Alpha Activity Reflects the Effort to Compensate an Individual Bias in Human Perception

Laetitia Grabot[a,1], Christoph Kayser[a,2]
[a] Department for Cognitive Neuroscience, Faculty of Biology & Cognitive Interaction Technology, Center of Excellence, Bielefeld University, Bielefeld, Germany

Email:
[1] laetitia.grabot@gmail.com
[2] christoph.kayser@uni-bielefeld.de

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Abstract

Biases in sensory perception can arise from both experimental manipulations and personal trait-like features. These idiosyncratic biases and their neural underpinnings are often overlooked in studies on the physiology underlying perception. A potential candidate mechanism mediating such idiosyncratic biases is spontaneous alpha activity, a prominent brain rhythm known to influence the processing of upcoming information in general. Using a time perception task, we here tested the hypothesis that alpha power reflects the compensation for an idiosyncratic bias. Importantly, to understand the interplay between idiosyncratic biases and contextual (temporary) biases induced by experimental manipulations, we quantified this relation before and after temporal recalibration. Using EEG recordings in human participants, we found that pre-stimulus alpha power correlates with the tendency to respond relative to an own idiosyncratic bias, with stronger alpha leading to responses matching the bias. In contrast, alpha power did not predict response correctness. These results also held after temporal recalibration and were specific to the alpha band, suggesting that alpha power indexes the cognitive effort to overcome an individual's momentary bias in perception.

Significance statement

The brain is a biased organ, frequently generating systematically distorted percepts of the world, leading each of us to evolve in our own subjective reality. However, such biases are often overlooked or considered noise when studying the neural mechanisms underlying perception. We show that spontaneous alpha band activity predicts the degree of biasedness of human choices in a time perception task, suggesting that alpha power indexes the effort needed to overcome an individual's idiosyncratic bias. This result provides a window onto the neural underpinnings of subjective perception, and offers the possibility to quantify or manipulate such priors in future studies.

Introduction

Perception is not only driven by the incoming information but is also shaped by expectations, knowledge and other individual and flexible biases. These can arise from both temporary contextual effects and long-term priors. Temporary biases can be experimentally manipulated by changing the probability of one response over another, or through contextual recalibration paradigms (Summerfield & Egner, 2009; de Lange, Heilbron, & Kok, 2018). The long-term priors comprise life-long learned and stable assumptions about the world, such as the sun shining from above (Sun & Perona, 1998). These priors may vary between individuals, but are stable for a given individual, and reflect idiosyncratic biases. These are often unknown to the experimenter and hence may be shadowed by experimental manipulations or may be regarded as inter-individual noise that is eliminated during data analysis (Kanai & Rees, 2011; Wexler, Duyck, & Mamassian, 2015; Grabot & Wassenhove, 2017; Rahnev & Denison, 2018; Lebovich, Darshan, Lavi, Hansel, & Loewenstein, 2019). We here argue that such inter-individual variability in temporary and idiosyncratic biases provides key perspectives on the neural mechanisms underlying perception. In particular, we ask whether pre-stimulus oscillatory activity reflects the neural underpinnings of such idiosyncratic biases, and if so, how these interact with those reflecting temporary biases.

The influence of prior expectations and knowledge on perceptual decisions is often thought to arise from high-level prefrontal and parietal regions, and is conveyed to sensory areas via top-down mechanism (Engel, Fries, & Singer, 2001). One neural signature involved in this process supposedly is alpha band activity (van Kerkoerle, et al., 2014; Michalareas, et al., 2016; Sherman, Kanai, Seth, & VanRullen, 2016; Mayer, Schwiedrzik, Wibral, Singer, & Melloni, 2016), generally known to shape the perception of forthcoming stimuli (Ergenoglu, et al., 2004; Hanslmayr, et al., 2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Recent studies have suggested that pre-stimulus alpha activity may reflect the criterion used to commit a specific response and may hence reflect a perceptual or decisional bias (Limbach & Corballis, 2016; Iemi, Chaumon, Crouzet, & Busch, 2017; Craddock, Poliakoff, El-deredy, Klepousniotou, & Lloyd, 2017; Iemi & Busch, 2018; Rohe, Ehlis, & Noppeney, 2019). Along such a role in perceptual decision making, alpha activity was shown to correlate with subjective awareness (Benwell, et al., 2017; Lange, Oostenveld, & Fries, 2013; Gulbinaite, İlhan, & VanRullen, 2017) and decision confidence (Samaha, Iemi, & Postle, 2017; Wöstmann, Waschke, & Obleser, 2018). Still, it remains unclear whether pre-stimulus activity indeed reflects an individual's intrinsic bias, or reflects processes that facilitate veridical sensory encoding, as previous work did not unambiguously quantify the relation of spontaneous brain activity to idiosyncratic and temporary biases.

We have previously proposed the hypothesis that alpha band activity compensates for an individual's idiosyncratic bias: low alpha power enhances the probability to respond against the bias, while high power increases the tendency to follow the bias (Grabot & Wassenhove, 2017; Grabot, Kösem, Azizi, & Wassenhove, 2017). To directly test this hypothesis, we here used a temporal order (simultaneity) judgement task, in which perception is shaped by idiosyncratic biases (Freeman, et al., 2013; Ipser, Karlinski, & Freeman, 2018; Grabot & Wassenhove, 2017) and can be manipulated by inducing temporary biases through temporal recalibration. Importantly, our paradigm was designed to dissociate intrinsic biases from overall task performance, allowing us to test whether pre-stimulus activity is predictive of the correctness or the degree of biasedness of a response. Our results confirm that a decrease in pre-stimulus alpha power enhances the probability to respond against the individual idiosyncratic bias and that inter-individual fluctuations in alpha power correlate with the magnitude of this perceptual bias. Furthermore, by testing the influence of contextual recalibration (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Vroomen, Keetels, Gelder, & Bertelson, 2004; Van der Burg, Alais, & Cass, 2015; Van der Burg, Alais, & Cass, 2013), we show that this relation persists after temporal recalibration, suggesting that alpha power reflects both idiosyncratic and temporary biases.

Results

Temporary and idiosyncratic biases in time perception

The participants' task was to judge which of two stimuli in an audiovisual pair of asynchronous stimuli was presented first. In an initial screening session, we determined the idiosyncratic bias of each participant. If a participant exhibited the tendency (across a set of balanced stimulus-onset asynchronies) to perceive the flash first more often, we would deem the flash-first response (Vfirst) as matching this individual's bias (matching-bias) and the sound-first response (Afirst) as against-bias (Fig. 1B). We computed the Point of Subjective Simultaneity (PSS) as a proxy for an individual's bias (Grabot & Wassenhove, 2017) and the Just Noticeable Differences (JNDs) for each individual and condition (Fig. 1B). In a planned sample, 12 participants were biased towards Vfirst responses (negative PSS, mean ± SD = -44 ± 46ms) and 12 were biased towards Afirst responses (positive PSS, mean ± SD = 38 ± 31ms).

