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Moment-to-Moment Fluctuations in Neuronal Excitability Bias Subjective Perception Rather than Strategic Decision-Making

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Abstract

Perceiving an external stimulus not only depends on the physical features of the stimulus, but also fundamentally on the current state of neuronal excitability, indexed by the power of ongoing alpha-band and beta-band oscillations (8–30 Hz). Recent studies suggest that heightened excitability does not improve perceptual acuity, but biases observers to report the presence of a stimulus regardless of its physical presence. It is unknown whether this bias is due to changes in observers' subjective perceptual experience (perceptual bias) or their perception-independent decision-making strategy (decision bias). We tested these alternative interpretations in an EEG experiment in which male and female human participants performed two-interval forced choice (2IFC) detection and discrimination. According to signal detection theory, perceptual bias only affects 2IFC detection, but not discrimination, while interval decision bias should be task-independent. We found that correct detection was more likely when excitability before the stimulus-present interval exceeded that before the stimulus-absent interval (i.e. 8–17 Hz power was weaker before the stimulus-present interval), consistent with an effect of excitability on perceptual bias. By contrast, discrimination accuracy was unaffected by excitability fluctuations between intervals, ruling out an effect on interval decision bias. We conclude that the current state of neuronal excitability biases the perceptual experience itself, rather than the decision process.

Significance Statement: The current state of neuronal excitability, indexed by the power of ongoing low-frequency oscillations (8–30 Hz), has a strong influence on perception. However, the specific mechanism underlying this influence is a continuing subject of debate in neuroscience. Previous research showed that states of heightened excitability make observers report the presence of a sensory stimulus even when none is present. Heightened excitability may therefore indicate a state of strategic decision-making (i.e. observers prefer to report "Yes, I saw the stimulus") or a state of amplified subjective perception (i.e. observers experience a stimulus even when none is present). Here, we tested these alternative interpretations and found evidence that fluctuations in neuronal excitability bias the perceptual experience itself, rather than the decision strategy.

Introduction

Ongoing neuronal activity just preceding, or in the absence of experimental events, is ubiquitous in electrophysiological recordings in the form of "spontaneous" or "pre-stimulus" oscillations. A prominent type of such spontaneous activity is the α- and β-rhythm (8–30 Hz),

which plays a key role in regulating cortical excitation and inhibition (Jensen and Mazaheri, 2010; Spitzer and Haegens, 2017). Specifically, states of weak α- and β-power (in addition to other indices, such as specific α-phases) reflect increased excitability in sensory brain areas, as indexed by the spike-firing rate (Haegens et al., 2011; Watson et al., 2018), multiunit activity (van Kerkoerle et al., 2014), ongoing γ power (Spaak et al., 2012) and the hemodynamic fMRI signal (Goldman et al., 2002; Becker et al., 2011).

How do spontaneous neural oscillations interact with the processing of sensory events? Numerous studies have demonstrated that observers are more likely to detect visual targets that are preceded by weak pre-stimulus low-frequency power (8–30 Hz), reflecting stronger neuronal excitability (Ergenoglu et al., 2004; Chaumon and Busch, 2014). But does strong excitability help observers distinguish more *accurately* between target and non-target stimuli, or does excitability simply make all stimuli appear more target-like? Recent studies have demonstrated that in visual detection tasks, strong excitability increases the hit rate in stimulus-present trials as well as the false alarm rate in stimulus-absent trials (Limbach and Corballis, 2016; Iemi et al., 2017). Moreover, recent studies found that this effect is specific to tasks requiring the detection of target presence vs. absence, while tasks requiring discrimination between two alternative target types are unaffected by excitability (Iemi et al., 2017; Samaha et al., 2017b). In sum, these findings indicate that contrary to the previously dominant view in the literature (van Dijk et al., 2008; Romei et al., 2008; Payne and Sekuler, 2014), heightened excitability does not lead to an increased perceptual precision, but to a more liberal detection bias.

These findings could be regarded as evidence refuting an effect of excitability on perception proper, showing instead an effect on observers' strategic *decision bias*: a deliberate preference to report "yes, I saw the target" in both target-present and -absent trials. Accordingly, false alarms induced by a decision bias during states of strong excitability are due to a shift in decision strategy. However, not every change in bias implies a change in deliberate decision strategy (Witt et al., 2015); alternatively, excitability might modulate *perceptual bias*: a change in the amplification of the neural representation of both target and non-target stimuli. In tasks requiring the detection of target presence vs. absence, this process boosts the perception of target presence in both target-present and -absent trials. Accordingly, false alarms induced by perceptual bias during states of strong excitability are due to genuine, albeit false, impressions of seeing a target. Evidently, decision bias and perceptual bias each lead to very different theoretical interpretations of how

spontaneous brain activity is related to perception and behavior.

The present study was conducted in order to determine whether spontaneous fluctuations in pre-stimulus low-frequency power (i.e. 5–30 Hz, a proxy for neuronal excitability) affect either precision, perceptual bias or decision bias. To this end, we used a two-interval forced choice (2IFC) paradigm, in which each trial includes a target and a non-target interval. In 2IFC detection, a stimulus is presented in the target interval and no stimulus is presented in the non-target interval, and observers report the interval comprising the stimulus. In 2IFC discrimination, a target-stimulus (e.g. a left-tilted grating) is presented in one interval, and a non-target stimulus (e.g. a right-tilted grating) in the other interval, and observers report the interval comprising the target.

We tested three models that represent alternative hypotheses on how weak pre-stimulus low-frequency power, reflecting strong neuronal excitability, influence performance (see Methods for details). If greater excitability improved perceptual *precision*, performance in both 2IFC detection and discrimination should be most accurate when power in both intervals is weak. If greater excitability leads to a more liberal *perceptual bias*, performance in 2IFC detection should be most accurate when power is weak in the target-interval (enhancing correct impression of stimulus-presence), but strong in the non-target interval (inhibiting false impression of stimulus presence), implying that excitability during the stimulus-present interval exceeds excitability during the stimulus-absent interval. Since this effect reflects a bias in the perception of stimulus presence vs. absence, it should be specific to the detection task. If greater excitability leads to a more liberal *decision bias*, performance in both 2IFC detection and 2IFC discrimination should be most accurate when power is weak in the target-interval compared to the non-target interval, indicating a strategic tendency to report the interval with the weakest power.

The results confirmed the predictions of the perceptual bias model, implying that spontaneous fluctuations in excitability, indexed by α- and β-power, bias subjective perceptual experience rather than strategic decision-making or precision.

