# Individual Alpha Frequency Predicts the Sensitivity of Time Perception

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**Abstract:** A growing body of research links individual differences in the frequency of alpha-band oscillations to temporal aspects of perception. However, whether the human alpha rhythm is a correlate of time perception itself has remained controversial. This multi-day study combined EEG with multiple duration estimation and discrimination tasks in order to evaluate whether individual alpha frequency (IAF) is associated with sensitivity or bias in judging visual durations across a range of peri-second durations (spanning 1200 to 100ms). In a temporal estimation task, participants (n = 55) reported the duration of a single stimulus between 300-1200ms. In a temporal discrimination task, participants reported which of two stimuli was longer: a standard (100, 600, or 1200ms) or comparison (50-150% of the standard). Stimuli also varied in whether their luminance was static or dynamic (varying randomly over time). We found that IAF was significantly related to the variance of duration estimates, a measure of precision (or sensitivity), but not average duration estimates, a measure of bias. Further supporting this relationship, psychometric function slopes obtained from independent duration discrimination tasks were correlated with IAF, particularly for the static stimulus conditions. These effects were largely consistent across the range of stimulus durations tested and held when controlling for participant age. Taken together, these results suggest that IAF plays a role in shaping individual differences in the sensitivity of time perception. However, we did not observe effects of spontaneous fluctuations in single-trial alpha frequency, suggesting the effect is primarily observable at the cross-subject level.

**Significance Statement:** Brain waves in the 8-13 Hz range, known as alpha waves, have long been hypothesized to modulate our perception of time, yet the evidence remains unclear. This study investigates the relationship between an individual's alpha frequency (IAF) and temporal sensitivity using a wide range of time perception tasks and stimulus durations to address gaps in the literature. We demonstrate that IAF is significantly associated with the precision of duration estimates and sensitivity in duration discrimination, particularly for static unchanging stimuli. These findings provide novel evidence that IAF shapes individual differences in time perception, emphasizing its role as a neural marker of temporal sensitivity.

**Keywords:** alpha oscillations, individual differences, duration estimation, duration discrimination, time perception

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## Introduction

The neural mechanisms underlying the perception of stimulus duration have long intrigued psychologists since, unlike other sensory features, time has no dedicated sensing organ. One view is that intrinsic neural dynamics act as an internal clocking mechanism that contributes to the perceived passage of time (Ivry & Schlerf, 2008). Alpha-band (8-13 Hz) neural oscillations have garnered interest as a potential neural clocking mechanism given its relatively stable rhythmic characteristics, intrinsic genesis, and the fact that the typical alpha period (~100ms) is within the range of many low-level sensory binding phenomenon, leading early researchers to debate the idea that the alpha rhythm reflects the minimum "psychological moment" (Ellingson, 1956; Treisman, 1984; White, 1963). If true, the frequency of occurrence of these moments, as indexed by an individual's alpha frequency (IAF) should be predictive of individual variation in duration perception.

Early research (for a review, see van Wassenhove et al., 2019) reported medium-to-small relationships between IAF and the degree of misperception of intervals lasting several seconds (Legg, 1968; Werboff, 1962), but findings have not always been consistent. For instance, Cahoon (1969) found a positive relationship between endogenous alpha (driven by internal processes), but not exogenous alpha (driven by external stimulation), on verbal timing estimates and on the timing of motor tapping, but not on reproductions of temporal intervals. Other research found weak or no evidence linking intra- or inter-individual fluctuations in alpha frequency to estimates of 10s-time intervals Surwillo (1966). Recent work, however, has highlighted the relationship between IAF and the temporal discriminability of brief sequential visual stimuli (Battaglini et al., 2020; Drewes et al., 2022; Samaha & Postle, 2015) as well as temporal windows in cross-modal binding (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020; Stevenson et al., 2012; Venskus & Hughes, 2021), suggesting a relationship between alpha frequency and the duration of temporal binding windows in perception (see Samaha & Romei (2024) for a review and see Schoffelen et al., (2024) for critique). Additionally, recent work related to the so-called rhythmic perception theory suggests that alpha oscillations (among other rhythms) phasically modulate the strength of sensory representations (Dou et al., 2022; Keitel et al., 2022; Mazaheri & Jensen, 2010; VanRullen, 2016) which may explain why individuals with faster IAF, or more frequent increases in sensory representation strength, are more sensitive at discriminating brief visual stimuli. However, whether the human alpha rhythm serves as a more general clocking mechanism for the passage of time itself has remained controversial.

Since the initial wave of research in the 1960s, few studies have looked at how alpha oscillations relate to time perception, and the results are not always comparable given variations in methodology. It

was found that bias in duration perception of durations around 400ms, as measured by the point of subjective equality (PSE) in a temporal judgment task, was related to IAF and the phase of prestimulus alpha (Milton & Pleydell-Pearce, 2016). However, IAF was not related to sensitivity, as measured by the slope of individual psychometric functions (Milton & Pleydell-Pearce, 2016). Similarly, administering tACS above or below one's IAF during a temporal generalization task led to a bias to overestimate or underestimate ~half-second durations respectively, but had no effect on sensitivity (Mioni et al., 2020). Finally, the frequency of alpha bursting episodes was found to be related to retrospective, but not prospective, time estimates of intervals around 2 minutes, but neither task was related to IAF (Azizi et al., 2023). Taken together, these studies found that alpha oscillations may play some role in biasing duration perception, but link these biases to different characteristics of alpha (i.e., phase, frequency, or bursting).

Overall, the current literature does not clearly point to a link between IAF and time perception. A variety of tasks (e.g., discrimination or estimation) are used in different groups of participants and attempts are not always made to tease apart effects on sensitivity or bias in time perception. Moreover, most studies have examined estimates or discriminations of intervals that include multiple alpha cycles (i.e., over 100ms), and typically use static stimuli or empty intervals where there is minimal visual information for alpha to potentially sample. Thus, the goal of the current study was to use a more comprehensive set of tasks to rigorously evaluate the role of alpha frequency in duration perception. Here, participants performed duration discrimination tasks that expanded on prior work by including "short", "medium", and "long" standard durations and by introducing a temporally dynamic stimulus. We also included both estimation and discrimination tasks in the same subjects to test for differences in tasks that rely on an internal (estimation) versus external (discrimination) reference of time. We hypothesized that higher IAF would relate to greater sensitivity in discriminating durations as well as higher precision estimates.

## Method

### Participants

This study was approved by the University of California Santa Cruz (UCSC) Institutional Review Board. Fifty-five participants with a mean age of 21.46 (SD = 5.16) were recruited from UCSC's online participant portal, SONA systems, as well as from the Samaha Lab. This sample size was chosen to achieve 90% power to detect a correlation in the range suggested by a recent meta-analysis of the correlation between IAF and temporal binding measures (mean r ~ 0.45; Samaha & Romei, 2024). The study consisted of two days of testing; the first day of testing took no more than 1.5 hours and involved

the completion of questionnaires and behavioral tasks. Participants received 1.5 SONA research credits and a $10 Amazon gift card. The second day of testing, which had to be completed within 12 days of the first, took no more than 3.5 hours and involved the completion of several duration perception tasks with simultaneous EEG recording. Participants were rewarded with 3.5 SONA research credits and a $30 Amazon gift card. The sample consisted of 68.52% of participants who identified as female, 24.07% who identified as male, and 7.41% who identified as non-binary. The participant sample was 45.45% White/Caucasian, 25.45% Asian (35.71% did not specify further, but of those who did specify, Indian-identifying participants made up 14.29% and those who identified as either Chinese, Cambodian, Filipino, Japanese, Persian, Taiwanese, or Vietnamese each made up 7.14%), 20% Hispanic/Latino, and 9.09% multiracial (20% Black/Southeast Asian, 20% White/Indian, 20% White/Filipino, 20% White/Taiwanese, and 20% White/Chinese). Participants all reported having normal or corrected-to-normal vision.

**Duration Estimation Task**

In the duration estimation task participants provided estimates of the duration of a simple visual stimulus (Figure 1A). In both the practice and experimental blocks, participants observed a dark gray dot presented on a medium gray background either 3 degrees of visual angle (DVA) above or below the central fixation. The dot duration was pseudo-randomly chosen between 300-1100ms in 100ms intervals with equal probability. Participants estimated each stimulus duration using a slider, controlled via computer mouse, that displayed a number line of possible durations, ranging from 100-1400ms in 100ms intervals. The slider provided numbers outside of the range of actual durations to reduce bias when reporting the shortest and longest possible durations. The current value was displayed on the screen in numerical values and was represented on the slider by a green dot which appeared at a random starting location on each trial. The inter-trial interval (ITI) ranged between 1.2-1.8s after the response was input. The practice block was 48 trials long and provided feedback displaying the actual stimulus duration if participants were incorrect in their estimate or “Correct!” if participants were correct. The two experimental blocks lacked feedback and were 90 trials long with each possible duration presented 10 times, totaling 180 trials.

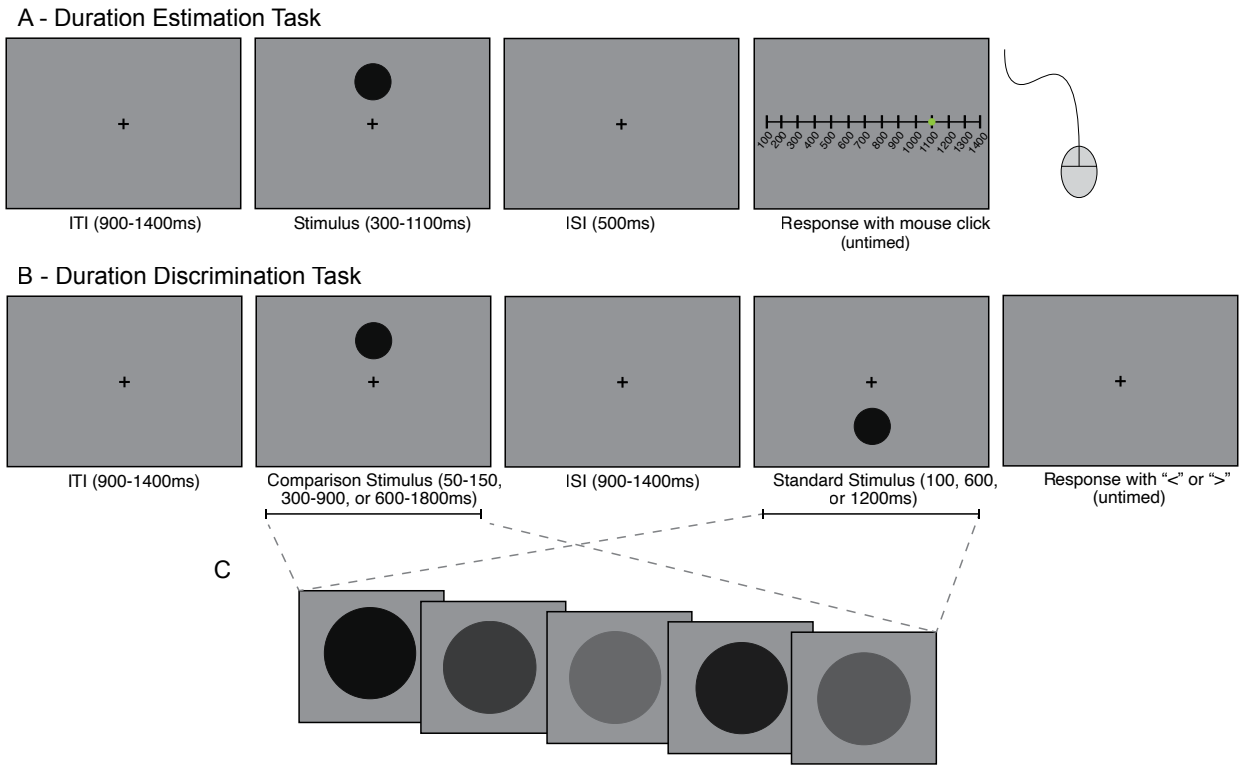


*Figure 1: Diagram of duration perception tasks. (A) Duration estimation task. Participants were shown a dot of variable duration either above or below the central fixation and reported their estimate of the duration of the dot via mouse click along a slider of possible durations. (B) Duration discrimination task. Participants were presented with a dot above fixation, followed by a dot below fixation, or vice versa (dot presentation alternated by block) and reported, via button press, whether the first or second dot was longer. (C) A schematic of the dynamic stimulus condition. The luminance value of the stimulus in the dynamic version of the task varied randomly between black and gray on every screen refresh (120 Hz) throughout the stimulus presentation.*