To induce a temporary bias, we tested participants' perception after prolonged exposure to constant audio-leading or visual-leading delays of 200ms (A200V and V200A conditions). As expected, recalibration significantly changed the perceived simultaneity (Table S1). A repeated-measure one-way ANOVA showed that there was a significant effect of recalibration on PSS ($F(2,23) = 3.48$, $p = 0.039$; Fig. 2A). A post-hoc t-test revealed that the PSS after A200V recalibration significantly decreased compared to V200A recalibration ($t(23) = -2.51$, $p = 0.019$, CI95 = [-23, -2]ms, effect size = 12ms, BF = 2.80). In addition, the PSS significantly differed between the A200V and no recalibration conditions ($t(23) = -2.34$, $p = 0.028$, CI95 = [-29, -2]ms,

effect size = 16ms, BF = 2.04), but not between the V200A and no recalibration conditions (t(23) = -0.45, p = 0.657, CI95 = [-17, 11]ms, effect size = 3ms, BF = 0.23).

Recalibration also induced a change in perceptual sensitivity, as measured by the difference between JND1 and JND2 (denoted ΔJND). A repeated-measure one-way ANOVA showed that there was a significant effect of recalibration (F(2,23) = 3.85, p = 0.028). A post-hoc t-test revealed that the ΔJND during no recalibration differed significantly from the A200V (t(23) = -2.30, p = 0.031, CI95 = [-54, -3]ms, effect size = 28 ms, BF = 1.90) and V200A conditions (t(23) = -2.22, p = 0.037, CI95 = [-63, -2]ms, effect size = 32 ms, BF = 1.66), showing that the temporal order judgements became less sensitive after recalibration.

Behavioral results from the EEG sessions

The same participants then performed the same temporal order judgment task while EEG was recorded. Here, the JND1/2 extracted from each condition of the screening session (no-, A200V- and V200A- conditions) were used as fixed SOAs. The behavioral data confirmed that the selection of JNDs for the EEG experiment was appropriate and resulted in the expected percentage of Vfirst responses (30% for JND1 and 70% for JND2; Fig. 2B): a one-sample t-test indicated that the difference between the actual percent of Vfirst responses and the *a priori* percentage was not statistically different (t(143) = 1.23, CI95 = [-0.009, 0.038], p = 0.220, BF = 0.19). Using a sound-leading (JND1) and a flash-leading (JND2) delay for each individual allowed us to orthogonalize the correctness and the biasedness of the responses, while ensuring a sufficient number of trials per response (Fig. 1D).

Pre-stimulus alpha reflects the effort to overcome an idiosyncratic bias

Given the presumed role of pre-stimulus alpha band activity in shaping subsequent perceptual responses, we quantified the relation between alpha activity and the idiosyncratic biases. To investigate whether alpha power predicted the correctness or biasedness of a subsequent response, we extracted alpha power from -600 to -200ms before the onset of the first stimulus in no recalibration condition and entered this into a 2x2 ANOVA combined with a spatio-temporal cluster-based permutation test (Fig. 3A). Importantly, the contrasts for correctness and biasedness were orthogonal given the experimental design and were controlled for the physical order of stimuli presentation. We found a significant positive cluster for biasedness over left fronto-central sensors (-598 to -438ms, cluster-value = 291.50, p = 0.044), suggesting that an increase in alpha power predicts a matching-bias response (Fig. 3A, right). No effect (even at a reduced p<0.15) was found for correctness, nor was there any significant interaction. A Bayesian analysis revealed that there is positive or substantial evidence that alpha power averaged across the left frontal cluster do not differ between correct and incorrect response (BF = 0.21), that there is no interaction effect (BF = 0.27), and it confirmed a strong and decisive evidence for a biasedness effect (BF = 112).

To localize the neural generators underlying the effect of biasedness, we performed a source reconstruction on pre-stimulus alpha activity and contrasted matching-bias and against-bias responses. This revealed a cluster in left temporo-frontal areas, consistent with the left frontal topography (Fig. 3B). The center of mass of this cluster (at an uncorrected $p<0.05$) was located in the left rolandic operculum (MNI coordinates: -60 +5 +6, corresponding to Brodmann area 44). Based on the AAL atlas, this cluster comprised prominent parts of the left frontal inferior operculum, rolandic operculum and temporal superior area, with 64% of the grid points contained in the cluster falling in left frontal areas, 27% in left temporal areas, and 9% in the left postcentral area and the insula (Fig. 3B).

If pre-stimulus alpha power indeed reflects the effort to overcome an idiosyncratic bias, the difference in power between responses (Afirst and Vfirst) should scale with the degree of the individual bias, hence the magnitude of the individual PSS. To test this, we computed a Spearman rank correlation between the difference in pre-stimulus alpha power (Afirst-Vfirst) and the individual PSS extracted from the no recalibration condition (Fig. 3C). This revealed a significant cluster over left fronto-central sensors (-578 to -458ms, cluster-value = 426.81, $p = 0.036$), the location of which was consistent with the results from the ANOVA above. Within this cluster, the alpha power difference between Afirst and Vfirst response was $R = 0.60$ (bootstrap-based CI95% = [0.27, 0.82], Pearson: $R = 0.58$, BF = 11, Fig. 3C). As a control, we also tested within the same cluster whether the alpha power difference between correct and incorrect response correlates with the PSS, and found no evidence for correlation (Spearman: $R = 0.01$, $p = 0.942$, Pearson: $R = -0.04$, $p = 0.864$, BF = 0.16).

We explored whether this result was specific to the alpha band, by repeating the above analysis for the theta, low beta and high beta bands (Fig. S1). No significant clusters were found for biasedness in any of these bands (see SI Results and Table S2 for a Bayes Factor analysis). However, high beta band activity was related to correctness (-298 to -218ms, $p=0.002$), with decreased beta power in occipital central electrodes predicting a correct response.

We also investigated whether the phase of alpha activity was predictive of whether the following response was correct or biased, since previous studies suggested a link between alpha phase, detection performance and prior expectation (Busch, Dubois, & VanRullen, 2009; Sherman, Kanai, Seth, & VanRullen, 2016). A non-parametrical permutation-based procedure on the Phase Opposition Sum index - POS (VanRullen, 2016) - revealed no significant cluster for correctness or biasedness (Fig. 3D).