Materials and Methods

Participants

Previous studies on the relationship between neuronal excitability and perception (Busch et al., 2009; Lange et al., 2013; Chaumon and Busch, 2014; Iemi et al., 2017, e.g.) have typically reported samples of 12–33 participants. To ensure a robust estimate of our neurophysiological effect, we recruited a sample of 25 participants (mean: 29.3, SEM = 0.75 year old, 16 females, 2 left-handed). All participants had normal or corrected-to-normal vision and no history of neurological disorders. Each participant took part in two sessions, one for each task, on two separate days within a 7-day period. One participant was excluded before EEG preprocessing and behavioral analysis, because she could not participate in the second experiment. Two participants were excluded after EEG preprocessing because of excessive artifacts. A total of 22 participants were included in the analysis. Prior to the experiment, written informed consent was obtained from all participants. All experimental procedures were approved by the ethics committee of the German Psychological Society.

Stimuli

The experiment was written in MATLAB (RRID:SCR_001622) using the Psychophysics toolbox 3 (RRID:SCR_002881; Brainard, 1997; Pelli, 1997). Stimuli were presented on a black background, using a gamma-linearized cathode ray tube monitor operated at 100 Hz and situated in a dark room. Low-contrast Gabor patches tilted by 10° clockwise or counterclockwise from the vertical meridian with a diameter of 0.75° visual angle were displayed at 10° to the left or to the right (counterbalanced across conditions) of the fixation dot.

Each trial included two successive intervals, separated by a 2 s gap. Each interval lasted two frames (0.02 s) and was indicated by a 50% reduction in the diameter of the fixation point (Figure 1). A Gabor stimulus was presented in one or both intervals for a duration of two frames (0.02 s). After a delay of 0.4 s following the second interval, the fixation dot turned into a question mark, which instructed participants to deliver a response with their dominant hand via button-pressing, in accordance with the task instructions. After the button press, the question mark disappeared and participants received color-coded feedback: correct/incorrect responses were indicated by a

green/red fixation dot, lasting 0.2 s. After the feedback, the fixation dot turned white and a new trial started.

For each participant and task, an adaptive staircase procedure (QUEST; Watson and Pelli, 1983) was used to find the stimulus contrast yielding 75% accuracy. To ensure that the analysis included only trials of similar contrast, we rejected outlier trials in which the difference between the presented contrast value and the final threshold estimated by QUEST exceeded $\pm$10%. Using this procedure, we ensured that the 2IFC detection and discrimination tasks were equally difficult.

Experimental Design

Participants performed a 2IFC detection and a 2IFC discrimination task in two separate sessions. Task order was counterbalanced across participants. Each session lasted approximately 1,5 h with breaks and included 700 trials divided into 14 blocks of 50 trials each. For both tasks, each trial included a target-interval and a non-target interval. The order of target and non-target intervals within a trial was counterbalanced and randomized across trials, such that half of the trials were target-first (T1) and non-target-first (nT1), respectively.

In the 2IFC detection task, a Gabor stimulus was presented in the target interval and a blank screen was presented in the non-target interval (Figure 1a). Participants were informed that each trial contained a stimulus, which could appear in either interval, and were instructed to report in which interval they perceived the stimulus ("first" vs. "second").

In the 2IFC discrimination task, each of the two intervals contained a Gabor stimulus: a left-tilted Gabor appeared in the target interval and a right-tilted Gabor appeared in the non-target interval (Figure 1c). Participants were informed that each trial contained two stimuli characterized by different tilts, and were instructed to report in which interval they perceived the left-tilted target ("first" vs. "second").

EEG recording and preprocessing

EEG was recorded with a 64-channel Biosemi ActiveTwo system at a sampling rate of 1024 Hz. Electrodes were placed according to the international 10-10 system (electrode locations can be found on the Biosemi website: https://www.biosemi.com/download/Cap_coords_all.xls)

The horizontal and vertical electro-oculograms were recorded by additional electrodes at the lateral canthi of both eyes and below the eyes, respectively.

The EEGLAB toolbox version 11, running on MATLAB (R2010b), was used to process and analyze the data (Delorme, 2004). Data were re-referenced to the average of all electrodes, epoched from -3.7 to 0.7 s relative to the second interval onset and down-sampled to 256 Hz. The data were then filtered using an acausal band-pass filter between 0.25 and 80 Hz. Gross artifacts (eye blinks, and noisy data segments) were removed manually, and entire trials were discarded when a blink occurred within a critical 0.5 s time window preceding interval onset, to ensure that participants' eyes were open at interval onset. After rejecting trials with EEG artifacts and contrast outliers, the total number of trials analyzed was 680 (5.5 SEM) and 645 (10.5 SEM) for the detection and discrimination session, respectively.

Noisy channels were selected manually on a trial-by-trial basis for spherical spline interpolation (Perrin et al., 1989). In the detection task we interpolated on average 8.1 channels (SEM = 1.13) in 22.3 trials (SEM = 4.74) in 21 out of 22 participants. In the discrimination task we interpolated on average 8.5 channels (SEM = 0.85) in 21.7 trials (SEM = 3.71) in 19 out of 22 participants. Furthermore, the EEG data were transformed using independent component analysis (ICA), and SASICA (Chaumon et al., 2015) was used to guide the exclusion of IC related to noisy channels and muscular contractions, as well as blinks and eye movements occurring before or after the critical intervals.

We then re-epoched the trials relative to the onsets of target and non-target interval of each trial, enabling us to analyze within-trial, between-interval fluctuations in oscillatory power. Time-frequency analysis was carried out using a wavelet transform (Morlet wavelets, 30 frequencies, frequency range: 1–30 Hz, number of cycles increasing linearly from 1 to 12). Thus, a wavelet at 10 Hz was 4.4 cycles long and had a temporal resolution σ_t of 0.14 s and a spectral resolution σ_f of 4.53 Hz. Since wavelet analysis is computed by convolving the data with a function that is extended in time, it is possible that pre-stimulus effects close to stimulus onset are actually affected by post-stimulus data. Iemi et al. (2017) determined the extent of this contamination by estimating the wavelet's temporal resolution σ_t (Tallon-Baudry et al., 1996). Thus, we consider effects as truly "pre-stimulus", only if they occur at time points earlier than interval onset - σ_t (indicated with a red line in Figure2a/c, 3a/e, 4a/d/f/h).

Modeling the relationship between oscillatory power and behavioral performance

Signal Detection Models

Signal detection theory (Macmillan and Creelman, 2005, Figure 1b/c) provides an account of behavioral performance and perceptual decision making in 2IFC detection and discrimination tasks.

For a 2IFC detection task (Figure 1a), SDT posits that observers sample an internal response in each interval, compare the two internal responses, and report whichever interval yielded the stronger response. Thus, if the internal response during the target (stimulus-present) interval exceeds the response during the non-target (stimulus-absent) interval, the participant makes a correct detection. Across trials, overall accuracy in 2IFC detection depends on the relative distance between the response distributions for stimulus-present and stimulus-absent intervals (the two-dimensional Gaussian distributions in Figure 1b).

