate with IAF, once again confirming the independence of IAF in accounting for precision estimation rather than perceptual bias in time estimation.

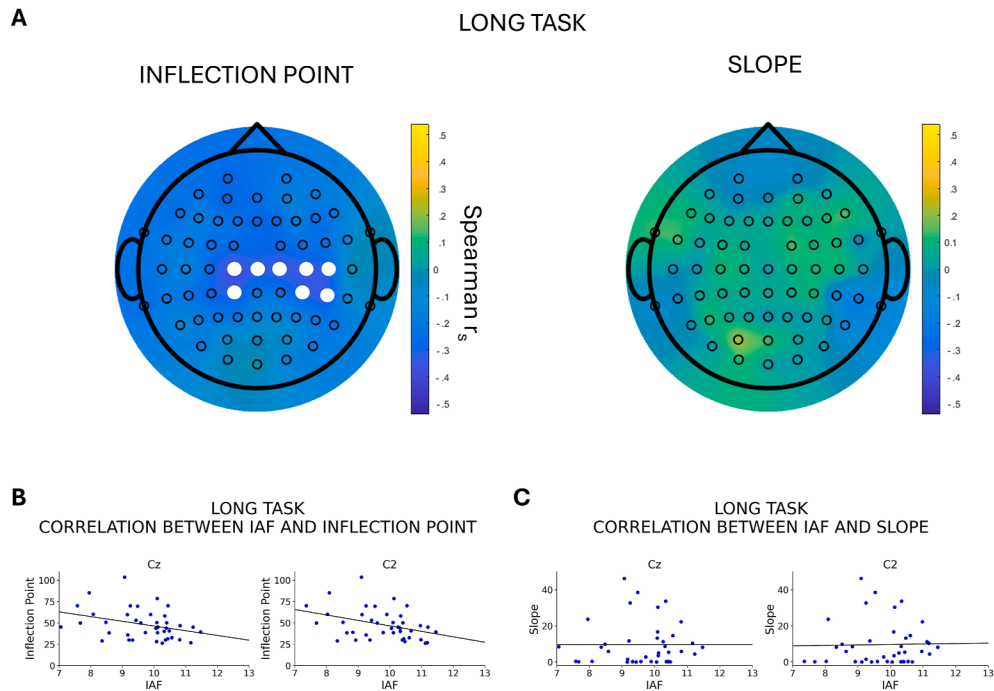
To assess potential time-order effects, we compared PSE values between trials where the standard appeared first versus second. In the short-duration task, PSE was 105.42 msec (SD = 31.07,  $N = 49$ ) for standard-first trials and 110.41 msec (SD = 20.27,  $N = 43$ ) for standard-second trials ( $t(90) = -.92$ ,  $p = .36$ ). Similarly, in the long-duration task, PSE was 495.10 msec (SD = 86.34,  $N = 49$ ) for standard-first and 534.41 msec (SD = 180.39,  $N = 46$ ) for standard-second trials ( $t(93) = -1.37$ ,  $p = .17$ ). These non-significant differences suggest that time-order effects are unlikely to systematically drive the observed shifts in PSE or the modulation by alpha activity.

Overall, these findings challenge the hypothesis that alpha frequency influences subjective perceived duration, while supporting the idea that faster (vs slower) alpha oscillations are linked to higher (vs lower) precision in the perception of interval differences.