**Duration Discrimination Task**

The duration discrimination task was a two-interval forced choice (2IFC) design in which participants were asked to report which of two visual stimuli they perceived to be longer in duration (Figure 1B-C). This task had two conditions: a "static" condition, where the stimulus was the same gray dot as presented in the duration estimation task, and a novel "dynamic" condition where the dot varied randomly in luminance between medium gray (0.5 luminance) to black (0 luminance) on every monitor refresh (120 Hz). There is evidence that changes in luminance are cross correlated with the broadband EEG signal in a manner related to the participant's IAF (VanRullen & Macdonald, 2012), suggesting that a dynamically modulating stimulus should elicit a strong response at the alpha frequency and potentially strengthen any link between IAF duration discrimination. To make the dynamically modulating stimulus, we created random luminance sequences for each dot presentation on each trial, and then normalized the sequence amplitude in the Fourier domain before performing an inverse Fourier transform to ensure the

dot had equal energies at all frequencies. Besides the introduction of a flickering dot, the dynamic task was identical to the static task. The order of these conditions was counterbalanced across experimental sessions.

In both duration discrimination conditions, participants observed the first dot either 3 DVA above or below the central fixation, and then a second target on the opposite side of fixation (to avoid any adaptation effects), with the presentation order counterbalanced across blocks so that participants could always expect the location of the first dot as well as the second dot. In other words, whether the first stimulus was presented above or below fixation alternated from block to block but was held constant across the block. For all blocks, one target (the "standard") was presented for a standard duration of 100, 600, or 1200ms, and the other target (the "comparison") was presented for a fraction of the standard duration (either 50%, 70%, 90%, 110%, 130%, or 150% of the standard duration). In this way, the comparison was always proportional to the standard, scaling the comparison durations to be longer for the longer standard durations and shorter for the shorter standards in order to equate difficulty for the different standard durations as predicted by Weber's Law (Haigh et al., 2021). There was a total of 30 presentations of each standard and comparison pair for each task condition. The practice blocks used comparison durations that were 50%, 80%, 120%, and 150% to give participants exposure to some of the easier discriminations and allow them to learn the task, as well as some discriminations of medium difficulty as practice for the experimental block. There were 48 practice trials total where participants received feedback in the form of a tone if they selected the wrong stimulus. For all blocks, the presentation order of the standard and comparison varied each trial. Participants responded with a button press to indicate whether the first ("<") or the second (">") target was longer in duration.

**Critical Flicker Frequency (CFF)**

The CFF - defined as the frequency at which continuously flickering illumination is perceived as constant - was used as a marker of an individual's temporal resolution in their vision (Cass et al., 2011; Eisen-Enosh et al., 2017). Temporal resolution is an aspect of visual processing that is often correlated with IAF in seemingly related tasks such as the two-flash fusion illusion (Drewes et al., 2022; Samaha & Postle, 2015). Individual differences in CFF are also related to IAF in clinical populations with hepatic encephalopathy (Baumgarten et al., 2018; Butz et al., 2013; May et al., 2014). We thus explored whether the CFF task might relate to IAF as well as the other duration perception measures in our non-clinical sample, and administered this task across both days of testing. The CFF was measured with the Flicker-Fusion system by Lafayette Instruments, which is designed to provide a quick (1-2 minutes) measure of an individual's CFF. Participants viewed a flashing light through a viewing chamber and reported

whether they perceived the light as flashing or continuous. The light was presented binocularly at the same rate to each eye and the rate of presentation adaptively changed according to participant responses. Initial changes were on the magnitude of +/-5 Hz, with final changes on the magnitude of +/- 0.1 Hz. Participants performed the task until the Flicker-Fusion system had identified the participant's CFF.

**Questionnaires**

Participants were asked to complete two questionnaires, the Comprehensive Autistic Trait Inventory (CATI; English et al., 2021) and the Prodromal Questionnaire-Brief (PQ-B; Loewy et al., 2005), so that we could assess the extent to which autistic and prodromal schizotypal traits in a typical college sample relate to variations in IAF and duration perception. Cognitive differences can vary widely in the Autism Spectrum Disorder (ASD) population and may be linked to variations in IAF (Dickinson et al., 2018). Research indicates that some individuals with ASD have atypical sensory processing, characterized by improved perception of local features, or detail, and impaired perception of global structure, or contextual information (Chung & Son, 2020; Dakin & Frith, 2005). However, there is conflicting evidence around whether individuals with ASD have typical or enhanced processing of time intervals (Poole et al., 2022; Wallace & Happé, 2008). Individuals with schizophrenia and schizotypal disorders, on the other hand, tend to have impairments in visual perception and visual working memory (Tek et al., 2002), which are thought to underlie difficulties in temporal processing and time perception (Roy et al., 2012), and have lower IAF on average (Ramsay et al., 2021; Sponheim et al., 2023; Trajkovic et al., 2021). Particularly, a meta-analysis suggests that individuals with schizophrenia are less accurate at discriminating durations and have the tendency to overestimate durations (Thoenes & Oberfeld, 2017). Thus, we wanted to explore varying amounts of autistic and schizotypal traits in our college sample related to variations in temporal perception.

To measure autistic traits in our college sample, we used the CATI (English et al., 2021), a 42-item inventory that asks participants to rate how much they agree with statements associated with traits typically seen in the ASD population. Responses are given via a 5-point scale ranging from "Definitely Disagree" to "Definitely Agree". The items come from one of six main categories of traits (Social Interactions, Communication, Social Camouflage, Cognitive Rigidity, Repetitive Behavior, and Sensory Sensitivity) and include statements like, "Metaphors or 'figures of speech' often confuse me," and "I feel discomfort when prevented from completing a particular routine." Answers for each of the items were totaled for each participant, providing a score between 42-210.

The PQ-B (Loewy et al., 2005) was used to measure schizotypal or prodromal traits in the neurotypical population, an inventory consisting of 21 items asking about thoughts, feelings, and experiences within the past month. Items were responded to with a "yes" or "no" and included statements such as, "Do familiar surroundings sometimes seem strange, confusing, threatening or unreal to you?" and "Have you felt that you are not in control of your own ideas or thoughts?". If the participant responded "yes", a follow-up distress scale item asked whether the experience caused the participant to feel "frightened, concerned, or it causes problems" on a 5-point scale ranging from "Strongly Disagree" to "Strongly Agree". Participant scores were computed in two ways: 1) by totaling the number of "yes" responses to get a score between 0-21, and 2) by totaling the values of the distress scale responses to get a score between 21-105. We were primarily interested in the first score which provided a numerical range of the prodromal experiences across individuals.

**Procedure**

Each day, participants signed a written consent form and filled out some basic questions about their state that day (e.g. tiredness, hours since they last ate, etc.) before completing additional tasks. On day one, participants answered demographic questions and completed the CATI and PQ-B questionnaires and the CFF task. Participants then completed at least two practice blocks of each duration task (more if their performance was low or participants reported having difficulty with the task) followed by one experimental block of each task where there was no feedback. On day two, participants quickly completed the CFF task before they were fitted with the EEG cap. They then completed one practice block and two experimental blocks of the duration estimation task, followed by one practice block and five experimental blocks of each duration discrimination task, with the static and dynamic task conditions counterbalanced. Finally, participants sat with their eyes closed for two minutes in order to collect resting state data at the end of the session. Participants were allowed to take breaks between blocks, as needed.

**Behavioral Data Analysis**

For the duration estimation task, we derived two standard measures of time estimation bias and precision by calculating each participant's average estimates at each possible duration and their coefficient of variation (CV) in estimates at each possible duration, respectively. The CV provided an unbiased measure of the variance in estimates, as it corrects for the larger variance inherent in estimates of longer durations. This measure can be interpreted as a precision measure (as variation in estimates decreases, precision increases). We also took the mean estimate and CV by collapsing across durations so that we had a single measure of estimation bias and precision for each participant.

Duration discrimination sensitivity was quantified from the discrimination tasks by fitting a logistic psychometric function (Palamedes toolbox version 1.10.4) to the proportion of times participants chose the comparison stimulus as "longer" for each of the possible comparison durations. This was done separately for each standard duration and each condition (static or dynamic). For all data fitting, the threshold parameter (reflecting the PSE) was bounded by the range of comparison values, the slope parameter of interest (β) was set to -10 to 100 to capture the expected positive slope, and the "lapse rate" parameters (lambda and gamma) values were fixed at 0.05 to denote the lower and upper bounds. Slopes were not normally distributed, so we applied a log10 transformation to each slope parameter. Thus, we derived a slope parameter as a measure of sensitivity for each participant and condition (100ms, 600ms, and 1200ms standards, static and dynamic conditions). Psychometric functions fit the duration discrimination data well for all participants and tasks except one participant who did not have a fit for the 1200ms dynamic condition. Given that there was a correlation among slopes from the different tasks (see Figure 4B), we imputed missing data by averaging the participant's 1200ms static slope and 600ms dynamic slope.

**EEG Data Collection and Analysis**

Continuous EEG was acquired from 63 active electrodes (BrainVision actiCHamp, iMotions A/S, Copenhagen, Denmark), with impedance kept below 20kΩ. Recordings were digitized at 1000 Hz, and FCz was used as the online reference. EEG was processed offline using custom scripts in MATLAB (version R2019b) and using EEGLAB toolbox (Delorme & Makeig, 2004).