For a 2IFC discrimination task (Figure 1c), SDT posits that in each interval, observers sample the internal responses of two feature detectors selective for the target and non-target stimulus, respectively. The relative strength of these two responses serves as an index of evidence of target-presence in a given interval. Observers compare this evidence between both intervals and report whichever interval yielded the strongest evidence (Figure 1d). If the strength of evidence for target-presence in the target-interval exceeds the strength of evidence in the non-target interval, the participant makes a correct response. Across trials, overall accuracy in 2IFC discrimination depends on the relative distance between the response distributions for target and non-target intervals (two-dimensional Gaussian distributions in Figure 1d). Note that 2IFC detection is based on comparing the responses of a single signal detector across two intervals, while 2IFC discrimination is based on comparing the relative strength of two feature detectors across two intervals.

As described in the Introduction, different models hypothesize that pre-stimulus low-frequency power (i.e. 5–30 Hz, a proxy for neuronal excitability) affects either perceptual accuracy, perceptual bias, or decision bias. Importantly, these models make specific, testable predictions regarding the relationship between pre-stimulus power and performance in 2IFC detection and discrimination tasks.

According to the precision model, weak pre-stimulus power (i.e. greater excitability) improves the accuracy in perceptual tasks by increasing the relative distance between the response distributions in the target and non-target intervals, possibly via reduction of the trial-by-trial response variability (Iemi et al., 2017). In 2IFC detection stronger excitability results in a greater distance between the response distributions of stimulus-present and -absent intervals. In 2IFC discrimination stronger excitability results in a greater difference in target evidence between target and non-target intervals. Thus, the precision model predicts that greater accuracy is related to weaker overall power in both the target and the non-target interval in both detection and discrimination.

According to the perceptual bias model, weak pre-stimulus power (i.e. greater excitability), amplifies internal responses to any kind of stimulus. In 2IFC detection, such an amplification would improve accuracy if amplification happened to be stronger in the stimulus-present compared to the stimulus-absent interval, thus increasing the relative distance between the internal responses in target and non-target intervals (Figure 1b). In other words, 2IFC detection accuracy should be influenced by the balance of excitability and inhibition between the stimulus-present and stimulus-absent interval. In 2IFC discrimination, stronger amplification in either target or non-target interval would simultaneously increase internal responses of both target and non-target feature detectors in that interval, leaving the relative distance between their response distributions (i.e. target evidence) unchanged (Figure 1d). In sum, the perceptual bias model predicts that 2IFC detection accuracy is greater when pre-stimulus power is weaker in the stimulus-present interval compared to the stimulus-absent interval, while 2IFC discrimination accuracy is expected to be unaffected by between-interval fluctuations of pre-stimulus power.

[Figure 1 about here.]

According to the decision bias model, weak pre-stimulus power influences observers' strategic decision making, rather than their perception, by increasing their tendency to report the interval with weakest power (i.e. strongest excitability). Importantly, this tendency should be task-independent. For 2IFC detection, this interval bias improves accuracy if pre-stimulus power is weaker in the stimulus-present compared to the stimulus-absent interval (similar to a perceptual bias). Likewise, interval bias improves 2IFC discrimination accuracy if pre-stimulus power is weaker in the target interval compared to the non-target interval. Thus, in contrast to the perceptual bias model, the decision bias model predicts that *both* 2IFC detection and 2IFC discrimination accuracy is

greater when pre-stimulus power is weaker in the stimulus-present/target interval compared to the stimulus-absent/non-target interval, respectively.

Statistical analysis

The analysis included oscillatory power at all electrodes, at frequencies between 5 and 30 Hz and between -0.5 and 0 s relative to interval onset.

Generalized linear modeling The predictions of the precision model concern the *overall* oscillatory power in the two intervals within a trial. Thus, for each single trial, time point, frequency, and electrode, we computed a measure, P_{ave}, reflecting power averaged across the two intervals within a trial.

The predictions of the perceptual bias and decision bias models concern the *relative* oscillatory power between the two intervals within a trial. Thus, for each single trial, time point, frequency, and electrode, we computed a measure, P_{rel}, comparing oscillatory power between the two intervals as:

$$P_{rel} = \frac{P_T}{P_{nT}} \tag{1}$$

where P_T is power in the stimulus-present interval in 2IFC detection, and target interval in 2IFC discrimination and P_{nT} is power in the stimulus-absent interval in 2IFC detection and the non-target interval in 2IFC discrimination. Thus, $P_{rel} > 1$ indicates that power was relatively stronger in the to-be-reported interval. P_{rel} and P_{ave} were rank-scored to mitigate the influence of extreme values.

Next, we modeled the relationship between single-trial oscillatory power and response accuracy and interval order using multilevel generalized linear modeling (GLM) (Cohen and Cavanagh, 2011; Samaha et al., 2017b). Including interval order as a regressor enabled us to remove any possible contribution of the interval order from the estimation of the accuracy predictor. For each participant and for each electrode, frequency, and time point, we fit a regression model of the form:

$$X = \beta_0 + \beta_1 A + \beta_2 O + \varepsilon \quad (2)$$

where X is a continuous measure of oscillatory power (i.e. P_{ave} for the precision model and P_{rel} for the bias models), A the accuracy (correct/incorrect) coded as a 1/-1 variable, O the interval order (target first or non-target first) coded as a 1/-1 variable, β_0, β_1, and β_2 the estimated coefficients, and ε the residual error. This GLM corresponds to a linear regression model, where the coefficients β_1 and β_2 represent the independent contributions of the accuracy and the interval order predictors, respectively, in explaining the observed power (P_{rel} or P_{ave}). GLMs were fit separately for detection and discrimination tasks.

Statistical testing and effect size We then tested whether the regression coefficients β_1 and β_2 at each electrode, frequency, and time point were significantly different from zero within participants, and consistent across the sample of participants, using separate statistical tests at the participant level and at the group level. Again, this procedure was carried out separately for the 2IFC detection and 2IFC discrimination task.

At the participant level, we permuted the mapping between single trial power and single trial accuracy/interval order 1000 times, recomputing the beta coefficients each time. This procedure creates a within-participant null hypothesis distribution of the β coefficients. The β coefficients associated with the true data mapping were then converted to a z-statistic relative to the mean and standard deviation of the distribution of the permuted data, resulting in a z-score for each participant and time-frequency-electrode point.

At the group level, we then tested whether z-scores of the β_1 and β_2 coefficients were significant across participants (i.e. whether their signs were consistent) using a non-parametric cluster based permutation test, which also addresses multiple comparisons across time points, frequencies and electrodes (Maris and Oostenveld, 2007). We obtained a distribution of z-scores under the null hypothesis by randomly permuting their signs 5000 times. On each iteration, we tested the resulting z-scores with a two-tailed t-test against zero and assessed the sum of the t-values within largest contiguous cluster of significant time-frequency-electrode points (cluster p-value = 0.01), resulting in a distribution of t-sums expected under the null hypothesis. A final p-value was calculated as the proportion of t-sums under the null hypothesis larger than the sum of t-values

within clusters in the observed data. Thus, p-values smaller than 0.01 indicate that the observed β coefficients were significantly different from zero (two-sided).