Pre-stimulus alpha reflects both idiosyncratic and temporary biases

Next, we investigated the interplay between the idiosyncratic bias and the temporary biases induced by recalibration. In particular, decreased alpha power could allow overcoming an idiosyncratic bias independently of any influence of contextual recalibration, or, on the contrary, could reflect an idiosyncratic bias modulated by temporary biases. To address this, we focused on

the cluster (i.e. electrodes and time points) that showed a significant alpha effect both for the ANOVA contrast and the correlation analysis in the no recalibration condition (-578 to -478ms, 23 electrodes, Fig. 3A and 3C).

To quantify whether alpha power is predictive of either the original idiosyncratic bias, or a updated bias emerging from recalibration, we split trials from A200V and V200A conditions i) according to correctness and biasedness relative to the recalibrated biases (PSS_{A200V} and PSS_{V200A}), or ii) relative to the original idiosyncratic bias (PSS_{no}).We then entered these alpha power values into a linear mixed-effect model with the factors correctness, biasedness, their interaction, and participants as a random effect (Fig. 4A). When using the adapted PSSs, alpha was significantly related to biasedness ($X^2(1) = 5.16$, $p = 0.023$, BF = 1.31), but not to correctness ($X^2(1) = 0.12$, $p = 0.726$, BF = 0.17), and the interaction was not significant ($X^2(1) = 1.11$, $p = 0.292$, BF = 0.38). When using the non-adapted PSS, no factors were significant (biasedness: $X^2(1) = 0.30$, $p = 0.586$, BF = 0.18; correctness: $X^2(1) = 0.12$, $p = 0.731$, BF = 0.17; interaction: $X^2(1) = 0.49$, $p = 0.482$, BF = 0.28). Furthermore, a model comparison based on a likelihood ratio test showed that the full model using the adapted PSSs (LL = 96.1) was explaining significantly more variance than the non-adapted model (LL = 94.5, $X^2 = 3.05$, $p < 10^{-3}$). An estimated Bayes factor suggested that the model with the adapted PSSs was 10 times more likely to occur than the model with the PSS_{no}. These results suggest that pre-stimulus alpha power predicts whether a subsequent response will follow or not the momentary and contextually adapted bias.

Trial-by-trial dependencies

Temporal recalibration is not only observed after prolonged exposure but can also emerge on a trial-by-trial basis (Van der Burg, Alais, & Cass, 2013; Van der Burg, Alais, & Cass, 2015). We investigated whether and how the previous trial influenced the alpha band activity prior to the subsequent trial and contributed to the behavioral response in the subsequent trial. First, we asked whether the previous stimulus (stimN-1) or the previous response (respN-1) significantly influenced the subsequent response (respN), by comparing the ability of distinct linear models based on different combinations of these predictors to predict the subsequent response (Table S3). The model providing the most parsimonious account of the data (according to the group-level BIC criterion) was the model with stimN and respN-1 as predictors (group-level likelihoods and criteria: LL = -21 660, AIC = 43 463, BIC = 43 848, Table S3). The model estimates and t-values averaged across participants were β(intercept) = -0.97 ± 0.84, $p < 0.05$ for 21/24 participants; β(stimN = Alead) = 1.63 ± 0.76, $p < 0.05$ for 23/24 participants; β(respN-1 = Afirst) = 0.06 ± 0.97, $p<0.05$ for 20/24 participants; df = 1 546 ± 70 (mean ± SD, Fig. 4B). Although a previous study has suggested that temporal recalibration is driven by the previous stimulus rather than the previous response (Van der Burg, Alais, & Cass, 2018), further analyses suggested that in the present data subsequent responses are more tied to the previous response than the previous stimulus (cf. SI Results).

We then asked whether the alpha activity before the subsequent trial was related to the stimuli or behavior in the previous trial (Fig. 4C). We sorted trials according to either the stimulus order

(Alead vs. Vlead), the response (Afirst vs. Vfirst), and the biasedness (matching-bias vs. against-bias) of the previous trial. A spatio-temporal cluster-based permutation test revealed no significant effects. In particular, for biasedness, one cluster over frontal electrodes came not even close to significance ($p = 0.111$; -498 to -418ms), suggesting that the previous stimuli or responses did not influence the pre-stimulus alpha activity for the subsequent trial.

Using additional analyses we further ruled out that alpha mediates, or modulates, the influence of the response in the previous trial on the current trial: A mediation analysis on alpha power from the left frontal cluster, revealed no significant mediation (path from respN-1 to the alpha power: $a=0.022$, $p = 0.051$; path from the alpha power to the respN: $b=0.05$, $p =0.031$; mediation term: $ab=5.2e-5$, $p=0.424$). Further, logistic modelling of the subsequent response revealed no interaction between alpha and the previous response (β(intercept) = -0.01 ± 0.53, $p < 0.05$ for 20/24 subj; β(respN-1=Alead) = 0.07 ± 0.78, $p < 0.05$ for 20/24 subj; β(alpha) = 0.04 ± 0.07, $p < 0.05$ for 2/24 subj, β(alpha*respN-1) = -0.04 ± 0.12, $p < 0.05$ for 3/24 subj; df= $1\,546 \pm 70$; mean $\pm$ SD).

Discussion

Although understudied, idiosyncratic biases are ubiquitous in behavior (Matthews & Meck, 2014; Kosovicheva & Whitney, 2017; Ipser, et al., 2017). Their origin is largely unknown but the persistency of these biases over time implies that they arise from structural or functional characteristics of an individual's brain (Kanai & Rees, 2011). Indeed, previous work has speculated about the relation of inter-individual differences in genotypes, neurotransmitters levels, brain structure or signatures of spontaneous brain activity (Kanai & Rees, 2011; Mennes, et al., 2011; Kleinschmidt, Sterzer, & Rees, 2012; Romei, Murray, & Thut, 2013; Matthews & Meck, 2014; Haegens, Cousjin, Wallis, Harrison, & Nobre, 2014; Marshall, Bergmann, & Jensen, 2015; Chechlacz, Gillebert, Vangkilde, Petersen, & Humphreys, 2015).

We here focus on a prevailing signature of spontaneous brain activity, alpha band oscillations. Our results show that a decrease in pre-stimulus alpha power is associated with an increased chance that the subsequent response will go against an idiosyncratic bias, but is not predictive of whether the response is correct. Further, the stronger an individual idiosyncratic bias, the larger the alpha power activity will differentiate between responses that (mis-) match the bias. Importantly, this relation also holds after temporal recalibration, a manipulation that affects contextual short-term biases in perception, and was specific to the alpha band. Hence, our results show that pre-stimulus alpha indexes the effort to overcome an individual's momentary, rather than stable and long-term, bias.