EEG signals were first high-pass filtered at 0.1 Hz, downsampled to 500 Hz, and re-referenced using a median reference (to avoid noisy channels contaminating the reference at this stage of pre-processing). Trials were epoched based on the onset time of the stimulus (or the first stimulus in the discrimination task) to include 2s of prestimulus data and at least 800ms of post-second-stimulus data based on the longest possible stimulus duration(s) for each task. We also epoched the eyes-closed resting data into 105 1s-long epochs prior to manual inspection. All task data was then manually inspected to identify trials with muscular artifacts within a -500 prestimulus to +500 post-stimulus window, eye-blinks overlapping the stimulus presentations, and channels with excessive noise. After removing bad trials (estimation task: M = 14.62, SD = 19.83; discrimination task: M = 67.30, SD = 54.98) and interpolating noisy channels (estimation task: M = 2.71, SD = 1.76; discrimination task: M = 3.56, SD = 1.86) using spherical interpolation, an independent components analysis (ICA) was conducted, and ocular artifact components removed (M = 1.71, SD = 0.72). Eyes-closed data were manually inspected for noisy channels (M = 2.13, SD = 1.42) and epochs (M = 5.46, SD = 7.09) to be interpolated and rejected,

respectively, but no ICA was run for this data. Finally, all data was average re-referenced and task data was baseline corrected using a 200ms prestimulus baseline window.

A fast-Fourier transform (FFT) was used to identify peak alpha frequency for each individual from their eyes-closed resting data (Figure 2). Each 1s epoch from the eyes-closed data was zero-padded, linearly detrended, and tapered using a Hamming window prior to applying the FFT. Power was then averaged across epochs using the electrodes with the highest group-level alpha power (O1, O2, PO7, and PO8) to identify the frequency within the alpha-band range (7-14 Hz) that had the most power for each participant, resulting in their IAF. If participants did not have a clear alpha peak (n=1), they were assigned a peak of 10 Hz.

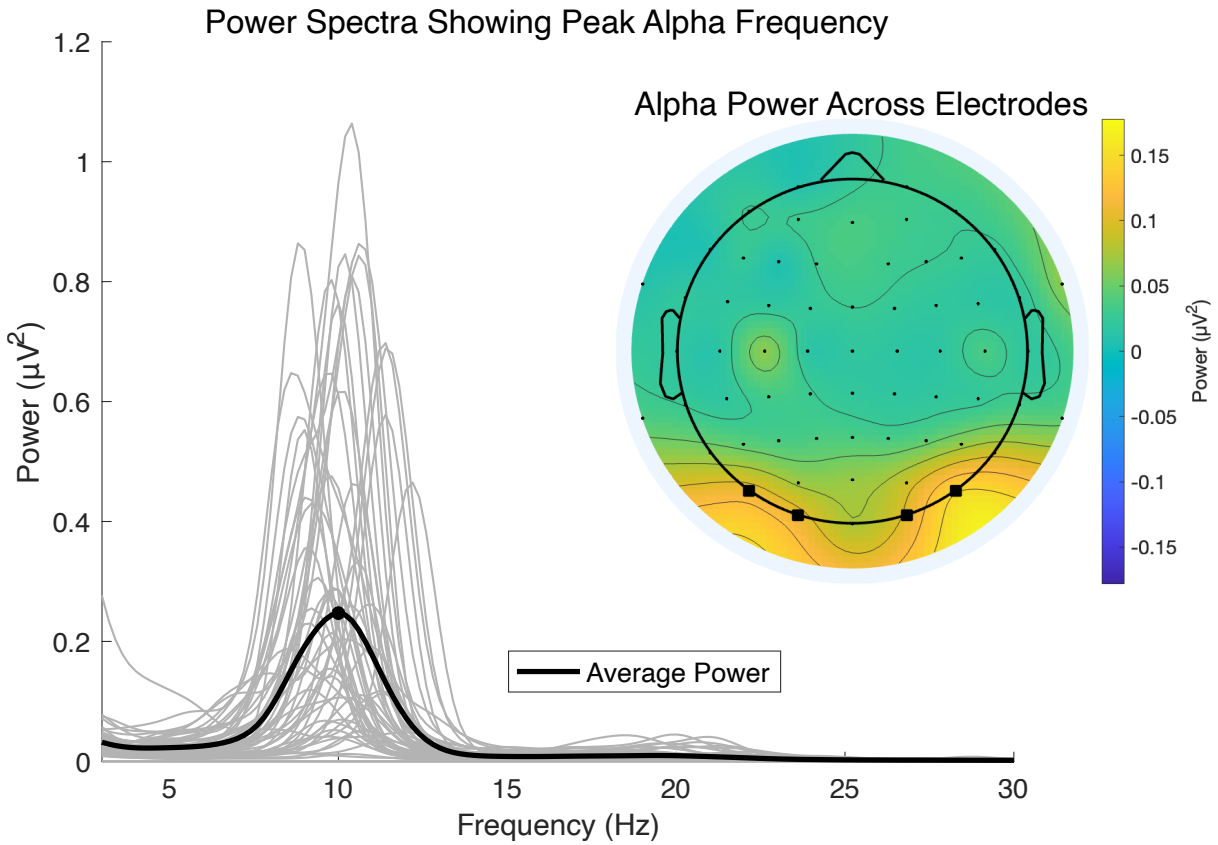


*Figure 2: Individual and group power spectra from eyes-closed resting state data. The average power spectrum (black line) shows the average peak alpha frequency (black dot) is at 10 Hz. Gray lines are power spectra for individual subjects and emphasize the variability in peak frequencies. The topographical map shows the distribution of alpha power (7-14 Hz) across the scalp. Electrode locations (from left to right: PO7, O1, O2, PO8) with the highest group-level alpha power are highlighted with squares and were used in the FFT analysis to determine each individual's peak alpha frequency.*

We additionally explored the relevance of within-subject variation in alpha frequency using the "frequency sliding" approach developed in Cohen (2014), which measures the instantaneous alpha frequency at the single trial level (our implementation can be found in the MATLAB function *dotheslide.m* at https://samahalab.ucsc.edu/resources). We computed the instantaneous alpha frequency for each trial and electrode, averaged across -600 to -200ms prestimulus range (to minimize post-stimulus contamination) and around each participant's IAF +/- 2 Hz. We reasoned that if IAF was linked to duration perception, this might also manifest in a link between trial-to-trial variation in alpha frequency and duration estimation or discrimination behavior. A higher or lower spontaneous prestimulus frequency may lead to a tendency to over- or under-estimate durations in the estimation task or lead to a change in sensitivity in the discrimination task. We also hypothesized that, in the discrimination task, a trial on which alpha frequency was higher prior to the comparison versus the standard stimulus might be more likely to result in a judgment that the comparison was longer, and thus result in a shift in the point of subjective equality (PSE) of the psychometric function.

To this end, we sorted trials by overall instantaneous frequency for both the duration estimation and duration discrimination tasks. For the estimation task, we binned the mean estimates and CV of estimates using a median split of instantaneous trial frequency. For the discrimination task, we averaged together the instantaneous prestimulus alpha frequencies prior to the standard and comparison stimuli (which we later refer to as the "trial frequency" analysis) to assess whether overall alpha frequency across the trial related to duration discrimination sensitivity. We then binned the slopes of psychometric fits from the discrimination task by trial frequency using a median split. We also computed the average instantaneous alpha frequency before each stimulus presentation, separately for standard and comparison stimuli (which we later refer to as the "prestimulus frequency" analysis) to evaluate whether having higher or lower prestimulus alpha frequency prior to the comparison relative to standard stimulus would introduce a shift in the PSE. Given the reduced number of trials for these analyses, some participants did not have a good psychometric fit for all conditions. Two participants were removed from the prestimulus frequency analysis, and one was removed from the trial frequency analysis for having a poor psychometric function fit for two or more conditions. Additionally, there were a total of 7 slopes for the prestimulus frequency analysis and 3 slopes for the trial frequency analysis, each from unique participants, that needed to be imputed. To do so, we averaged those same participants' data from the two most similar conditions.

**Statistical Analyses**

Our main goal was to evaluate the relationship between IAF and duration perception across individuals. We used Spearman correlations to examine the relationship between IAF and behavior in the duration estimation task (namely the mean estimates and CV of estimates). To further examine the link between IAF and estimation measures at each of the durations used in our estimation task, we ran t-tests on the mean estimates and CV comparing participants with high and low IAF (median split). For the duration discrimination task, we also used Spearman correlations to assess the relationship between IAF and the slopes for each of the conditions and the mean slopes across conditions. The mean duration discrimination performance (slope) was moderately correlated with age ($rho(53) = .28$, $p = .04$), and thus we performed all of the aforementioned correlations after correcting for age in each behavioral measure of performance using a linear model (both age-corrected and non-age corrected results can be found in Extended Data Table 1-1). Our main statistical inference, however, given the number of variables in question in the duration discrimination task and their potential relationships, came from a mixed-effects regression model to predict duration discrimination slopes using the main effects of IAF (mean-centered), standard duration (100, 600 ,1200), stimulus type (static or dynamic; dummy-coded), participant age (mean-centered), and the interactions between IAF and standard duration, and IAF and stimulus type as predictors.

We additionally performed within-subjects analyses on the instantaneous alpha frequency extracted from each trial. Specifically, we performed t-tests to evaluate mean estimates and CV of estimates in high versus low prestimulus frequency trials. We then performed t-tests comparing average slopes for high and low instantaneous frequency at the trial level and comparing average PSEs for high and low instantaneous frequency at the stimulus level.

We were also curious about the extent to which CFF, CATI, and PQ-B scores related to IAF and duration perception sensitivity, as well as how the sensitivity measures across tasks related to one another. Given the non-normal distribution of CFF, CATI, and PQ-B scores, we computed separate Spearman correlations between IAF and each of these variables. We also used a Spearman correlation to explore the relationship between the CATI and PQ-B scores and participants' mean estimates, CV of estimates, and duration discrimination slope values. Additionally, we wanted to compare our main behavioral measures of interest across tasks to see how duration estimation related to duration discrimination. We computed a Spearman correlation between the mean slope of the duration discrimination task (taken across all conditions) and the CV of estimates as well as between the mean slope of the duration discrimination task

and the grand mean of estimates from the duration estimation task. Lastly, we checked whether the CV of estimates and grand mean of estimates were correlated using a Spearman correlation.

## Results

### Duration Estimation

Mean and CV of duration estimates are shown in Figure 3. Mean duration reports were near veridical for medium durations (600-800ms) were underestimated at longer durations (900-1100ms), and overestimated at short duration (300-500ms), replicating a well-documented pattern in estimation and reproduction tasks thought to stem from a prior over durations centered on the mean of the stimulus distribution (Jazayeri & Shadlen, 2010). We were primarily interested in looking at participants' average estimates at each duration, as a measure of bias, and their variation around those estimates (CV), as a measure of precision. We found that age-corrected mean estimates (Figure 3) were not significantly related to IAF ($rho(52) = .08$, $p = .57$), nor were they significantly different when median split by IAF ($t(54) = .50$, $p = .62$). However, the age-corrected CV of estimates (Figure 3) was significantly negatively correlated with IAF ($rho(52) = -.30$, $p = .03$), such that faster IAF was associated with a lower CV, or greater precision in one's time estimation. Additionally, the CV (averaged across durations) was significantly different for groups with high IAF compared to low IAF, median split ($t(54) = -2.63$, $p = .01$), such that individuals with faster IAF had significantly lower CV of their estimates. This effect did not appear to interact with the duration being estimated (see Figure 3A, bottom row). Finally, we binned trials relative to the median of each participant's prestimulus alpha frequency to explore trial-to-trial variability in bias and precision. We found no significant difference between high and low trial frequency and mean estimates ($t(54) = -.95$, $p = .35$) or CV of estimates ($t(54) = 1.32$, $p = .19$).