We computed Cohen's d to estimate the effect size of significant clusters of interest. For each time-frequency-electrode point of the significant cluster, Cohen's d was estimated by dividing the t-statistics by the square root of the number of participants. Conventionally, Cohen's d indicates whether the effect size is small (if d < 0.2), medium (if $0.2 < d < 0.8$) or large (if d > 0.8) (Cohen, 1988; Lakens, 2013).

Bayes factor analysis The perceptual bias model predicts a relationship between P_{rel} and accuracy in 2IFC detection, but a null effect in 2IFC discrimination. However, in conventional inferential statistics, a non-significant result only indicates that the null hypothesis cannot be rejected. It does not necessarily follow that the null hypothesis is actually true; it is possible that the data might be inconclusive, e.g. due to insufficient statistical power. Thus, to directly estimate evidence supporting the null hypothesis, we estimated the JZS Bayes factor (BF; Jeffreys, 1961; Zellner and Siow, 1980; Rouder et al., 2009). The JZS BF is a Bayesian measures of evidence which takes the form of an odds ratio: i.e. the probability of the data under H_1 relative to that under H_0. Conventionally, BF indicates whether there is evidence supporting the alternative hypothesis (H_1: $\beta \neq 0$) if $BF > 3$, or supporting the null hypothesis (H_0: $\beta = 0$) if $BF < 1/3$, or whether the evidence is inconclusive (if $1/3 < BF < 3$). For example, a Bayes factor of BF $= 1/3$ indicates that the data are three times more likely under the H_0 than under the H_1. For the significant negative t-statistics, found by the cluster test, we set the prior on effect size following a Cauchy distribution with a scale factor 0.707, as recommended by Rouder et al. (2009). We then computed for each time point the proportion of cluster electrodes and frequencies yielding evidence for $H1$ and $H0$, respectively (see insets below the time-frequency plots in Figure 2a/c, 3e).

Results

Behavior

For each participant, an adaptive staircase procedure (see $Methods$) adjusted stimulus contrast to ensure a proportion of 75% correct responses in both the 2IFC detection and the discrimina-

tion task. The participants included in the analysis had a mean proportion of correct detection responses of 73.2 % (SEM = 0.002) and a mean proportion of correct discrimination responses of 72.5 % (SEM = 0.007), indicating that the staircase procedure was successful. On average, the stimulus contrast necessary for achieving this level of performance was higher in the 2IFC discrimination task than in the 2IFC detection task (two-tailed paired-sample t test: $t(21) = 5.77$, $p < 0.001$), which is consistent with previous work (Iemi et al., 2017). The group-average contrast was 7.2% (SEM = 0.2) and 41.6% (SEM = 6.1) in the detection and discrimination task, respectively.

EEG

This study aimed to test three models of the relationship between low-frequency oscillatory power as a measure of excitability and performance in 2IFC detection and discrimination. To recap, the precision model predicts that correct responses are associated with weak overall pre-stimulus power in both intervals (i.e. low P_{ave}). The perceptual bias model predicts that correct responses are associated with relatively weaker pre-stimulus power in the target interval compared to the non-target interval (i.e. low P_{rel}), but only in the detection task. The decision bias model predicts this association for both the detection and discrimination task (see Methods for details).

To test these models, we analyzed both tasks using GLM to model within each participant the contributions of response accuracy (β_1 regressor) and interval order (β_2 regressor; target-first vs. non-target first) on either P_{ave} (i.e. overall power averaged across the two intervals; to test the precision model), or on P_{rel} (i.e. power in the target interval relative to the power in the non-target interval; to test the perceptual bias and decision bias models). We then used a cluster permutation test to determine whether regressors were significantly different from 0 across participants.

Precision Model The group-level statistical test of β_1 (accuracy) identified significant clusters in neither 2IFC detection nor discrimination. In other words, 2IFC accuracy did not correlate with P_{ave} across participants. To provide evidence of a true null effect of accuracy on P_{ave}, as opposed to merely inconclusive evidence, we used Bayes Factor (BF) analysis to quantify the proportion of data points providing evidence of an effect (H_1) or evidence of a null effect (H_0). We restricted this analysis to the significant time-frequency-electrode cluster found for β_1 in the bias model for

2IFC detection (see below, Figure 3a). The BF analysis revealed that for both 2IFC detection and discrimination, the proportion of data points in favor of a null effect by far outnumbered the proportion of data points in favor of an effect ($H_0 > H_1$, bottom insets of Figure 2a/c). In sum, the relationship between P_{ave} and 2IFC detection and discrimination accuracy was not merely weak or inconclusive, but entirely absent. These findings reject the precision model.

The group-level statistical test of β_2 (interval order) identified a significant effect of interval order for 2IFC detection (p-value = 0.003), starting from -0.5 s relative to interval onset and at frequencies between 7 and 24 Hz with an occipital topography (Figure 4a/b). In other words, pre-stimulus 7–24 Hz P_{ave} was greater in trials when a stimulus was presented in the first interval (target-first: T1) relative to trials when it was presented in the second interval (non-target-first: nT1; Figure 4c). By contrast, no significant clusters were found for β_2 in 2IFC discrimination (see Figure 4d/e).

[Figure 2 about here.]

Perceptual and Decision Bias Model The group-level statistical test of β_1 (accuracy) in the 2IFC detection task yielded a significant negative cluster (p-value = 0.005) starting from -0.344 s before interval onset and at frequencies between 8 and 17 Hz (Figure 3a). In other words, correct detection was associated on a trial-by-trial basis with lower 8–17 Hz P_{rel}, i.e. reduced α- and β-power in the time window before the stimulus-present interval relative to the stimulus-absent interval (Figure 3b). The topography of this negative effect evolved from fronto-central to parieto-occipital electrodes (Figure 3c). The peak of this cluster was at electrode FC4, at 13 Hz and at -0.305 s before interval onset (t(21) = -5.20). Cohen's d estimated within this significant cluster had a median of -0.290, indicating a medium effect size (Figure 3d). Note that this effect in 2IFC detection is predicted by both the perceptual bias and the decision bias model.

No significant clusters were found for β_1 in the 2IFC discrimination task (Figure 3e). In other words, discrimination accuracy did not correlate with differences in P_{rel} (Figure 3f). We then tested whether there was evidence of a true null effect of accuracy on P_{rel}, using BF analysis as described above. We restricted this analysis to the significant time-frequency-electrode cluster found for β_1 in 2IFC detection (Figure 3a). The BF analysis revealed that the proportion of data points in favor of a null effect on 2IFC discrimination accuracy by far outnumbered the proportion

of data points in favor of an effect ($H_0 > H_1$, bottom insets of Figure 3e). Hence, the relationship between 2IFC discrimination accuracy and P_{rel} was not merely weak or inconclusive, but entirely absent. In sum, the results confirm the prediction of the perceptual bias model that for 2IFC detection, but not 2IFC discrimination, relatively weak power before the target interval and strong power before the non-target interval is related to higher accuracy.

[Figure 3 about here.]