A mechanistic role of alpha power

Alpha activity supposedly reflects a signature of neural excitability (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Klimesch, 2012) with reduced alpha power correlating with higher neural firing rates and stronger sensory excitability (Romei, et al., 2008; Haegens, Nácher, Luna, Romo, & Jensen, 2011; Klimesch, 2012; Thut, Miniussi, & Gross, 2012; Kayser, Wilson, Safaai, Sakata, & Panzeri, 2015) while higher alpha power would relate to the inhibition of sensory-perceptual functions (Sauseng, et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). In line with such a neural underpinning, a series of studies suggested that reduced alpha power correlates with enhanced perceptual sensitivity (Ergenoglu, et al., 2004; Hanslmayr, et al., 2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Busch, Dubois, & VanRullen, 2009; Obleser & Weisz, 2012). Yet, recent studies suggested a different picture whereby the alpha power does not modulate perceptual sensitivity or accuracy per se but rather reflects a bias in perceptual decision making (Limbach & Corballis, 2016; Iemi, Chaumon, Crouzet, & Busch, 2017; Samaha, Iemi, & Postle, 2017; Craddock, Poliakoff, El-deredy, Klepousniotou, & Lloyd, 2017; Iemi & Busch, 2018; Wöstmann, Waschke, & Obleser, 2018). While the precise role of alpha in a mechanistic cascade of sensory-decision processes remains debated, we here consider alpha oscillations from a new perspective, through the prism of idiosyncratic and temporary biases.

We can envision two potential accounts on how alpha implements, or at least reflects, the origin of an idiosyncratic bias. The first account is related to attention, a function usually associated with alpha (Worden, Foxe, Wang, & Simpson, 2000; Sauseng, et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). A stronger anatomical connectivity between visual and association areas could for instance generate an individual bias toward vision. Increased attention to audition, indexed by decreased alpha power in auditory areas, could alleviate the anatomical imbalance by strengthening auditory processing. If true, this mechanism implies relationships between alpha power and biased responses in both auditory and visual areas and that, in these two areas, these two relationships are in the opposite direction. However, the main alpha effect found here was localized to prefrontal and temporal but not occipital regions (consistently with Grabot et al., 2017), hence not supporting such an attention-based account.

Another hypothesis is related to top-down cognitive control, a function that has been associated to prefrontal alpha (Sauseng, et al., 2005; Sadaghiani & Kleinschmidt, 2016; Wöstmann, Alavash, & Obleser, 2019). Previous studies have suggested that prefrontal alpha increases reflect a mechanism that prevents external information from interfering with high-level cognitive processes (Sauseng, et al., 2005; Klimesch, Sauseng, & Hanslmayr, 2007; Jensen & Mazaheri, 2010). Our finding that increased alpha power predicts biased responses is consistent with such an idea, as increased alpha would reflect internal information processing, which is more sensitive to the intrinsic biases of the system. In contrast, when alpha activity is low, neural excitability is increased (Haegens, Nácher, Luna, Romo, & Jensen, 2011; Thut, Miniussi, & Gross, 2012; van Kerkoerle, et al., 2014; Kayser, Wilson, Safaai, Sakata, & Panzeri, 2015), which will facilitate

circumventing biases. Based on this account, the correlation of alpha power with the overall bias reflects the cognitive effort needed to overcome an idiosyncratic bias.

Distinct mechanisms mediating prolonged and single-trial recalibration

The neural correlates of temporal recalibration itself are poorly understood (Stekelenburg, Sugano, & Vroomen, 2011; Kösem, Gramfort, & Wassenhove, 2014; Simon, Noel, & Wallace, 2017; Simon, Nidiffer, & Wallace, 2018), and although we do not directly focus on this question, our study opens new avenues for studying them.

We found that pre-stimulus alpha power predicts biased perception after temporal recalibration, but does not mediate the effect of previous responses on behavior, suggesting that dissociated mechanisms underlie prolonged and single-trial recalibration. There is evidence from psychophysical experiments supporting this hypothesis in the temporal (Van der Burg, Alais, & Cass, 2015) and the spatial domain (Bruns & Röder, 2015; Bruns & Röder, 2017; Watson, Akeroyd, Roach, & S.Webb, 2019). A recent neuroimaging study showed that pre-stimulus alpha power predicted the tendency to bind audiovisual events, but played no role in mediating the influence of the recent history (Rohe, Ehlis, & Noppeney, 2019). This dissociation between prolonged and single-trial recalibration could stem from the need to strike a balance between the sustainability of an optimal processing state, and the flexibility necessary to cope with rapid changes. Alpha activity, associated with top-down control in order to maintain an internal state, would then interact with prolonged recalibration, but not with single-trial recalibration.

Alternatively, the perceptual dependencies often described as single-trial recalibration may in fact not be a genuine recalibration effect but reflect a simple decisional bias to repeat a response in consecutive trials (Roseboom, 2019; Keane, Bland, Matthews, Carroll, & Wallis, 2019). Our data revealed a significant choice-repetition bias, which is inconsistent with a recalibration effect (exposing participants to audio-leading stimuli would increase their tendency for Vfirst responses). The absence of relation between pre-stimulus alpha power and the observed choice-repetition bias here points to a role of alpha activity in perceptual rather than decisional stages. Since a genuine recalibration effect can be observed if the choice-repetition bias is controlled for (Keane, Bland, Matthews, Carroll, & Wallis, 2019), further investigations are needed to determine whether alpha power also compensates for single-trial recalibration.

Conclusion

The inter-individual variability in brain structures may generate idiosyncratic biases, which can help in understanding fundamental mechanisms underlying perception. We show that the prominent alpha rhythm in the brain interacts with idiosyncratic and temporary biases, and is predictive of the degree of biasedness of an upcoming response. Given the opportunity to manipulate alpha band activity using brain stimulation (Romei, Gross, & Thut, 2010; Romei, Murray, & Thut, 2013), future work can now test the neural basis of idiosyncratic behavioral biases in other contexts, and using mechanistic interventions to manipulate such biases.

Materials & Methods

Participants

Forty right-handed naive participants with normal or corrected-to-normal vision and normal hearing were tested in a first screening session (10 male, 30 female; mean ± SD age = 24 ± 3 years). Each provided written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013), and the study was approved by the local ethics committee of Bielefeld University. The screening session was designed to collect a planned sample of 24 participants, balanced according to their preferred temporal order (see below), and with a negative JND1 and a positive JND2 (defined as in Fig. 1B). 12 participants were excluded based on the screening data, including 10 whose JNDs fell outside the range of tested stimulus onset asynchronies (according to the criteria used in Spence et al., 2001), one whose JNDs were both negative, and one who did not complete the whole session. In total, 28 participants joined the EEG session, 4 of which had to be excluded because they had less than 20 trials in at least one condition. Thus, in the final analysis, we included 24 participants (7 male, 17 female; age = 24 ± 2 years mean ± SD).