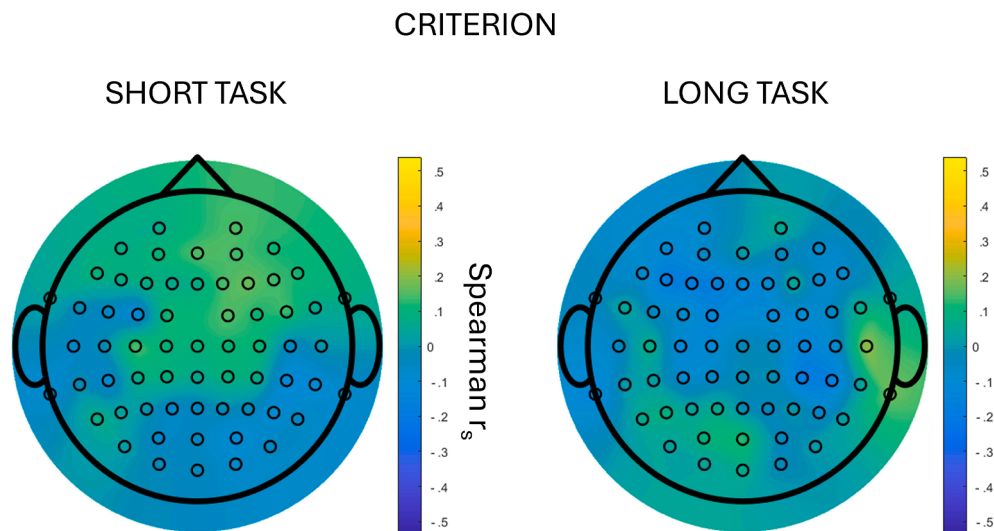
#### 4. Discussion

The aim of the present study was to investigate the oscillatory correlates of time perception, with a focus on the role of Individual Alpha Frequency (IAF) in temporal sensitivity and bias. Specifically, we examined whether higher IAF is associated with improved temporal sensitivity rather than introducing a perceptual bias when discriminating temporal durations of sub-second stimulus durations. Our findings support the notion that faster alpha oscillations enhance sensitivity in temporal judgments, particularly for durations close to the alpha cycle (i.e., 100 msec). This effect is most prominent in frontocentral regions, which are commonly involved in prospective timing tasks (Wiener, 2024).

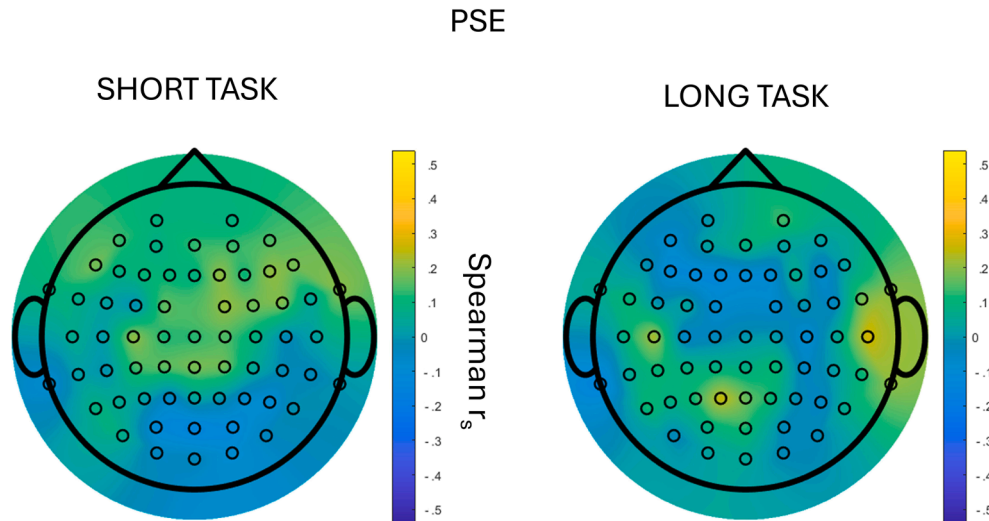
On the other hand, we could discard the alternative hypothesis that IAF could account for perceptual bias in time perception. Indeed, we did not find any relationship between indices of temporal bias and IAF. In particular, we have employed both classical measures of temporal bias (i.e., PSE) and signal detection theory derived measure of bias (i.e., criterion). Importantly, by examining the relationship between