The group-level statistical test of β_2 (trial order) found significant clusters in neither 2IFC detection (Figure 4f/g) nor discrimination (Figure 4h/i).

[Figure 4 about here.]

Discussion

Excitability modulates perceptual bias rather than decision bias

What are the perceptual consequences of spontaneous fluctuations in neuronal excitability? Accumulating evidence suggests that, during states of strong neuronal excitability, indexed by weak ongoing α- and β-power, observers are more likely to report the presence of a sensory target, irrespective of its actual physical presence. Thus, contrary to the previously dominant view (e.g. Ergenoglu et al., 2004; Payne and Sekuler, 2014), strong excitability reflects a state of liberal detection criterion/bias rather than of improved perceptual acuity/sensitivity. What is the mechanism linking fluctuations of excitability and bias? According to SDT, two alternative mechanisms are possible. On the one hand, strong excitability could indicate a state of more permissive detection strategy, during which observers prefer to report "yes, I saw the target". This mechanism is referred to as *decision bias*. On the other hand, strong excitability could reflect a state of increased baseline sensory processing, resulting in an amplification of the neural responses to both target and non-target stimuli. At the behavioral level, this is paralleled by an amplification of subjective perceptual experience, during which observers "perceive" the presence of a target even when it is not physically present. This mechanism is referred to as *perceptual bias*. Past studies using single-interval detection tasks (Iemi et al., 2017; Limbach and Corballis, 2016) were unable

to distinguish between these alternative interpretations of excitability, because standard SDT analysis cannot determine the underlying source of the bias, be it perceptual or decision-based (Wixted and Stretch, 2000; Witt et al., 2015).

In this study, we addressed the issue by analyzing the relationship between low-frequency oscillatory power (5–30 Hz), as a measure of neuronal excitability, and performance in 2IFC detection and discrimination tasks, which are differently affected by perceptual bias and decision bias. The predictions of a SDT model of perceptual bias are twofold. First, 2IFC detections should be most accurate when excitability in the stimulus-present interval exceeds that in the stimulus-absent interval, reflecting an amplification of the stimulus representation in the stimulus-present interval and a dampening of the representation in the stimulus absent interval. Second, in 2IFC discrimination, fluctuations of excitability between target and non-target intervals should not affect discrimination accuracy. This is because a change in global excitability (i.e. not specific to a certain feature value) affects the response of all feature detectors equally, without changing their relative strength, which determines the evidence for target presence. By contrast, a SDT model of decision bias posits that fluctuations in excitability influence the observer's strategic decision behavior, rather than perceptual processing. Note that a "yes"-bias, as in a single-interval detection task, cannot affect decisions in a 2IFC detection task, because "yes, I saw it" is not among the given options. However, an interval decision bias predicts a tendency to report the interval with stronger excitability, regardless of perceptual task, and should therefore be manifest in both 2IFC detection and 2IFC discrimination.

To test these alternative models, we analyzed how 2IFC detection and discrimination accuracy is related to excitability in target and non-target intervals (P_{rel}). We found that detection was most accurate when pre-stimulus α- and β-power was lower before the stimulus-present interval relative to the stimulus-absent interval (i.e. low P_{rel}). This effect rules out a "yes"-decision-bias that might have affected previous findings from single-interval detection tasks (e.g. Chaumon and Busch, 2014; Limbach and Corballis, 2016; Iemi et al., 2017). Moreover, using Bayes factor analysis we found evidence that discrimination accuracy was unaffected by between-interval fluctuations of excitability, ruling out an interval decision bias model. Taken together, the effect on 2IFC detection and the evidence of a null effect on 2IFC discrimination confirm the predictions of the perceptual bias model.

Excitability does not affect perceptual acuity

It is important to note that the effect of perceptual bias on 2IFC detection, i.e. when excitability is specifically strong (i.e. weak low-frequency power) in the stimulus-present interval, merely represents a serendipitous distortion of subjective perception "in the right direction" rather than an actual improvement in perceptual acuity. By contrast, the precision model predicts that overall excitability in both intervals improves detection and discrimination accuracy. However, using Bayes factor analysis we found that overall excitability (P_{ave}) affected neither 2IFC detection nor discrimination accuracy (Figure 2a). This result replicates, in a 2IFC paradigm, the findings of three recent studies, reporting a null effect of excitability on single interval yes/no detection sensitivity (Limbach and Corballis, 2016; Iemi et al., 2017) and 2AFC discrimination accuracy (Iemi et al., 2017; Samaha et al., 2017b). Taken together, these findings challenge the long-held notion that neuronal excitability affects the accuracy of perceptual decisions (van Dijk et al., 2008; Romei et al., 2008; Payne and Sekuler, 2014). This notion has been based on the observation that successful stimulus detection (hit-rate) is associated with relatively stronger excitability. Such findings have been obtained with visual (Ergenoglu et al., 2004; van Dijk et al., 2008), auditory (Leske et al., 2015) and somatosensory detection (Baumgarten et al., 2016) and for detection of TMS-induced phosphenes (Romei et al., 2008; Samaha et al., 2017a). However, without testing for an effect on the false-alarm rate on stimulus-absent trials, it is possible that excitability affects rather the bias to report a stimulus, irrespective of whether or not this is accurate. Indeed, recent studies analyzing signal detection measures found that increased excitability is associated with a more liberal detection bias in both vision (Limbach and Corballis, 2016; Iemi et al., 2017) and somatosensation (Craddock et al., 2017). Our results are also consistent with several experiments that found no effect of excitability on multiple-alternative-forced-choice (mAFC) *discrimination* performance (e.g. Bays et al., 2015; see Iemi et al., 2017 for a comprehensive literature review). A SDT model of perceptual bias, in fact, predicts these null findings because discrimination performance in mAFC tasks is unaffected by a "yes"-bias, and a modulation of excitability does not change the discriminability between response alternatives (Iemi et al., 2017).

Accumulating evidence suggests that spontaneous neural oscillations modulate subjective, rather than objective, measures of performance in perceptual tasks. While replicating the finding that states of heightened excitability do not improve objective perceptual accuracy, two recent studies additionally demonstrated that excitability instead biases observers to report higher confidence in

2AFC discrimination (Samaha et al., 2017b) and higher visibility ratings (Benwell et al., 2017). These results can be reconciled by a SDT model of perceptual bias. For example, in a 2AFC discrimination task, confidence, unlike accuracy, is thought to depend on the absolute amount of evidence in favor of the chosen stimulus alternative, regardless of the amount of evidence against this choice (Zylberberg et al., 2012; Maniscalco et al., 2016). According to a perceptual bias model, heightened excitability amplifies evidence for both stimulus alternatives simultaneously (Iemi et al., 2017). Thereby, a perceptual bias amplifies evidence for the chosen alternative and, in turn, amplifies subjective confidence and subjective visibility, while leaving objective accuracy unchanged. Taken together, these results provide suggestive evidence for the perceptual bias model.

Spectral and topographical characteristics of the experimental effects.