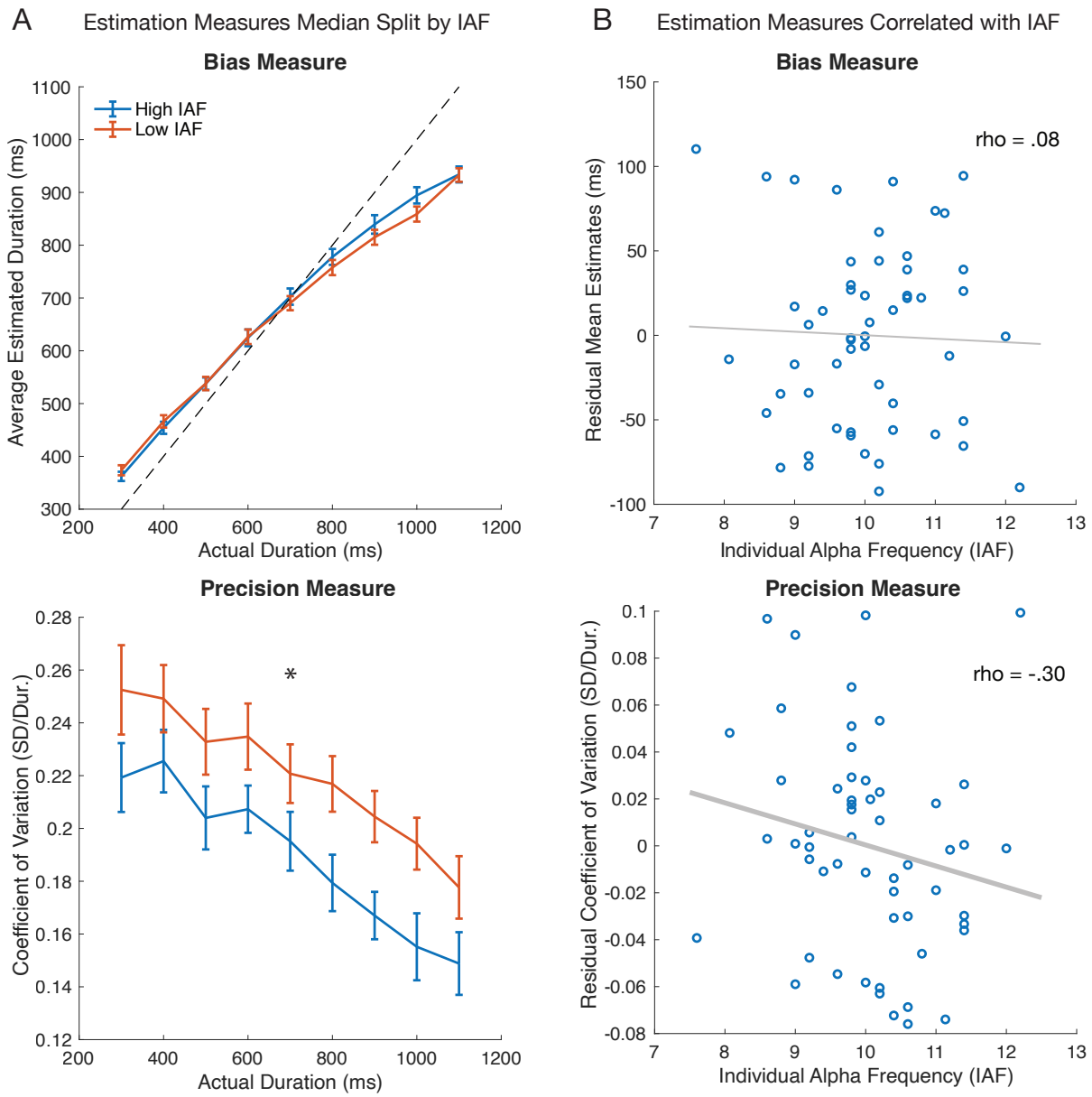


*Figure 3: Duration estimation behavior correlated with IAF and median split by IAF. Mean estimates (bias measures) are plotted in the top row and the coefficient of variation (CV) of estimates (precision measures) are plotted in the bottom row. (A) Participants were split by the median IAF, and their mean estimates and CV of estimates are plotted for every actual duration that was presented in the duration estimation task. Participants with high IAF are shown in blue and participants with low IAF are shown in red (error bars are SEM). Asterisks indicate significance ($p < .05$). (B) Mean estimates and CVs of estimates were averaged across all durations and corrected for age. Plots show the correlation between IAF and the residuals for mean estimates and CV of estimates, where each blue dot indicates an individual participant. Bolded fit lines indicate significance ($p < .05$).*

**Duration Discrimination**

Psychometric functions characterizing duration discrimination behavior were fit for each of the three standard durations (Figure 4A) and for low and high IAF individuals based on median split (Figure 4B). Performance in the discrimination task seemed to improve as durations became longer (Figure 4A), despite the comparison durations being proportionally matched to satisfy Weber's law (Haigh et al., 2021), implying a breakdown of Weber's law in duration discrimination at the shortest (100ms) duration. Despite this, we also found that individual differences in slopes across all standard durations were positively correlated with one another, ranging from *rho*(54) of .30-.79; see Fig. 4C).

To estimate the joint effects of age, IAF, standard duration (100, 600, or 1200ms) and stimulus type (static versus dynamic) on psychometric slopes using a single model that incorporates all the conditions of the discrimination task, we estimated a linear mixed-effects model (see Methods and Fig. 4D). We found that participant performance (non-age-corrected slopes since age is now a predictor in the model) could be predicted using IAF, age, standard duration, and stimulus type (static or dynamic) as predictor variables ($R^2 = .72$). Specifically, age ($\beta = 0.02$, SE = 0.005, $t(323) = 3.06$, $p = .002$), IAF ($\beta = 0.10$, SE = 0.03, $t(323) = 2.83$, $p = .005$), and standard duration ($\beta < 0.001$, SE < 0.001, $t(323) = 13.52$, $p < .001$) were significant predictors of slope as a measure of task performance. While stimulus type (static or dynamic) was not a significant predictor of performance, it significantly interacted with IAF to predict performance ($\beta = -0.05$, SE = 0.02, $t(323) = -2.42$, $p = .02$), indicating that the relation between the duration discrimination sensitivity and IAF was stronger for static compared to dynamic stimuli (as can be seen in Figure 4B). There was no significant interaction between IAF and standard duration as a predictor variable, suggesting that the IAF relation to duration discrimination sensitivity was not strongly dependent on overall stimulus duration. Thus, when pooling together the discrimination sensitivity measures from all conditions into a single model, we found a clear positive association between IAF duration discrimination sensitivity that remained relatively constant across the three standard intervals tested (Fig. 4D). This effect indicates that individuals with higher IAF are more sensitive (i.e., have a steeper psychometric function slope) in discriminating between two different visual stimulus durations.

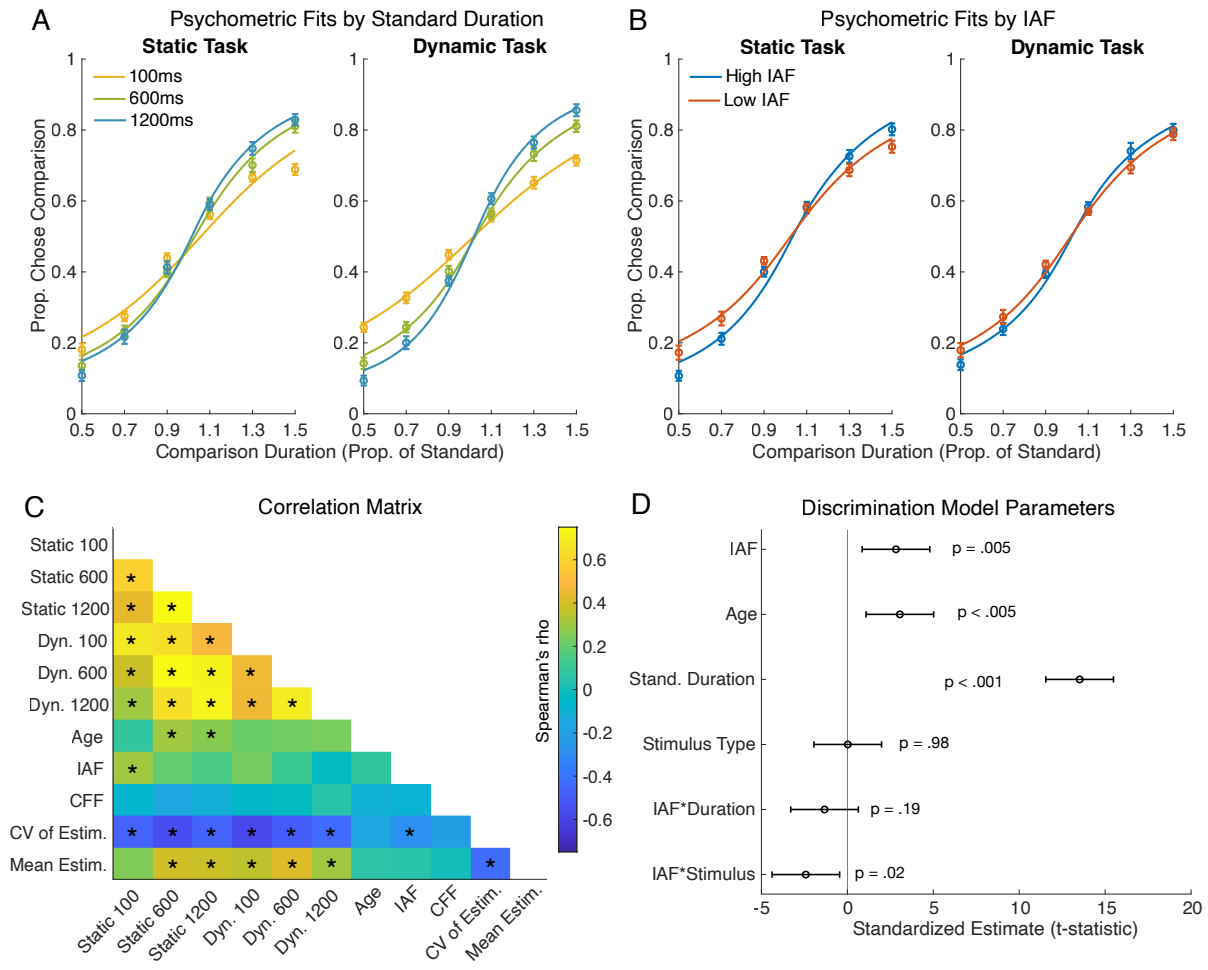


*Figure 4: Duration discrimination results. (A) The proportion of times participants chose the comparison stimulus as being "longer" than the standard stimulus is plotted against the comparison duration (expressed in fractions of the standard). Psychometric function fits (lines) are shown alongside group mean data (circles with SEM error bars) for the 100ms standards (yellow line), 600ms standards (green line), and 1200ms standards (blue line), separated by stimulus type. (B) Psychometric functions for participants with high IAF (blue line) and low IAF (red line) according to a median split shown separately for the static and dynamic tasks. (C) A correlation matrix showing the Spearman correlation between duration discrimination slopes from each condition (from top to bottom, or left to right: Static 100ms, Static 600ms, Static 1200ms, Dynamic 100ms, Dynamic 600ms, Dynamic 1200ms), Age, IAF, CFF, the CV of Estimates (the sensitivity measure in the estimation task), and the Mean Estimate (the bias measure in the estimation task). (D) The effects (t-statistics and 95% CI) from a linear mixed effects model that was used to predict duration discrimination sensitivity (i.e., slopes) using IAF, Age, Standard Duration, Stimulus Type and the interaction terms IAF * Standard Duration and IAF * Stimulus Type in the model. Asterisks indicate significance (p < .05). Note that the effects in the correlation matrix are not corrected for age.*