Stimuli

The experiment was controlled using the Psychophysics Toolbox (Version 3.0.14; http://psychtoolbox.org/) and run using MATLAB (Version R2017a; The MathWorks, Inc., Natick, MA). The visual stimuli were white rings (outer diameter = 12°, inner diameter = 8°, 275 cd/m²) presented for 25 ms (three frames) and centered on a grey LCD screen (refresh rate = 120 Hz, resolution = 1920 × 1080 pixels, 16 cd/m²). Participants were asked to fixate a black cross presented in the middle of the screen during the whole experiment. Auditory stimuli were sine-wave tones (2 kHz) presented for 25 ms (including 5-ms fade-in and 5-ms fade-out) at a comfortable hearing level (73 dB). They were presented trough speakers placed behind each side of the monitor screen to ensure a perceived co-localization of sound and visual stimuli. The relative timing of auditory and visual stimuli was tested to be precise up to ± 3ms using an oscilloscope and a photodiode.

Screening session

The experiment comprised a screening session and two EEG sessions based on a temporal order judgment (TOJ) task (Fig. 1A). The three sessions took place within approximately 10 days (7 ± 6 days between the screening session and the first EEG session, and 3 ± 2 days between the two EEG sessions). Experiments took place in a darkened and electrically shielded room (Desone Ebox; Germany), where the participant sat at 90 cm distance from the screen.

The screening session aimed at estimating the temporal thresholds associated with judging the temporal order of a pair of audiovisual stimuli (Fig. 1A, 1B). The individual thresholds were then used as stimulus onset asynchrony (SOA) in the following EEG sessions, ensuring a similar ratio of Afirst and Vfirst responses. In the screening session, the audiovisual stimuli were separated by 12 different SOAs: ± 20, ± 50, ± 80, ± 110, ± 160, ± 250 ms. Negative values indicate that the sound was presented first.

The task was performed in three conditions: without recalibration (no), after sound-leading recalibration (A200V) and after visual-leading recalibration (V200A). In the no recalibration condition, participants were presented with a pair of audiovisual stimuli and had to judge which of the two came first, in a two-alternative forced choice, by pressing a key on a keyboard. The trials in A200V- and V200A- recalibration conditions were split into 3 blocks per condition. Each block consisted of an exposure phase and a test phase. During the exposure phase, 84 audiovisual pairs with an identical SOA of 200 ms were presented at roughly 1 Hz (uniform distribution: 900-1100ms). In A200V- recalibration (resp. V200A) blocks, 80 trials were audio-leading (resp. visual-leading) while 4 deviant trials were visual-leading (resp. audio-leading). To enhance recalibration effects and to ensure that participants kept their attention focused they were asked to detect these deviant trials as fast as possible (Heron, Roach, Whitaker, & Hanson, 2010). The hit rate was on average 84 ± 10% and the false alarm rate was 1 ± 1 % (mean ± SD). The exposure phase was immediately followed by a test phase. Top-up trials were used to maintain recalibration (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Vroomen, Keetels, Gelder, & Bertelson, 2004). We used a minimum number of top-up trials sufficient to enhance recalibration effects (Cai, Stetson, & Eagleman, 2012) and tested two consecutive audiovisual pair at once. Three top-up trials were presented at roughly 1Hz (uniform distribution: 900-1100ms). 700ms after the last top-up trial, the black fixation cross turned green, indicating to the participant to judge the order of the two next pairs of AV stimuli.

For all conditions (no, A200V, V200A), inter-trial interval delays were uniform between 900 and 1100 ms. In the screening session, each SOA was repeated 24 times per condition. The screening session consisted of no recalibration block, followed by three A200V recalibration and three V200A recalibration blocks, with randomized order. Participants were allowed to take a short break between blocks. Before the experiment, they were trained with 10 repetitions of maximal SOAs (± 250ms) for each recalibration condition and received feedback. Button mapping for responses was balanced between participants.

PSS and JNDs estimation

In the screening session, we determined the order bias (PSS) and the just noticeable differences (JNDs) for each participant using the method of constant stimuli. For each recalibration condition (no, A200V and V200A), the percentage of Vfirst responses from the screening session was determined as a function of SOA and fit using a psychometric curve described by a logistic function with three parameters: bias, slope and lapse rate (Spence & Squire, 2003; Mégevand, Molholm, Nayak, & Foxe, 2013). We chose a three-parameter model based on a piloting test (n = 6) which revealed a lower Bayesian information and Akaike information criterion for this model

compared to two- (bias and slope) or four-parameter (bias, slope, lapse rate for auditory-leading stimuli, lapse rate for visual-leading stimuli) models. The goodness of fit (R^2) was 90.2 ± 8.3% on average across participants (mean ± SD). The PSS and JNDs were defined as shown in Fig. 1B, for each recalibration condition (no, A200V and V200A). To obtain a balanced design between correctness and bias (Fig. 1D), it was necessary that each individual's JND1 was negative (sound-leading SOA), and each JND2 positive (visual-leading). To achieve this, we had to adjust the definition of JNDs for 5 participants (the JNDs performance ratios deviating from 30/70 for these participants were respectively: 23/70 in V200A condition; 30/78 in no condition, 30/87 in A200V condition, 30/78 in V200A condition; 30/93 in V200A condition; 30/95 in no condition, 30/82 in A200V condition, 30/90 in V200A condition; 30/92 in no condition, 30/75 in A200V condition).

EEG sessions

Each EEG session consisted of two no recalibration, four A200V recalibration and four V200A recalibration blocks. Here we used the three pairs of JND's derived from the screening session as SOAs, and each SOA was repeated 200 times per condition. The ITI preceding test trials was randomly drawn from a uniform distribution between 1.5-1.7s. Four catch trials (SOA = ± 250ms) were introduced in each block (~4% of the total number of trials) to test the involvement of the participants. 88 ± 7 % (mean ± SD) of the catch trials were correctly perceived. The no recalibration blocks were always presented first, followed by the 8 recalibration blocks in a randomized order.

EEG acquisition and preprocessing

EEG signals were recorded using an active 128 channel Biosemi system (BioSemi, B. V., The Netherlands), with additional four electrodes placed near the outer canthi and below the eyes to record the electro-occulogram (EOG). Electrode offsets were below 25mV.

Offline preprocessing and analysis were performed with MATLAB R2017a (The MathWorks, Natick, MA, USA) using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The data were band-pass filtered between 0.2 and 90Hz, resampled to 50Hz and epoched from -1.5s before the first stimulus onset to 1s after. We removed ICA components that reflect eye movement artefacts, localized muscle activity or poor electrode contacts (12 ± 6 rejected components per block, mean ± SD). These were identified following definitions provided in the literature (Hipp & Siegel, 2013; O'Beirne & Patuzzi, 1999). Furthermore, trials with amplitude exceeding 150µV after 1Hz high-passed filtering and trials with reaction times shorter than 200ms were rejected. In total, 3 ± 5 % of trials (mean ± SD) were rejected across all participants. The EEG signals were not re-referenced to facilitate the analysis of local alpha power and phase effects (Yao, et al., 2005).