Correct detection was more likely when low-frequency power before the stimulus-present interval was weaker relative to the stimulus-absent interval (Figure 3a–c). The effect of between-interval power fluctuations on detection accuracy was widely distributed over many electrodes and spanned frequencies between 7-18 Hz. The topography of this effect evolved from a fronto-central to parieto-occipital topography (Figure 3c). This pattern is consistent with previous studies using single-interval perceptual tasks reporting either a fronto-central (Busch et al., 2009; Achim et al., 2013), parieto-occipital (Ergenoglu et al., 2004; van Dijk et al., 2008; Romei et al., 2008; Lange et al., 2013; Chaumon and Busch, 2014; Mathewson et al., 2014; Samaha et al., 2017b), or widespread topography (Iemi et al., 2017; Benwell et al., 2017). Furthermore, the broad frequency range of this effect (Figure 3a) is consistent with recent reports (Iemi et al., 2017; Samaha et al., 2017b; Benwell et al., 2017) and is in line with studies showing that α- and β-oscillations are typically comodulated in time and colocalized in space (Bastos et al., 2015; Lakatos et al., 2016; Michalareas et al., 2016). A recent study in rats demonstrated that low-frequency LFP power (10-30 Hz) is negatively correlated with firing rate (Watson et al., 2018). Therefore, it is possible that the β-oscillations exert an inhibitory function, similar to α-oscillations (Spitzer and Haegens, 2017). Taken together, these studies suggest that α- and β-power may reflect a similar function in regulating cortical excitability and perceptual decision-making.

In addition to detection accuracy, interval order (i.e. whether or not stimulus is presented in the first interval) was also related to low-frequency power (Figure 4a–c). In the detection task,

low-frequency pre-stimulus power averaged across first and second intervals (P_{ave}) was significantly greater in trials when a stimulus was presented in the first interval (T1 trials) relative to trials when it was presented in the second interval (nT1 trials; Figure 4a). During T1 trials, low-frequency synchronization (Kalcher and Pfurtscheller, 1995) induced by the stimulus in the first interval probably leaked into the pre-stimulus period of the second, stimulus-absent interval. Conversely, during nT1 trials, low-frequency desynchronization due to temporal expectation and attention (Rohenkohl and Nobre, 2011) following the first, stimulus-absent interval leaked into the pre-stimulus period of the second, stimulus-present interval. Including the interval order in our regression model ensured that the effect of accuracy on oscillatory power was independent of effects of interval order.

Within-trial fluctuations of excitability

Past studies on the relationship between perception and excitability have typically analyzed how differences in perceptual reports were related to differenced in pre-stimulus power *across* trials (e.g. Busch et al., 2009; Iemi et al., 2017; Limbach and Corballis, 2016). This across-trial approach treats individual trials as independent samples and therefore ignores the fact that data are collected in temporal order. This is potentially problematic, because it is known that both perceptual reports and excitability change over the course of an experiment. Specifically, behavioral measures such as hit rate (Boncompte et al., 2016; Carrasco-López et al., 2017) and sensitivity (Maniscalco et al., 2017) tend to decrease over time, possibly due to progressive fatigue, resulting from an exhaustion of cognitive resources. Likewise, ongoing α-power tends to increase over the course of an experiment (van Dijk et al., 2008), suggesting a decrease in excitability, possibly as a result of fatigue (Kaida et al., 2006). Since perceptual reports and excitability both covary across time, e.g. as a function of fatigue, their correlation could be epiphenomenal. Therefore, several studies have tried to rule out that the across-trial correlation between performance and α-power is confounded by fatigue by showing that the temporal factor does not explain the effect on performance (van Dijk et al., 2008; Mathewson et al., 2009).

To test the bias models in our study, we used a different approach and quantified the differences in excitability between two intervals *within* a trial (P_{rel}), instead of the differences in the absolute magnitude of excitability *across* trials. This approach ensures that our measure of excitability is not influenced by fatigue-related effects occurring over longer time scales. Crucially, our results

show a significant correlation between excitability and perceptual reports, even when the effects of fatigue are ruled out. This study thus confirms that the relationship between excitability and perception is not determined by fatigue.

Perceptual bias and selective stimulus processing

It is important to note that the present study focused on spontaneous, moment-to-moment fluctuations in oscillatory power and, in turn, of neuronal excitability and inhibition. To this end, the task was designed such that participants could not expect and selectively attend to a specific time interval, spatial location, or stimulus feature. Therefore, our finding that spontaneous, non-selective fluctuations in oscillatory power are associated with a perceptual bias rather than a change in precision or accuracy, does not exclude the possibility that this bias *can* serve to improve accuracy when the task allows for some form of selective stimulus processing.

Numerous studies have demonstrated that selective attention to a spatial location or to other stimulus aspects allows for a selective gating of the task-relevant information by adjusting α-power in task-relevant vs. irrelevant neuronal populations (see Foxe and Snyder, 2011, for a review). When subjects are instructed to selectively attend to a spatial location, α-power decreases in the contralateral relative to the ipsilateral hemisphere, indicating greater excitability in the task-relevant hemisphere and greater inhibition in the task-irrelevant hemisphere (Thut et al., 2006; Busch and VanRullen, 2010). For example, Händel et al. (2011) demonstrated that this lateralization serves to inhibit distracting stimuli in the unattended visual hemifield. Moreover, selective attention to a particular stimulus feature (orientation vs. identity; Jokisch and Jensen, 2007), modality (visual vs. auditory; Mazaheri et al., 2014), and timing (expected vs. unexpected; Rohenkohl and Nobre, 2011) induces a relative increase of α-power in the currently task-irrelevant areas.

Thus, our finding is consistent with the gating-by-inhibition account by Jensen and Mazaheri (2010) and the pulsed-inhibition account by Mathewson et al. (2011). Both models argue that the inhibitory effect of α-oscillations is not sustained, but pulsed as a function of α-phase, and that the inhibitory phase is more pronounced than the excitatory counterpart. Moreover, both models argue that top-down control can modulate both power and phase for selective information processing. In light of the present findings, we propose that the performance-modulating effect of top-down

controlled α-oscillations is associated with a selective perceptual bias, which dampens responses in those neuronal populations processing potentially distracting or task-irrelevant information.

Conclusions

We propose that the current state of neuronal excitability—indexed by spontaneous α- and β-oscillations—biases the observer's subjective perceptual experience, by amplifying or attenuating sensory representations, rather than the decision strategy.