We next explored the correlations between IAF and age-corrected duration discrimination sensitivity for different groupings of the discrimination task conditions. First, we evaluated whether IAF was related to duration discrimination sensitivity when averaging over all durations and stimulus types.

We found that condition-averaged sensitivity (slope) was significantly positively correlated with IAF (*rho*(52) = .29, *p* = .03), such that individuals with faster alpha frequency exhibited more sensitive time perception (steeper psychometric function slopes, after controlling for age). Breaking down this relationship further, we found a significant correlation between IAF and the average slope for the static condition (*rho*(52) = .37, *p* < .01), but not for the dynamic condition (*rho*(52) = .13, *p* = .35), consistent with the interaction effect observed in the mixed-effects model (Fig. 4D). Finally, there was a significant correlation between IAF and sensitivity discriminating 100ms standards (*rho*(52) = .30, *p* = .02) and a moderate correlation between IAF and sensitivity discriminating 600ms standards (*rho*(52) = .26, *p* = .05), but no significant relationship was found for the 1200ms standards (*rho*(52) = .17, *p* = .22). Note, however, that these correlations are not statistically different from one another as reflected in the lack of a significant IAF-by-duration interaction in the mixed-mode (Fig. 4C).

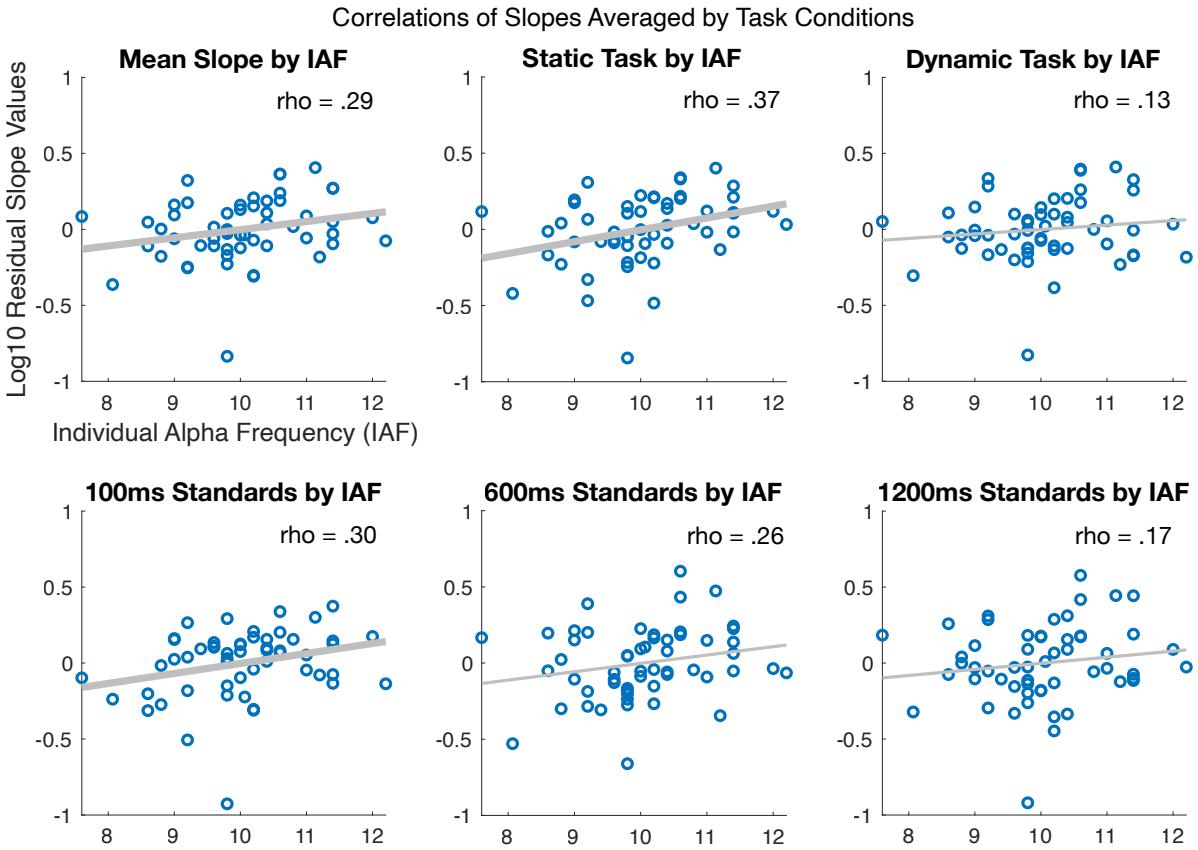


*Figure 5: Correlations between IAF and (age-corrected) slopes for different duration discrimination task conditions. The average discrimination slope across all conditions is plotted in the top left, with stimulus types plotted in the middle and top rightmost plots (static condition and dynamic condition, respectively). Slopes from each standard duration (averaged over static and dynamic tasks) are plotted in the bottom row (from left to right: 100ms, 600ms, 1200ms) and). Each blue dot indicates an individual participant. Bolded fit lines indicate significance (p < .05).*

The within-subjects analysis for the duration discrimination task looked at instantaneous alpha frequency at both the prestimulus frequency level (where trials were sorted by whether the comparison stimulus had higher or lower prestimulus alpha frequency than the standard stimulus) and at the trial frequency level (where trials were sorted by whether the average prestimulus frequency before each stimulus was higher or lower than the median frequency across trials). Slope, averaged across all conditions, was not significantly different for trials with higher prestimulus frequency compared to trials with lower prestimulus frequency ($t(53) = 0.26$, $p = .80$). The PSE, on average, was not significantly different on trials where the comparison stimulus had a higher prestimulus frequency compared to trials where the standard stimulus had a higher prestimulus frequency ($t(52) = 0.91$, $p = .37$). Similarly, no significant results were found comparing slopes or PSEs sorted by trial or prestimulus frequency when broken down further by standard duration or stimulus type.

**Exploratory Measures**

We were interested in evaluating whether IAF or duration perception performance related to questionnaire scores measuring Autistic-like traits and prodromal (schizotypal) experiences in each participant (Extended Data Figure 1-1). No significant correlation was found between IAF and individual's CATI scores or PQ-B scores. The CATI and PQ-B scores also did not significantly relate to any of the main performance measures of interest (mean estimates, CV of estimates, and duration discrimination slopes). Given the established relationship between CFF and IAF in clinical populations, we also compared CFF to various measures. First, we explored potential correlations between IAF with the CFF averaged across both testing days as well as the CFF from only the second day - the same testing session where we measured IAF. Neither CFF score was significantly correlated with IAF (average CFF: $rho(53) = -.09$, $p = .51$; day 2 CFF: $rho(53) = -.15$, $p = .26$). We also evaluated whether the CFF from the first day, the testing session where participants completed the trait questionnaires, was correlated with either questionnaire score (Extended Data Figure 1-1). We found a moderately weak, non-significant, correlation between CFF and CATI scores ($rho(53) = .24$, $p = .08$) and PQ-B scores ($rho(53) = .23$, $p = .09$).

Finally, we examined whether performance on the different discrimination tasks (estimation versus discrimination) was related across individuals. Since the CV derived from duration estimates and the slope measure derived from 2IFC discrimination are both sensitivity measures we would expect a relationship. Indeed, we found that the CV (averaged across durations) and the average slopes of the psychometric fits were significantly negatively correlated across participants ($rho(53) = -.56$, $p < .001$; Figure ), indicating that an individual with a steeper discrimination slope has lower estimation variability,

as expected (Fig. 4C). Interestingly, there were also relationships with the bias measure derived from the estimation task such that participant's average overall estimates correlated significantly with the average slopes of the psychometric fits (*rho*(53) = .41, $p < .01$).

## Discussion

This study measured individual differences in sensitivity and bias in duration perception using both discrimination and estimation tasks across a range of peri-second durations spanning 100ms to 1200ms. Our key finding is that IAF shows a medium-sized correlation with time perception sensitivity as measured by both estimation and discrimination tasks, and was not found to predict measures of duration bias (i.e., under- or over-estimation). Importantly, these two sensitivity measures were significantly related: less variance in estimates was associated with a steeper psychometric function slope, highlighting a relationship between duration perception tasks that has not yet been explored. Moreover, our effects hold when controlling for participant age, a confound that may have influenced the conclusions in prior research. Our duration discrimination findings are consistent with, and expand upon, the vast literature supporting the role of IAF in sensitivity discriminating quick successive visual and multisensory stimuli (Cecere et al., 2015; Cooke et al., 2019; Di Gregorio et al., 2022; Migliorati et al., 2020; Noguchi, 2022; Samaha & Postle, 2015; Venskus & Hughes, 2021), and our duration estimation findings provide novel evidence that IAF also plays a role in the overall precision of estimating the duration of visual events.

By exploring the relation between IAF and a range of mostly sub-second durations, we show that IAF predicts time perception sensitivity approximately equally across the tested range, both in estimation and discrimination tasks. However, particularly in the discrimination, there was a trend towards a larger effect of IAF at the shortest duration (100ms) and a smaller effect at the longest duration (1200ms), although this was not a significant interaction in our model. We speculate, however, that the effect of alpha frequency may become weaker as the interval in question increases since more cognitive factors, such as working memory, are expected to play a role at longer durations. In contrast, the stimulus durations tested here is within what is traditionally considered closer to the "perceptual" side of duration judgment. Moreover, the fact that our strongest correlation was found with 100ms standard, where Weber's law was observed to break down, reinforces the idea that the alpha frequency supports "short" duration discrimination which likely relies even more on sensory mechanisms such as those involved in temporal resolution and temporal binding of stimuli.