Logistic modelling of behavioral data

To quantify the influence of the current stimulus and the previous stimulus or response on single trial responses, we used generalized linear models using a binomial distribution with a logit link

function. The model parameters were estimated using maximum likelihood methods based on Laplace approximation for each participant. The outcome variable was the response of the current trial (respN: Afirst=1, Vfirst=0), the predictors were the physical stimulus of the current trial (stimN: Alead=1, Vlead=-1), the physical stimulus of the previous trial (stimN-1: Alead=1, Vlead=-1) and the response of the previous trial (respN-1: Afirst=1, Vfirst=-1). All variables were treated as categorical variables. We first determined which behavioral model was explaining best the variance of the dataset by comparing Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and log likelihood, after summing them across individuals (Table S3).

Time-frequency analysis

We extracted the single trial power in different frequency bands between -1.5s to 0.5s around the first stimulus onset. To avoid any post-stimulus contamination, each trial was windowed (with a function equal to zero after stimulus onset and equal to 1 before, with a 27.5ms transition realized by a Hann function). The alpha power was obtained by using Morlet wavelets (10Hz, 3.5 cycles, which gives a spectral bandwidth of 7.1-12.8Hz) and log-transformed. We also extracted the power from theta (6Hz, 3.5 cycles, spectral bandwidth = 4.3-7.7Hz), low beta (17Hz, 5 cycles, spectral bandwidth = 13.6-20.4Hz) and high beta bands (25Hz, 5 cycles, spectral bandwidth = 20-30Hz).

To investigate whether pre-stimulus alpha power was predictive of response correctness or biasedness, the alpha power was z-scored for each participant using the average and standard deviation across all trials and time points between -600 and -200ms for each sensor. The trials were then split into two groups depending on the contrast of interest (correct vs incorrect response, matching-bias vs against-bias responses). For the correlation analyses with the PSS, we used the raw alpha power differences between Afirst and Vfirst responses without baseline or z-scoring.

Source reconstruction

We performed source reconstruction on the pre-stimulus alpha activity (-600 to -200ms) using DICS and re-referenced data (Gross, et al., 2001). Cross-spectral density matrices were computed using multiple tapers in the alpha band (centered in 10Hz, spectral smoothing of 3Hz). We created a forward model by using a standard 3D source model with 6mm dipole spacing and a MRI template from Fieldtrip, on which we manually aligned the 128-electrode array. We then computed the common inverse filter from all trials using DICS and applied this filter to each condition.

Phase analysis

We used the phase opposition sum index (POS) to determine whether the instantaneous pre-stimulus alpha phase was concentrated around a mean value statistically different between two conditions (VanRullen, 2016). After equalizing the number of trials for each condition, we

computed first the inter-trial coherence (ITC) for each condition, sensor and time point between -600 and -200ms. The POS index is defined as followed:

$$POS = ITC_{cond1} + ITC_{cond2} - 2*ITC_{allTrials}$$

Statistical analyses

The power difference (-600 to -200ms) between conditions was tested using a non-parametric cluster-based permutation procedure based on an independent samples t-test (Fig. 2A) using the following parameters: two-sided t-test, alpha level for thresholding individual points at p=0.05, minimal number of neighbors in a cluster of 3, t-statistics performed on the maximal sum across cluster, 4000 randomizations. The same procedure was used to assess the significance of the Spearman correlation.

The phase difference between conditions was statistically assessed using a permutation-based approach (VanRullen, 2016). For each subject, a surrogate distribution was built by randomly shuffling the trials label and recalculating the POS for each new shuffling (number of repetitions: 1000). Then, a group-level surrogate distribution was built by randomly picking a POS sample for each subject distribution and averaging the samples across subjects (number of repetitions: 100 000). Last, a cluster-based permutation procedure was used to compare the empirical POS values to the group-level surrogate distribution (cluster threshold corresponding to the two-sided 95th percentile), ensuring a correction for the multiple comparison problem.

We computed the Bayes factor for paired t-tests and Pearson correlation using the *bayesFactor* toolbox in Matlab and the *BayesFactor* package with R (Version 3.5.3), and interpreted the Bayes Factor following (Jarosz & Wiley, 2014).

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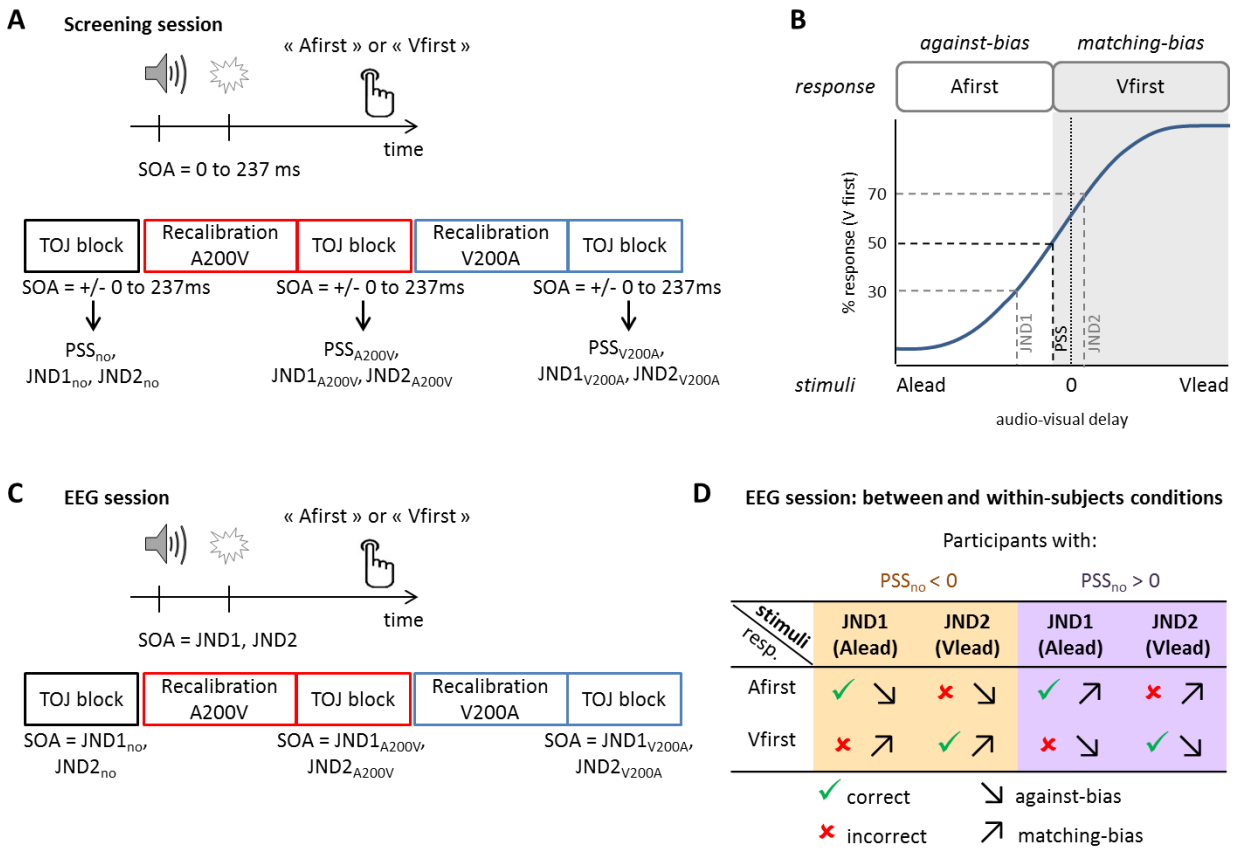