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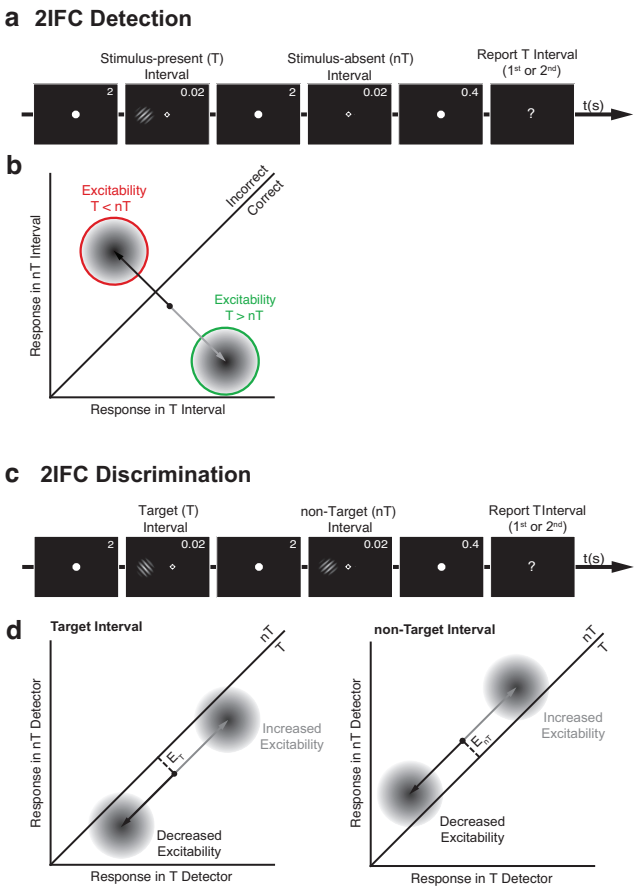

Figure 1: Effects of perceptual bias on 2IFC detection and discrimination performance according to signal detection theory (SDT). See Methods for predictions of the precision and decision bias model. **a**: in 2IFC detection, a target stimulus (T) appears in either one of two successive intervals and the task is to report which interval contained the stimulus. **b**: according to SDT, the internal response in the stimulus-present interval, R_T, is compared to the internal response in the non-target, stimulus-absent interval, R_{nT}, and the interval yielding the stronger response is reported. If $R_T > R_{nT}$ (below diagonal), the report is correct, otherwise incorrect. The perceptual bias model predicts that the accuracy of 2IFC detection reports is affected by the balance of excitability and inhibition between the stimulus-present and stimulus-absent intervals: weaker oscillatory power (i.e. stronger excitability) before the stimulus-present interval relative to before the stimulus-absent interval, is expected to boost detection accuracy (green circle); instead, stronger oscillatory power (i.e. stronger inhibition) before the stimulus-present interval relative to before the stimulus-absent interval, is expected to impair accuracy (red circle). **c**: in 2IFC discrimination, two successive intervals contain either a target (T) or a non-target (nT) stimulus and the task is to report in which interval the target was presented. **d**: according to SDT, for each interval, the difference between the internal responses of the target detector and non-target detector (i.e. distance from the diagonal; dashed line) represents the evidence of target presence in that interval (E), and the interval yielding stronger target-evidence is reported. If there is more target-evidence in the target interval, the response is correct, otherwise incorrect. The perceptual bias model predicts that increased excitability or inhibition in the target interval (left panel) or non-target interval (right panel) affects both target and non-target detectors equally, leaving target evidence in that interval unchanged (illustrated by shift parallel to the diagonal without affecting the distance to the diagonal). Thus, this model predicts that between-interval fluctuations of excitability do not affect 2IFC discrimination accuracy.

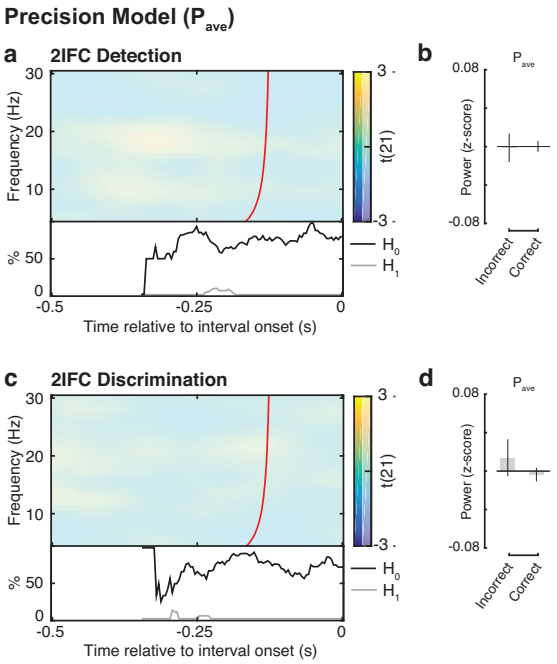

Figure 2: Relationship between overall oscillatory power (P_{ave}) and 2IFC accuracy; test of the precision model. **a/c**: Group-level t-statistics maps of the regression coefficient β_1, indicating the relationship between accuracy and P_{ave}, in 2IFC detection and discrimination, respectively. Accuracy in neither 2IFC detection nor discrimination is related to P_{ave}. This null effect is corroborated by the BF analysis, indicating that there is more evidence supporting the H_0 than supporting the H_1 (bottom insets). The maps in **a/c** are averaged across the electrodes comprising the cluster of significant effects illustrated in figure 3a/c and masked by a p-value of 0.01 using two-sided cluster permutation testing. Time 0 s indicates interval onset. The red line in **a/c** indicates the time points before which oscillatory activity is not contaminated by activity after interval onset (Iemi et al., 2017). **b/d**: Group-average P_{ave} in detection (**b**) and discrimination (**d**), shown separately for correct and incorrect trials, normalized by the P_{ave} in all trials. The bar plots are shown for illustrative purposes for the cluster of significant effects illustrated in figure 3a/c. These results refute the prediction of the precision model that low P_{ave} is related to higher accuracy.