The role of IAF in duration discrimination was, however, found to be specific to the static stimulus condition, as supported by a significant interaction between IAF and stimulus type in our mixed

effects model. In our dynamic stimulus condition, we randomly modulated the luminance of the stimulus according to a white noise (equal energy at all frequencies) sequence, which has previously been shown to induce a strong alpha "echo" in the luminance-by-EEG cross correlation (VanRullen & Macdonald, 2012). We anticipated that this may enhance any link between IAF and duration discrimination although this was admittedly speculative. Instead, randomly modulating stimulus luminance seems to interfere with the relationship between IAF and time perception sensitivity, perhaps by inducing a stimulus-driven alpha rhythm separate from each individual's endogenous alpha. Alternatively, these stimuli may have simply been more cognitively demanding for participants to observe and duration perception in this task may have recruited more cognitive mechanisms, or participants may have used different strategies for the dynamic conditions such as trying to count notable luminance changes. Overall, it seems that the role of IAF may depend on the type of stimulus whose duration is being estimated, and future research should further explore what stimulus properties engage IAF for duration perception.

We also performed single-trial analyses to explore whether within-subject changes in alpha frequency relate to duration perception. We found no relationship between spontaneous changes in instantaneous prestimulus frequency and any of our duration perception measures. Specifically, there was no effect of trial frequency on bias (mean estimates) or precision (CV of estimates) in the estimation task, or on sensitivity (slope) in the discrimination task. Additionally, prestimulus frequency differences between the comparison and standard stimulus did not affect bias (PSE) in the discrimination task. Despite IAF modulating precision and sensitivity in these tasks at the subject level, it seems that duration perception may be relatively stable within an individual despite spontaneous changes in alpha frequency. On the one hand, this finding is supported by theories of time perception that suggest alpha acts as an internal clock that can calibrate to fluctuations in alpha frequency (Karmarkar & Buonomano, 2007; Surwillo, 1966; Treisman, 1963; Treisman et al., 1990). However, it could also be that spontaneous variation in single-trial instantaneous frequency is small and noisy and using it to sort behavioral data is not an optimal analysis approach. Indeed, prior work using instantaneous frequency measures have tended to condition the results on the behavior (i.e., correct versus incorrect) and look back at the instantaneous frequency, rather than the other way around (e.g., Samaha & Postle, 2015). This approach seemed less suitable for our case, though, since the behavioral measures we designed our experiment to assess are themselves based on trial-averaged response (i.e., psychometric function slope or CV of duration estimates) and don't provide single-trial measures. However, the lack of robust within-subject effects when relying on spontaneous variation in alpha frequency make clear the need for casual manipulations of alpha frequency at the within-subject level to test for a true causal relationship.

The final analyses examining IAF's relationship to the CFF and CATI and PQ-B scores and the CATI and PQ-B scores to task performance were somewhat exploratory in nature, and we failed to find any significant relationships across the measures. Research on patients with hepatic encephalopathy shows that IAF correlates with CFF (Baumgarten et al., 2018; May et al., 2014). However, it is possible that CFF and IAF are uniquely correlated in these clinical populations, perhaps due to other underlying mechanisms that drive these patients to have lower IAF on average compared to healthy controls (Butz et al., 2013; Götz et al., 2013; May et al., 2014). Similarly, IAF varies in populations with ASD (Dickinson et al., 2018) and schizotypal disorders (Ramsay et al., 2021; Sponheim et al., 2023; Trajkovic et al., 2021), and duration perception varies in populations with ASD (Poole et al., 2022; Wallace & Happé, 2008) and schizotypal disorders (Roy et al., 2012; Tek et al., 2002; Thoenes & Oberfeld, 2017). However, there were no significant correlations between IAF and the magnitude of ASD traits (CATI) or prodromal traits (PB-Q) in our population, perhaps due to the non-normal distribution of trait scores whereby individuals tended to score low in both of these traits (see Extended Data Figure 1-1). While we found lower IAF to be associated with reduced duration perception sensitivity, it does not seem to be directly related to ASD or prodromal traits. The lack of correlation between IAF and CFF, however, does fit with a recent paper that replicated the correlation between IAF and another measure of temporal resolution (the two-flash fusion paradigm) but not with CFF, suggesting these two measures tap different aspects of temporal resolution (Haarlem et al., 2024).

Our main results contradict some recent literature exploring the role of IAF in duration perception, which found evidence that IAF and alpha phase relates to bias, but not sensitivity (Milton & Pleydell-Pearce, 2016; Mioni et al., 2020). However, both tasks used a similar standard duration (400ms or 600ms) which was either learned before viewing comparisons, or always presented as the first stimulus. Perceptual training research (Navarra et al., 2005; Powers et al., 2009; Stevenson et al., 2013) and research on the temporal order effect (Grondin, 2010) suggest that these design considerations have important implications for how participants may have performed on those duration tasks. We also note that our sample size was considerably larger than those prior papers and we found consistent results across two distinct time perception tasks and across different stimulus durations.

Overall, our results support the idea that rhythmic alpha sampling drives sensitivity in time perception, as the theory would suggest that individuals with faster IAF have more frequent excitatory perceptual windows and therefore more frequent updating of sensory information to be used for estimating stimulus duration. Further supporting this theory and interpretation of our findings is the fact that the sensitivity measures (CV of estimates and slope in discriminations) were significantly negatively

correlated across tasks: as discrimination sensitivity increased, the amount of variance in estimates decreased. While this correlation is not sufficient to conclude that these processes are supported by the same underlying mechanism, it is a necessary relationship to observe if IAF is indeed the mechanism driving the magnitude of sensitivity across participants in both tasks. Finally, we note that many important future directions stem from this work, such as considering the role of IAF in filled versus empty intervals, as has often been done in behavioral duration perception studies (Buffardi, 1971; Hasuo et al., 2014; Wearden et al., 2007; Williams et al., 2019). Examining whether IAF plays a role in perceiving durations for non-visual stimuli is also critical to establish. Critically, though, casual methods are needed to establish the mechanistic role of alpha oscillations in time perception.

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**Extended Data**

| | **Age-corrected** | | **Non-age-corrected** | |
|---|---|---|---|---|
| | ***rho(52)*** | ***p*** | ***rho(54)*** | ***p*** |
| **Duration Estimation Measures** | | | | |
| Mean Estimates | .08 | .57 | .05 | .72 |
| CV of Estimates | -.30* | .03* | -.28* | .04* |
| **Duration Discrimination Measures** | | | | |
| Mean Slope | .29* | .03* | .21 | .12 |
| Mean Static Slope | .37* | .005* | .31* | .02* |
| Mean Dynamic Slope | .13 | .35 | .09 | .52 |
| Mean 100ms Slope | .30* | .02* | .26 | .05 |
| Mean 600ms Slope | .26 | .05 | .18 | .19 |
| Mean 1200ms Slope | .17 | .22 | .07 | .63 |

*Table 1-1: Age-corrected and non-age-corrected statistical results of duration estimation and duration discrimination analyses. Each measure was corrected for age using a linear model to account for the amount of variance explained in the performance measure by participant age. These measures were used in the main correlation analyses described in Chapter 5. Non-age-corrected correlations were also performed and are provided in the final two columns of the table. Asterisks indicate significant correlations ($p < .05$).*