Fig. 1: Experimental design. A. The screening session was based on a temporal order judgment task and comprised three conditions: no adaptation, audio-leading adaptation (A200V) and visual-leading adaptation (V200A). We assessed the individual bias in temporal order perception (PSS_{no}), adapted PSSs (PSS_{A200V} and PSS_{V200A}) and JNDs. **B.** Schematics of a psychometric curve obtained after the screening session. The PSS was defined as the SOA for which a participant's performance was at chance level (50%). The JNDs were defined as the SOAs for which a participant's performance was at 30 % (JND1) and 70% (JND2) of performance. If a participant has a negative PSS, i.e. the sound needs to be presented first so that s/he can perceive simultaneity, s/he has an increased tendency to reply Vfirst (matching-bias response) compared to Afirst (against-bias response). **C.** In the EEG session, the JNDs derived in the screening session were used as SOAs. **D.** The correctness and biasedness contrasts are fully orthogonal, and they comprise the same number of audio-leading and visual-leading pairs.

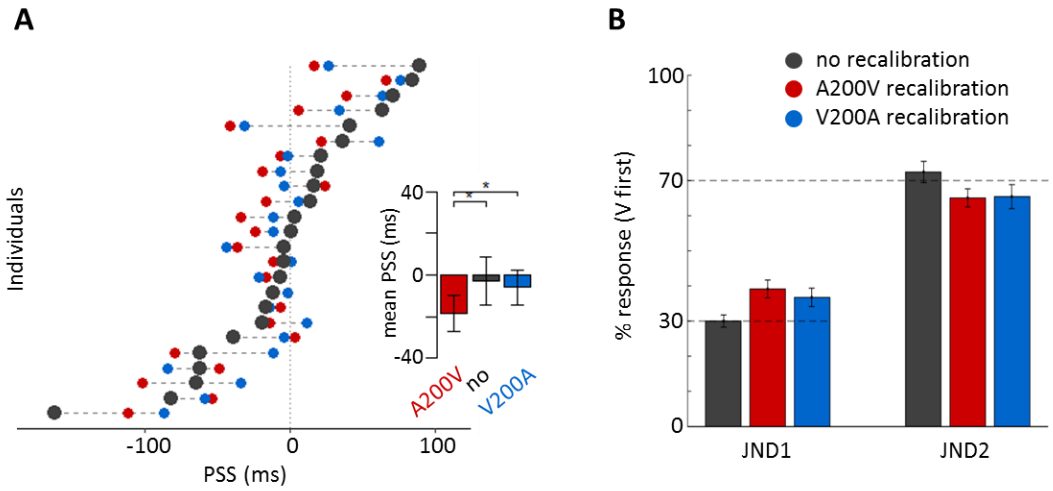

Fig. 2. Behavioral results. A. Each line shows individual's PSSs for each condition (grey: no, red: A200V, blue: V200A). The insert depicts the group-averaged PSS for each condition (error bars shows ± 1SEM). Asterisks indicate the significance level of the repeated-measure one-way ANOVA (with *$p < 0.05$) **B.** Behavioral results of the EEG session. The percentage of flash-first responses is shown for each SOA (JND1 and JND2) and adaptation condition (error bars show ± 1SEM).