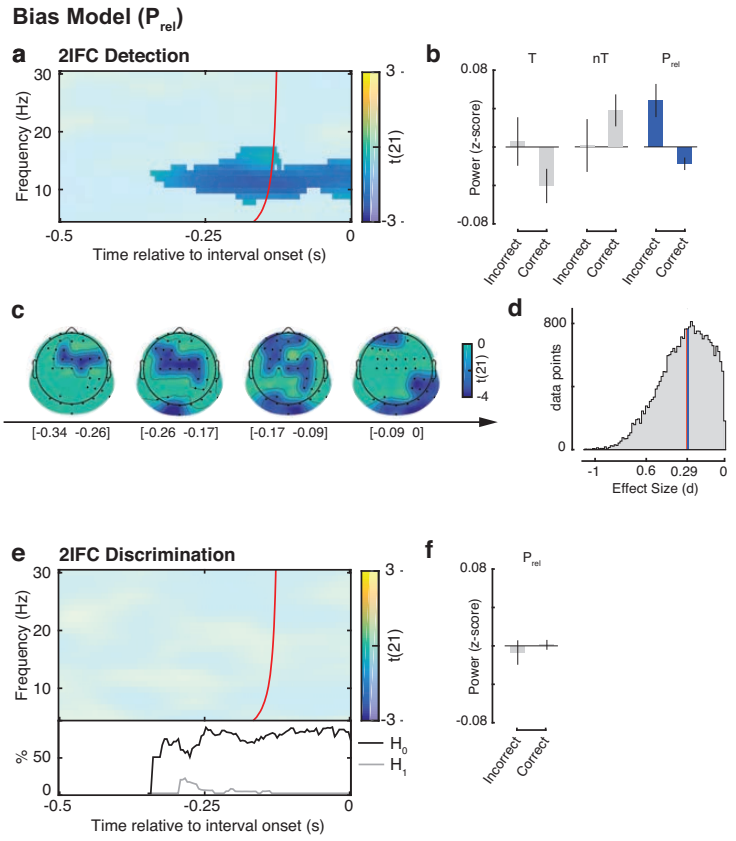

Figure 3: Relationship between relative oscillatory power (P_{rel}) and 2IFC accuracy; test of the perceptual bias and decision bias models. **a**: Group-level t-statistics maps of the regression coefficient β_1, indicating the relationship between 2IFC detection accuracy and P_{rel}. Correct performance is related to lower 8–17 Hz P_{rel}, i.e. reduced α- and β-power preceding the stimulus-present interval relative to that preceding the stimulus-absent interval. **b**: Group-average power averaged across the window before the target interval (left panel) or that before the non-target interval (middle panel), shown separately for correct and incorrect 2IFC detections, normalized by the average power in all trials. Group-average P_{rel} (right panel) shown separately for correct and incorrect trials, normalized by the average P_{rel} in all trials. **c**: a time-course of topographies of the significant negative cluster. Black dots represent cluster electrodes. **d** Histogram of the effect size, estimated as Cohen's d, for the data within the time-frequency-electrode cluster of significant negative effects. The median value is highlighted by the blue vertical bar. **e**: Group-level t-statistics maps of the regression coefficient β_1, indicating the relationship between 2IFC discrimination accuracy and P_{rel}. 2IFC discrimination accuracy is not related to P_{rel}. This null effect is corroborated by the BF analysis, indicating that there is more evidence supporting the H_0 than supporting the H_1 (bottom inset). **f**: Group-average P_{rel} shown separately for correct and incorrect 2IFC discriminations, normalized by the average P_{rel} in all trials. The maps in **a/e** are averaged across the electrodes comprising the cluster of significant effects illustrated in a/c and masked by a p-value of 0.01 using two-sided cluster permutation testing. Time 0 s indicates interval onset. The red line in **a/e** indicates the time points before which oscillatory activity is not contaminated by activity after interval onset (Iemi et al., 2017). The plots in **b/f** are shown for illustrative purposes for the cluster of significant effects illustrated in a/c. The negative relationship between P_{rel} and accuracy in 2IFC detection, but not in 2IFC discrimination, confirms the perceptual bias model.

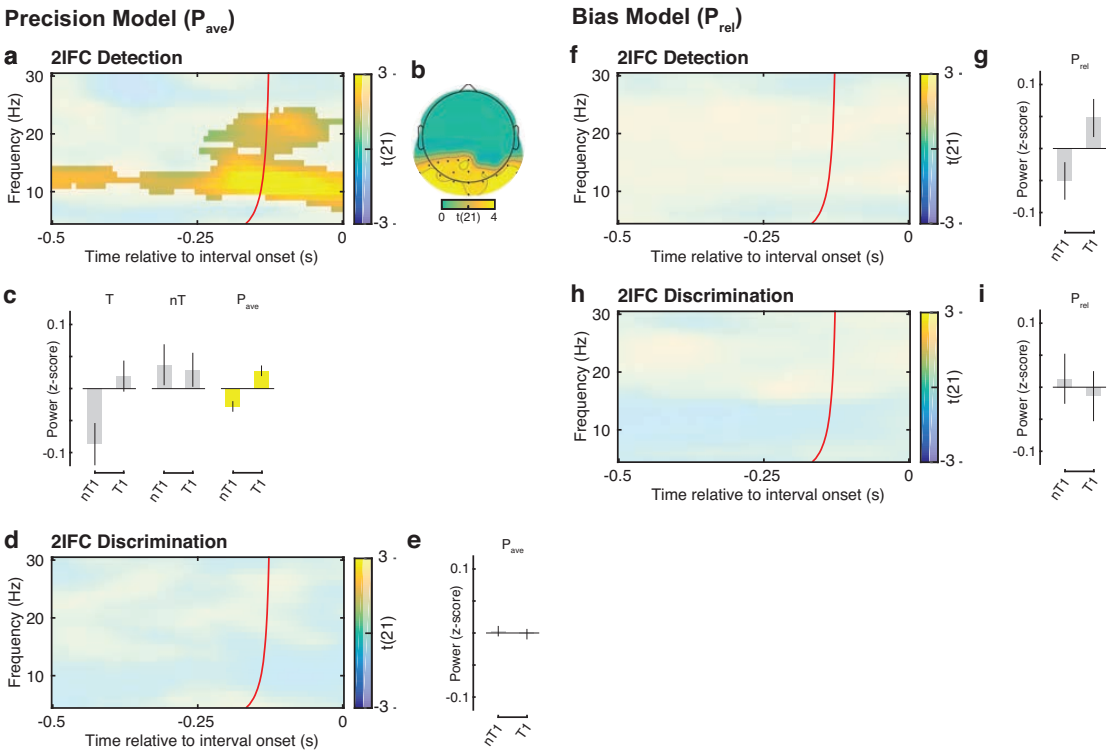

Figure 4: Relationship between oscillatory power (P_{ave} and P_{rel}) and interval order in 2IFC detection and discrimination. **a/d**: Group-level t-statistics map of the regression coefficient β_2, indicating the relationship between interval order and P_{ave} in 2IFC detection and discrimination, respectively. **b**: Topography of the significant positive cluster in 2IFC detection. Black dots represent cluster electrodes. **c**: Group-average power averaged across the window before the stimulus-present interval (left panel) or that before the stimulus-absent interval (middle panel), shown separately for non-target first (nT1) and target first (T1) trials, normalized by the average power in all trials. Group-average P_{ave} (right panel) shown separately for nT1 and T1 detection trials, normalized by the average P_{ave} in all trials. **f/h**: Group-level t-statistics map of the regression coefficient β_2, indicating the relationship between interval order and P_{rel} in 2IFC detection and discrimination, respectively. **g/i**: Group-average P_{rel} shown separately for nT1 and T1 trials, normalized by the average P_{rel} in all trials in 2IFC detection and discrimination, respectively. The maps in **a/d/f/h** are averaged across the electrodes comprising the cluster of significant effects illustrated in a/b and masked by a p-value of 0.01 using two-sided cluster permutation testing. Time 0 s indicates interval onset. The red line in **a/d/f/h** indicates the time points before which oscillatory activity is not contaminated by activity after interval onset (Iemi et al., 2017). The plots in **c/e/g/i** are shown for illustrative purposes for the cluster of significant effects illustrated in a/b. nT1: trials with non-target in the first interval; T1: trials with target in the first interval.