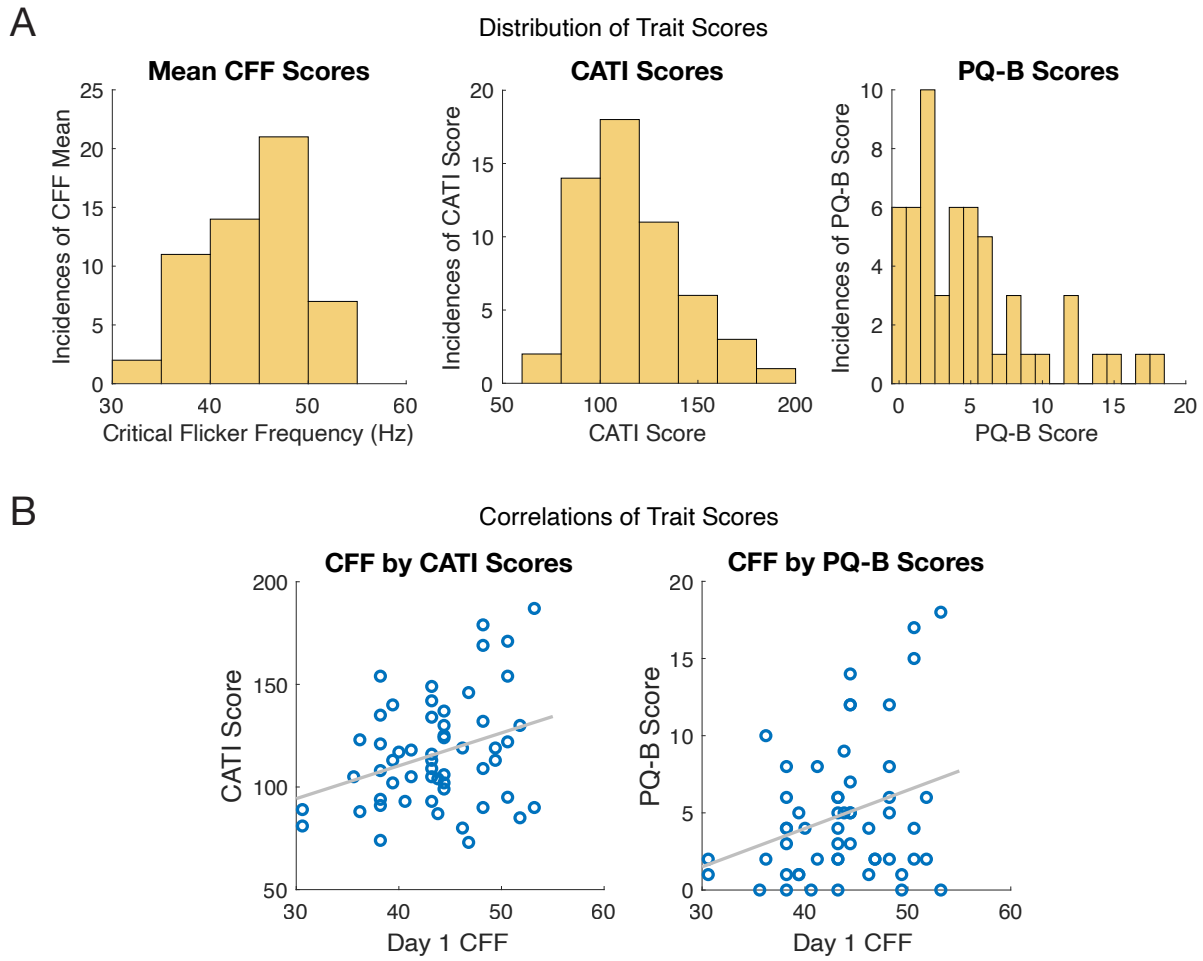
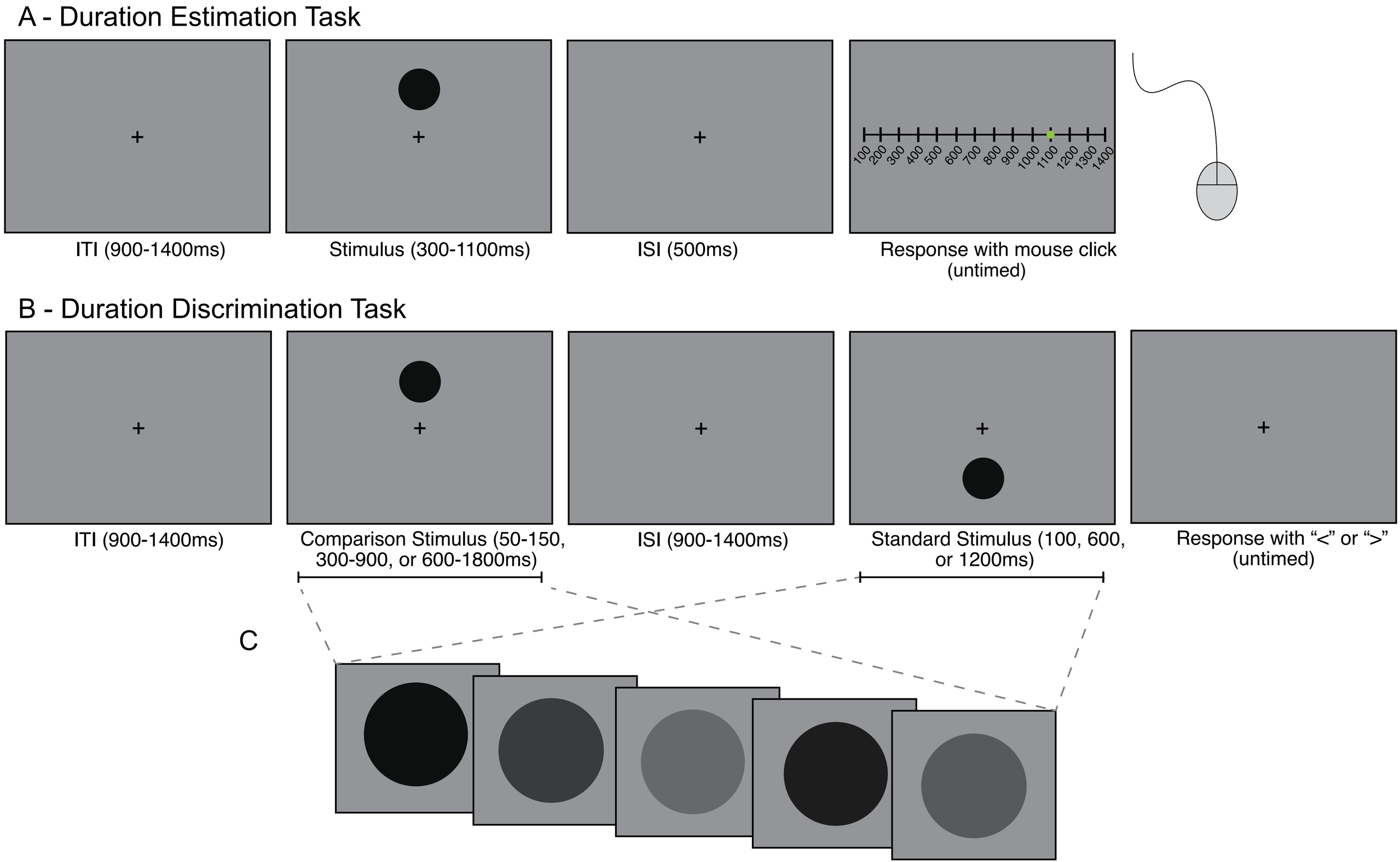
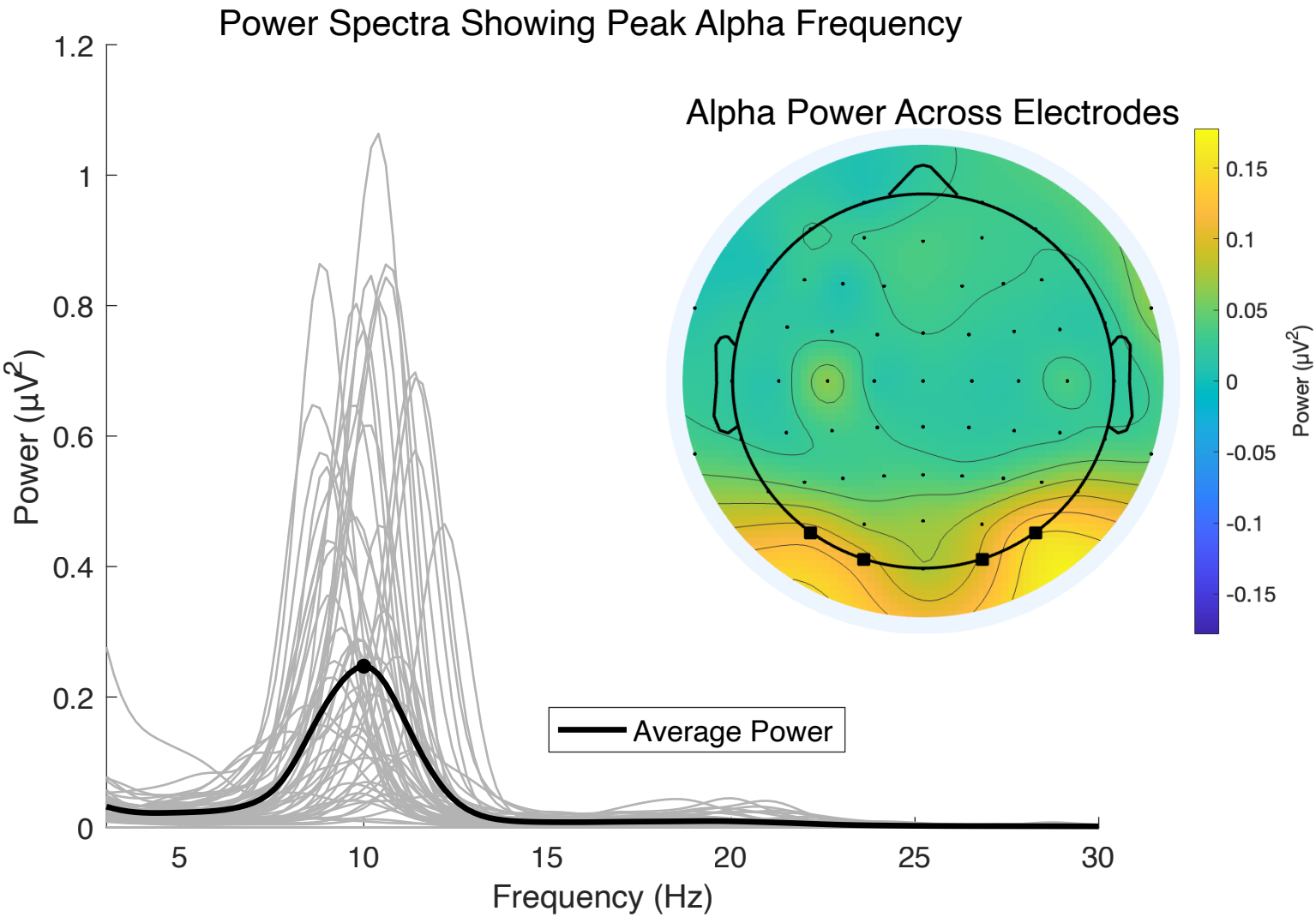
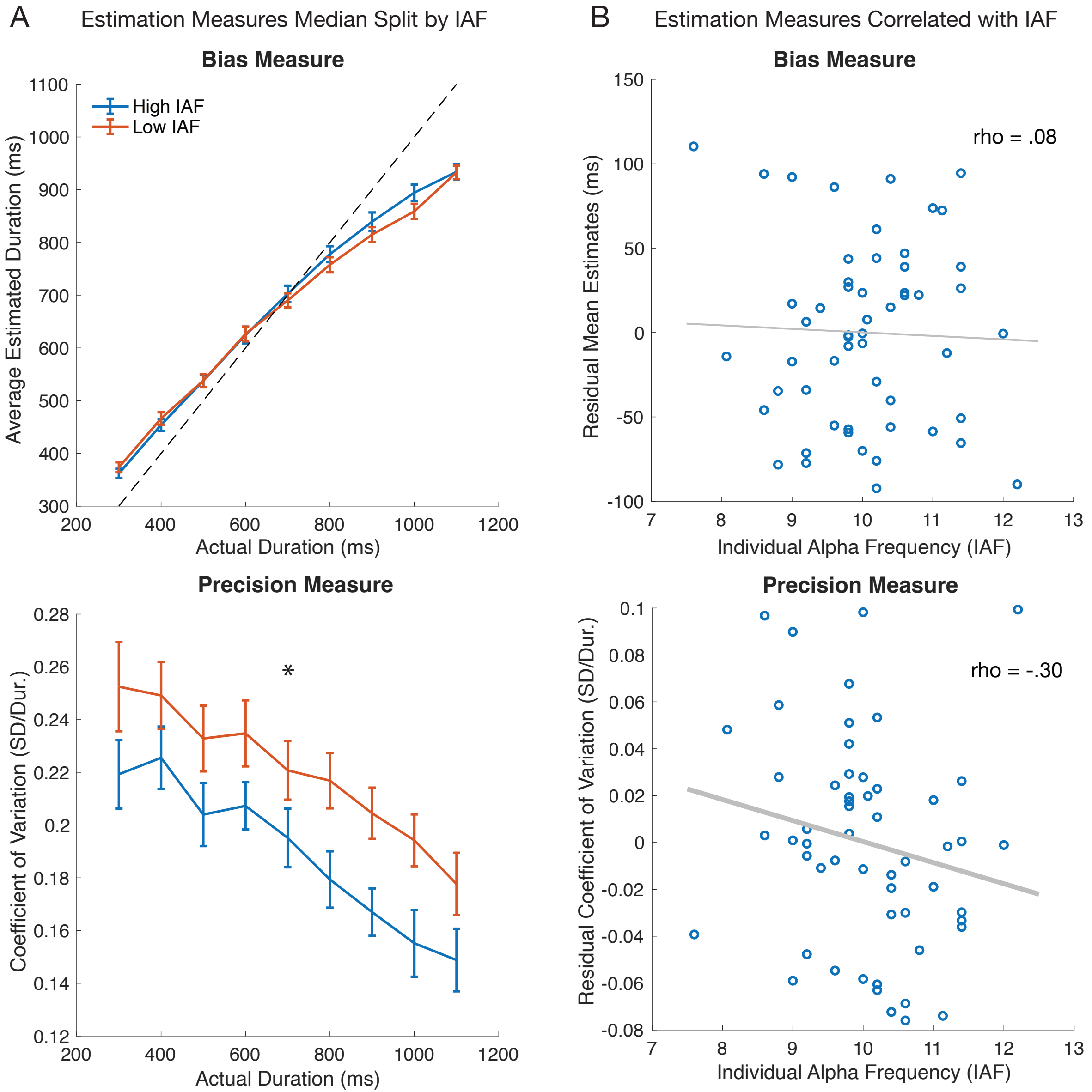
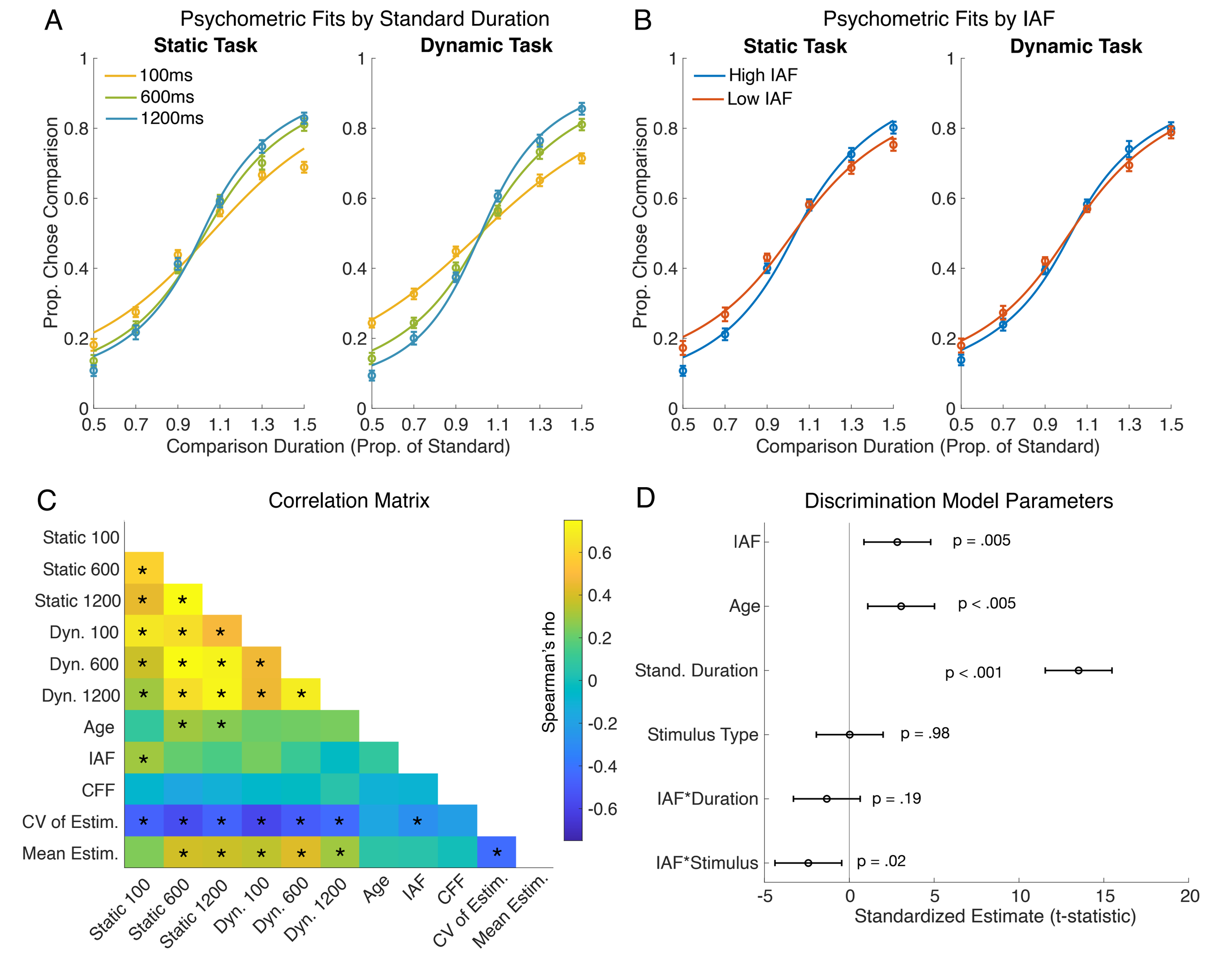