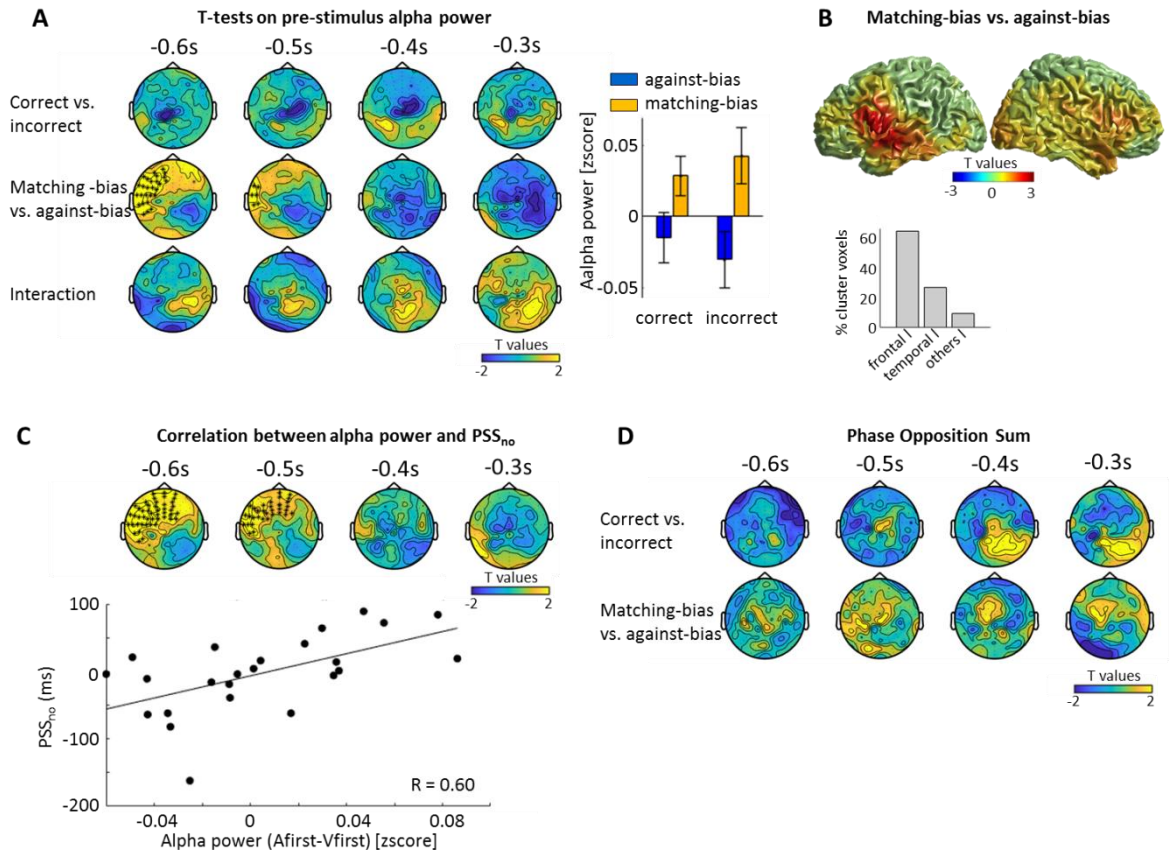

Fig. 3. Pre-stimulus alpha power and idiosyncratic bias. A. ANOVA t-maps for main effects (correctness, matching bias) and interaction performed for the no-recalibration condition on pre-stimulus alpha power. One positive significant cluster for biasedness (-598 to -438ms, p = 0.044) was found. Each topography shows the average t-map across a 100ms temporal window starting at the indicated time point. The bar graph shows alpha power averaged across the significant cluster, for each response. **B.** Prestimulus alpha power contrasted between matching-bias and against-bias responses in source reconstructed data from -600 to -200ms. The center of mass of the cluster corresponding to uncorrected $p<0.05$ is located in the left rolandic operculum. 64% of the cluster covers left frontal areas, 27% left temporal areas and 9% left postcentral areas and insula (based on the AAL atlas). **C.** Correlation between PSS_{no} and the difference of prestimulus alpha (Afirst-Vfirst) tested using a spatio-temporal cluster based permutation test. One significant cluster was found (p = 0.036; -578 to -458ms). **D.** The phase opposition sum (POS) index was used to determine whether the instantaneous alpha phase has different concentration between two conditions. No significant cluster was found.

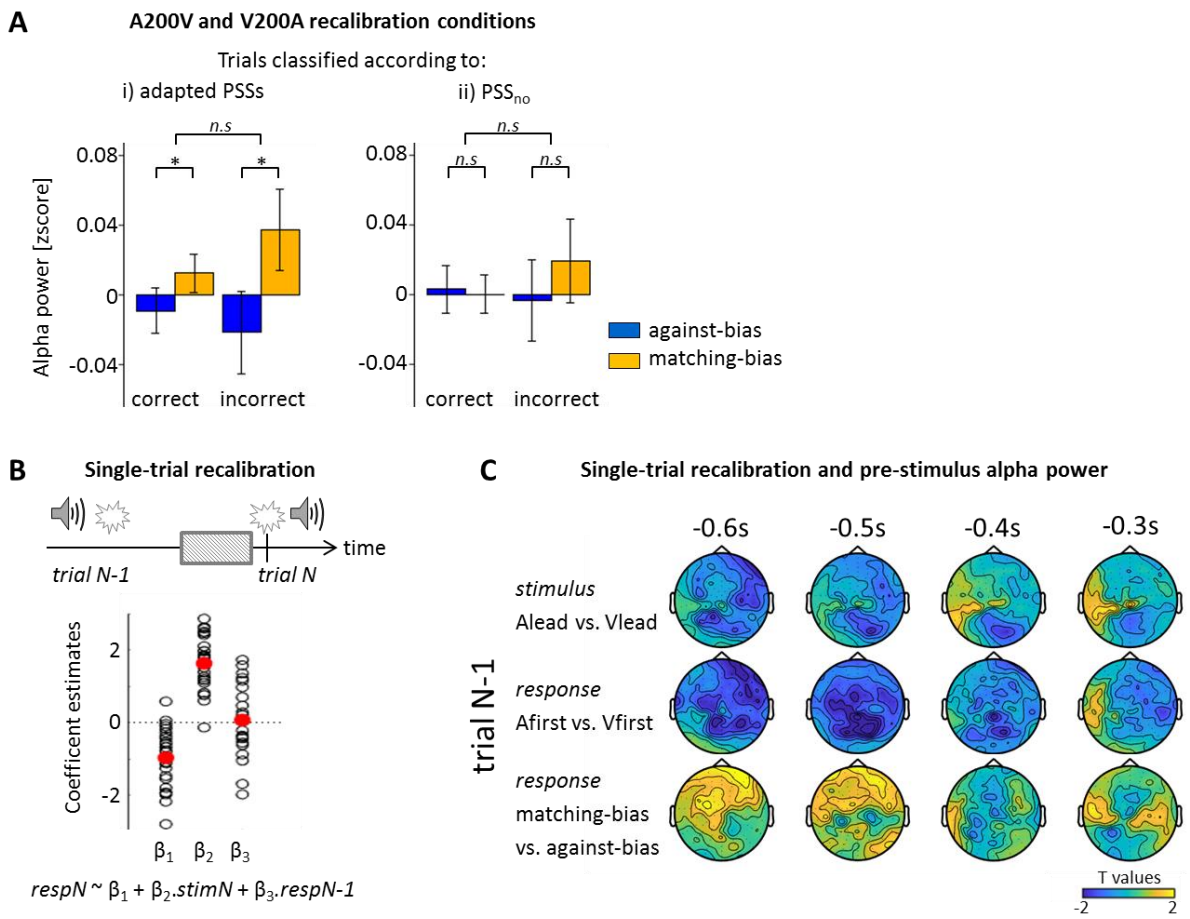

Fig. 4. Pre-stimulus alpha power and temporary biases. A. The trials in A200V and V200A conditions were either classified following i) the adapted PSSs (PSS_{A200V} and PSS_{V200A}) or ii) the non-adapted PSS (PSS_{no}). The alpha power was computed according to biasness and correctness for these two classifications and averaged across the conjunction cluster derived from the ANOVA and the correlation analysis (Fig. 3A and 3C). A two-way ANOVA (factors: biasness, correctness) showed that the biasedness factor was significant only when trials were classified according to adapted PSSs (*: $p < 0.05$, *n.s.*: non-significant). **B.** A single trial model was used to explain the response in the current trial N (respN) based on the current stimulus (stimN) and the previous response (respN-1). The coefficient estimates for each individual (black dots) and the mean across individuals (red) are shown. **C.** The relationship between pre-trial N alpha power and the response of trial N-1 was investigated by splitting trials according to either stimulus, response or biasedness of the response in trials N-1. No significant clusters were found.