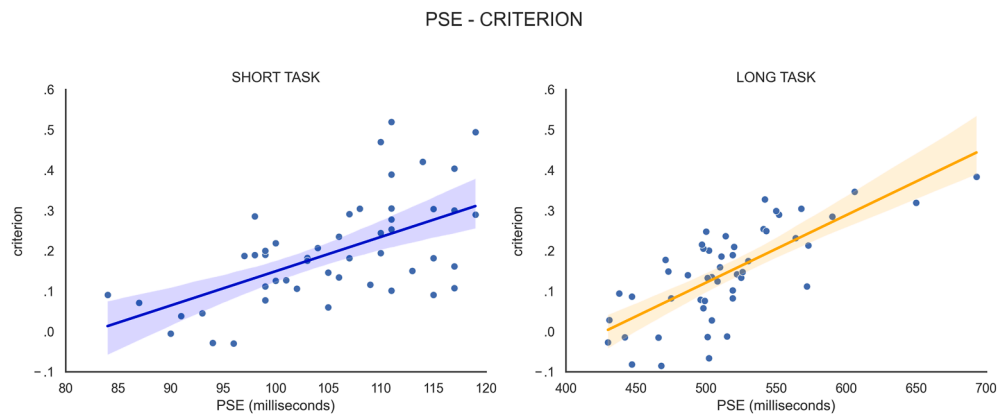
**Fig. 5 – Results of the sensitivity analysis for the Long Temporal Task. A.** Topographical maps showing significant negative correlations between individual alpha frequency (IAF) and two sensitivity measures: inflection point (left) and slope (right). White markers indicate electrodes where permutation-based cluster analysis identified significant effects ( $p < .05$ , cluster corrected). In the Long Temporal Task (500 msec), a faster IAF was associated with an earlier inflection point (left panel), while no significant correlation was found with slope (right panel). **B.** Scatterplots depicting the relationship between IAF and inflection point at two representative electrodes: Cz (left) and C2 (right). Each blue dot represents an individual participant's data point, with IAF on the x-axis and inflection point on the y-axis. The black line shows the best-fitting linear trend. Higher IAF values correspond to lower inflection points, indicating that faster alpha rhythms are linked to earlier temporal sensitivity (Spearman correlations: Cz:  $r_s = -.33$ ,  $p < .05$ ; C2:  $r_s = -.36$ ,  $p < .05$ ). **C.** Scatterplots illustrating the correlation between IAF and slope index in Cz (left) and C2 (right). Unlike the Short Temporal Task, no significant associations were found between IAF and slope in the Long Temporal Task (Spearman correlations: Cz:  $r_s = .01$ ,  $p = .94$ ; C2:  $r_s = .08$ ,  $p = .61$ ).



**Fig. 6 – Absence of a relationship between criterion and IAF across the two tasks.** Colors represent the Spearman correlation coefficient ( $r$ ), indicating the strength and direction of the correlation between Individual Alpha Frequency (IAF) and response bias, with no evidence of significant channels.



**Fig. 7 – Absence of a relationship between the Point of Subjective Equality (PSE) and IAF across the two tasks. The colors represent the Spearman correlation coefficient ( $r_s$ ), indicating the strength and direction of the correlation between Individual Alpha Frequency (IAF) and the PSE, with no significant channels observed.**



**Fig. 8 – Correlation between Point-of-Subjective Equality (PSE) and criterion in both tasks. Scatterplots show the relationship between PSE (x-axis) and criterion (y-axis) for the Short Temporal Task (left panel) and the Long Temporal Task (right panel). We observed a significant positive correlation in both tasks, indicating that participants with a more conservative criterion (tending to judge comparison intervals as shorter than the standard) also exhibited higher PSE values (requiring longer comparison intervals to perceive equality).**

these two independent indices of temporal bias we observed a significant positive correlation. This finding reinforces the interpretation of criterion as a genuine indicator of perceived duration distortion (i.e., temporal underestimation) rather than as a simple response or positional bias.

It should be noted that perceptual bias may also account for time-order error (i.e., first vs second stimulus presented) as described by [Bausenhardt et al. \(2018\)](#) and we acknowledge that analyzing trials based on stimulus order could help isolate this specific effect. This being said, our goal was to capture overall perceptual bias across the task, independently of presentation order, which was counterbalanced for standard and test stimuli. As such, our current analysis allowed us to focus on

net under- or overestimation tendencies, independent of order effects.