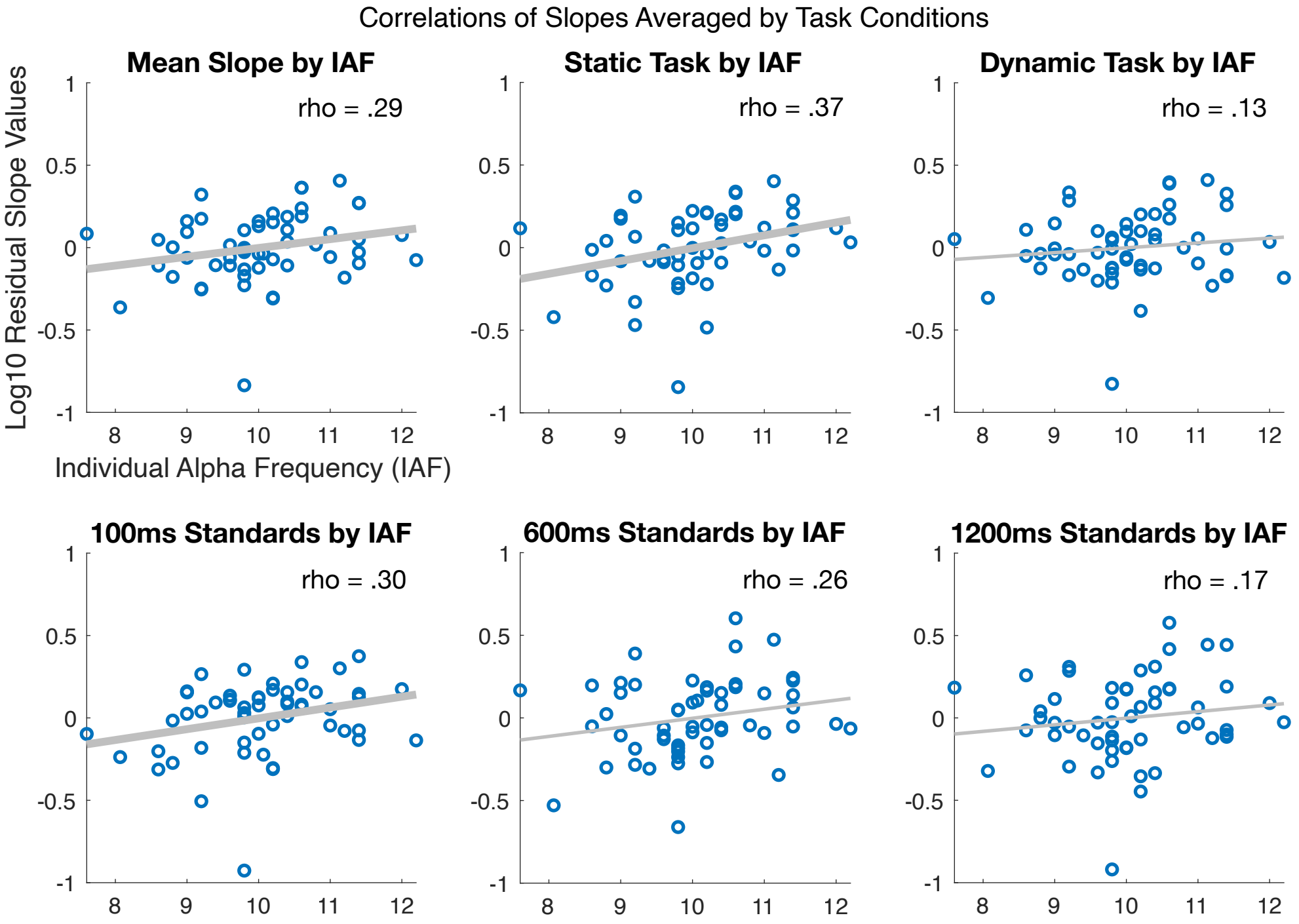

*Figure 1-1. The distribution of CFF, CATI, and PQ-B scores across the sample, and correlations between Day 1 CFF and the CATI and PQ-B scores. (A) Histograms demonstrate the number of participants with each trait-like score that was measured in the experiment: critical flicker frequency (CFF), Comprehensive Autistic Trait Inventory (CATI) and the Prodromal Questionnaire (PQ-B). (B) A Spearman correlation was computed between the Day 1 CFF scores and the CATI scores (left) and PQ-B scores (right) as an exploratory measure of the relationship between traits that were expected to, but did not relate to, IAF. Neither correlation reached statistical significance.*


A - Duration Estimation Task
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
ITI (900-1400ms)
Stimulus (300-1100ms)
ISI (500ms)
Response with mouse click
(untimed)
B - Duration Discrimination Task
ITI (900-1400ms)
Comparison Stimulus (50-150,
300-900, or 600-1800ms)
ISI (900-1400ms)
Standard Stimulus (100, 600,
or 1200ms)
Response with “<” or “>”
(untimed)
C


Power Spectra Showing Peak Alpha Frequency
Alpha Power Across Electrodes
Power (μV²)
Frequency (Hz)
Average Power
0
0.2
0.4
0.6
0.8
1
1.2
5
10
15
20
25
30
0.15
0.1
0.05
0
-0.05
-0.1
-0.15


A
Estimation Measures Median Split by IAF
Bias Measure
High IAF
Low IAF
Average Estimated Duration (ms)
Actual Duration (ms)
Precision Measure
*
Coefficient of Variation (SD/Dur.)
Actual Duration (ms)
B
Estimation Measures Correlated with IAF
Bias Measure
rho = .08
Residual Mean Estimates (ms)
Individual Alpha Frequency (IAF)
Precision Measure
rho = -.30
Residual Coefficient of Variation (SD/Dur.)
Individual Alpha Frequency (IAF)


A
Psychometric Fits by Standard Duration
Static Task
Dynamic Task
100ms
600ms
1200ms
Prop. Chose Comparison
Comparison Duration (Prop. of Standard)
B
Psychometric Fits by IAF
Static Task
Dynamic Task
High IAF
Low IAF
Prop. Chose Comparison
Comparison Duration (Prop. of Standard)
C
Correlation Matrix
Static 100
Static 600
Static 1200
Dyn. 100
Dyn. 600
Dyn. 1200
Age
IAF
CFF
CV of Estim.
Mean Estim.
Spearman's rho
D
Discrimination Model Parameters
IAF
Age
Stand. Duration
Stimulus Type
IAF*Duration
IAF*Stimulus
p = .005
p < .005
p < .001
p = .98
p = .19
p = .02
Standardized Estimate (t-statistic)


Correlations of Slopes Averaged by Task Conditions
Mean Slope by IAF
rho = .29
Static Task by IAF
rho = .37
Dynamic Task by IAF
rho = .13
100ms Standards by IAF
rho = .30
600ms Standards by IAF
rho = .26
1200ms Standards by IAF
rho = .17
Log10 Residual Slope Values
Individual Alpha Frequency (IAF)
1
0.5
0
-0.5
-1
8
9
10
11
12