A key point in the understanding of our results concerns the specific paradigm employed in our study as compared to alternative paradigms, such as the same/different task used by [Mioni et al. \(2020\)](#). While such methods provide valuable insights into perceptual thresholds, we deliberately chose a 2AFC discrimination task with SDT modeling for its strong psychometric basis and its ability to disentangle sensitivity from bias. This design allowed us to derive continuous measures of sensitivity ( $d'$ ), criterion ( $c$ ) and PSE, which we could then correlate with neurophysiological markers (IAF) in a principled manner. At the same time, we acknowledge that

our 2AFC design with variable standard position introduces interpretative complexity regarding time-order effects and internal standard updating (Dyjas et al., 2012). However, our analyses revealed no significant differences in PSE between standard-first and standard-second trials, suggesting that such effects did not systematically influence our findings.

While this paradigm may not fully control for the different aspects contributing to time perception, it provides a valid index of temporal discrimination ability under cognitively naturalistic conditions, emphasizing temporal discrimination rather than absolute timing or introspective reports.

Our data show a general bias toward underestimation across participants, which does not correlate with IAF. This dissociation suggests that mechanisms underlying temporal underestimation differ from those driving alpha-related modulation of perceptual sensitivity - while bias may reflect strategic or decisional tendencies, the modulation of discrimination performance by IAF likely reflects perceptual-level processes.

Previous research on visual temporal resolution has demonstrated that alpha oscillations regulate the temporal sampling of sensory input strongly advocating for a positive link between sensitivity (rather than perceptual bias) and IAF. Studies using two-flash fusion tasks (Samaha & Postle, 2015), the sound-induced flash illusion (Cecere et al., 2015; Cooke et al., 2019; Keil & Senkowski, 2017), temporal segregation paradigms (Ronconi et al., 2018), and more recently contrast detection tasks (Romei & Tarasi, 2025, preprint), all converge on the notion that individuals with higher IAF exhibit finer temporal resolution in vision. Specifically, Tarasi and Romei (2024) showed that contrast detection sensitivity could be accounted for by IAF, such that the faster the IAF the lower the contrast threshold needed for accurate perception. Moreover, Noguchi (2023), employed SDT to test for the contribution of IAF in accounting for sensitivity ( $d'$ ) versus criterion ( $c$ ) in the sound-induced flash illusion paradigm, confirming that IAF positively correlated with  $d'$  but not  $c$ , again supporting the idea that faster alpha oscillations enhance perceptual discrimination across modalities.

Back to comparative tasks employed in the investigation of time perception, Mioni et al. (2020) employed a temporal generalization task in which participants first learned a standard interval (600 msec) and subsequently judged whether a series of comparisons matched the learned standard. During the task, occipital transcranial Alternating Current Stimulation (tACS) was applied at participants' IAF or at off-peak alpha frequencies ( $IAF \pm 2$  Hz). Faster alpha stimulation in posterior regions resulted in longer perceived durations, aligning with the “counter” clock model, where more pulses result in the perception of longer durations (pace-maker-accumulator hypothesis; Treisman, 1994). It is important to note, however, that the experimental design did not fully disentangle sensitivity from criterion measures, potentially introducing confounding factors. For example, in a temporal generalization tasks, responses might be influenced by a tendency to systematically judge durations as “same” rather than accurately discriminating between intervals (Klapproth, 2018).

Our results did not reveal a temporal bias associated with IAF. Instead, we observed a relationship between faster alpha

oscillations and improved sensitivity to temporal differences, highlighting the importance of distinguishing sensitivity (stimulus discrimination ability) from bias (systematic over- or underestimation of duration). While our task required participants to compare two alternatives rather than judge against a memorized standard, vision may become more critical in the latter case, potentially explaining the discrepancies in occipital effects. Although Mioni et al. (2020) reported interesting behavioral modulations, it is important to note that they did not provide direct evidence of modulation of oscillatory activity, as EEG was not recorded concurrently with stimulation. A plausible alternative interpretation of the observed effects may lie in the indirect effects produced by tACS at the retinal level, which could have established an external rather than an internal timing signal. Although the authors controlled for the presence of phosphenes, it remains uncertain whether the absence of reported phosphenes fully excludes interference with visual processing.

It might be surprising that there are not coherent reports of an association between IAF and time perception and even more so in terms of temporal resolution as the one identified in the current study. It should be noted, once again, that a potential confounding factor is indeed the lack of experimental manipulation and hence control of the differential dimensions contributing to time perception which may depend on the experimental design and task instructions, as well as on the way the dependent variables are defined. Surprisingly, SDT has never been employed in the study of time perception and this may indeed explain some of the inconsistencies so far, by confounding sensitivity and perceptual bias. For example, our findings apparently differ from those reported by Venskus and Hughes (2021), who found no association between IAF and time perception. However, their study relied on the filled duration illusion—a subjective estimation task that is more likely to reflect perceptual bias than temporal precision (Block et al., 2018). This would not be at odds (but actually in line) with our findings as we did not find any relationship between criterion (or PSE) and IAF. More recently, Mokhtarinejad et al. (2024) employed a similar temporal generalization task as the one used by Mioni et al. (2020), using a 1000 msec standard interval. They reported a negative correlation between difference limen (DL; i.e., a measure of precision indicating the smallest physical difference between two stimuli that a participant can just detect; Bausenhardt et al., 2018) and posterior IAF. Specifically, the smaller the DL, the faster the IAF, leading to greater precision and resolution in perceiving 1 s. Moreover, in line with our current findings, they could not find any relationship between IAF and subjective measures of time perception. Finally, they could not establish a causal link between alpha modulation via tACS and time perception, suggesting that active tACS (but not SHAM) interfered with DL. These findings further support the interpretation of a potential confounding factor of retinal interference in Mokhtarinejad et al. (2024) and Mioni et al. (2020) which may alternatively explain their findings.

Despite the scant evidence so far, there is increasing interest and more systematic assessment on the topic in recent years. In this respect, a recent study found measures of precision (such as coefficient of variation and variance in duration estimates) and slope indices to correlate with IAF in both

a single-stimulus duration judgment task and a two-alternative forced-choice (2AFC) task (Morrow et al., preprint), in line with our findings.

Another element that may emerge from our current findings is that faster IAF enhances sensitivity in temporal interval discrimination, with a more pronounced effect observed in the short-duration compared to the long-duration stimuli. For longer durations, which span multiple alpha cycles, we expected the influence of IAF to diminish and the results align with our predictions. This is likely because longer durations involve additional cognitive processes and fluctuations in spontaneous alpha frequency, which likely contribute to variations in IAF. This may call into question the concept of a “golden duration” or critical interval in the subsecond range (Grondin, 2019) which states a different type of neural processing below and above the 1 s duration accounting for time estimation. According to our results and hypothesized mechanism, rather than a specific critical interval accounting for differential time processing, our effect may rather reflect a gradient that diminishes as duration increases. We speculate that beyond 1 s, alpha frequency variations may introduce a substantial amount of noise when it comes to precise estimate of the neural underpinning of temporal computations, thus increasing variability in detecting such relationship. In other words, the effect of IAF on temporal discrimination may build up as a gradient shading off from sensory sampling to cognitive control, where other subjective interpretative mechanisms get in place to build up a representation of time passing. Our study also highlights a topographical specificity of the alpha effect, with prominent activity in frontocentral regions. These areas have been well-documented in the literature as crucial for time perception (Wiener, 2024; Wiener et al., 2010) and overlap with key regions such as the supplementary motor area (SMA; FC1 and FC2). The SMA has been extensively implicated in timing tasks (Betancourt et al., 2023; Coull et al., 2004; Ferrandez et al., 2003; Macar et al., 2006; Pouthas et al., 2005), with different portions showing duration-specific activity arranged in a rostro-caudal gradient (Protopapa et al., 2019). Alpha effects were also observed in adjacent frontocentral electrodes (e.g., C1, C2, CP1, CP2, CP4, CPz, Cz, FC6), corresponding to pre- and postcentral gyri—regions previously linked to timing tasks (Bader & Wiener, 2024). Moreover, pre- and postcentral gyri structural and functional properties have been shown to predict individual time-learning abilities (Bueti et al., 2012). Our results align with these findings, demonstrating that resting-state alpha frequency in these areas is associated with temporal sensitivity. While previous studies have primarily focused on posterior brain regions, where alpha rhythms are dominant, our findings extend this framework by showing that faster alpha oscillations in frontocentral regions also enhance temporal sensitivity. This raises an important question: if alpha oscillations are typically linked to visual perception, how can they also influence frontocentral regions responsible for internal timing? We propose that alpha rhythms do not operate as a localized “clock” but rather as part of a distributed network spanning frontocentral regions associated with motor planning and supramodal processing, as well as posterior areas responsible for sensory input. This perspective aligns with theories emphasizing temporal processes across regions rather than specific loci (Paton & Buonomano, 2018).

#### 4.1. Limitations of the study

While this study provides important insights into the role of individual alpha frequency (IAF) in time perception, several limitations should be acknowledged.

First, the exclusive use of resting-state EEG, which, while valuable for assessing interindividual differences, does not capture within-subject fluctuations during the task. Future research should incorporate ongoing EEG recordings to track trial-by-trial variations in alpha oscillations and better dissociate the contributions of instantaneous IAF to perceptual sensitivity versus decision bias.

Second, the relatively small sample size limits the generalizability of our findings. Replication with a larger sample, combined with ongoing EEG measures, would provide a more comprehensive understanding of how alpha oscillations dynamically shape time perception and decision-making.

Third, while our 2AFC design provides a valid index of temporal discrimination ability and allows us to disentangle temporal sensitivity from temporal biases, it does not necessarily control for all components of time perception. Alternative paradigms, such as temporal reproduction, may target other components of time perception. However, these approaches also come with limitations, including greater susceptibility to memory confounds and central tendency biases (Grondin, 2010). Future research employing comprehensive approaches that tackle multiple aspects of time perception would further expand our understanding of temporal information processing.

Finally, the study lacks causal evidence. While correlational findings strongly suggest a link between IAF and time perception, direct manipulation of alpha frequency would be necessary to establish a causal relationship. However, previous studies using transcranial alternating current stimulation (tACS), such as Mioni et al. (2020) and Mokhtarnejad et al. (2024), have yielded mixed results, highlighting the challenges of modulating perceptual timing through online neural stimulation. A promising alternative would be to manipulate alpha frequency in an offline manner, incorporating pre- and post-stimulation phases. This approach would help mitigate potential confounds associated with online stimulation, which can introduce uncontrolled transient effects on timing computations.

Taken together, these considerations highlight the need for future studies to refine methodological approaches, integrating task-based EEG recordings and controlled neural manipulations to further elucidate the causal role of alpha oscillations in time perception.

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## 5. Conclusion

In conclusion, our study reinforces the relationship between individual alpha frequency and temporal sensitivity. Higher IAF in frontocentral areas was associated with improved performance in sub-second temporal discrimination tasks. These results challenge the pacemaker hypothesis and instead suggest a distributed mechanism where alpha oscillations enhance the precision of temporal sampling. Future research employing brain stimulation techniques (Di Luzzo

et al., 2022; Romei et al., 2016) could further elucidate the causal role of alpha rhythms across different brain regions in time perception. While the exact nature of this relationship remains to be fully understood, our findings contribute to a growing body of evidence supporting the role of alpha oscillations in temporal sensitivity and time perception.

### CRediT authorship contribution statement

**Matteo Frisoni:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luca Tarasi:** Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sara Borgomaneri:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Vincenzo Romei:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

### Scientific transparency statement

**DATA:** All raw and processed data supporting this research are publicly available: <https://doi.org/10.5281/zenodo.15677346>.

**CODE:** All analysis code supporting this research is publicly available: <https://doi.org/10.5281/zenodo.15682746>.

**MATERIALS:** All study materials supporting this research are publicly available: <https://doi.org/10.5281/zenodo.15683467>.

**DESIGN:** This article reports, for all studies, how the author (s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.

**PRE-REGISTRATION:** No part of the study procedures was pre-registered in a time-stamped, institutional registry prior to the research being conducted. No part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted.

For full details, see the *Scientific Transparency Report* in the supplementary data to the online version of this article.

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### Declaration of competing interest

None.

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### Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2025.09.008>.

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