INTRODUCTION

Human perception is not stable over time but is influenced by the functional state of the brain. Alpha oscillations have been considered as indicators of the functional state of the brain (Pfurtscheller et al., 1996). A number of studies have revealed that high posterior alpha power before stimulus onset reduces detection rates in challenging visual perception tasks for widely different stimulus types. Ergenoglu et al. (2004) showed participants a short visual stimulus at their detection threshold. Occipital oscillations in the alpha band are closely related to visual perception and attention. In multiple studies, increased alpha power has been shown to reduce detection rates of hard-to-detect visual stimuli. Recent studies explain this finding by a shift in perceptual bias. Moreover, the phase of alpha oscillations prior to stimulus onset appears to be critical for the detection of visual stimuli. This is explained by a shift in cortical excitability over the course of each alpha cycle. However, prior studies often used short presentation times of visual stimuli at the perceptual threshold. Here, we use longer presentation times to elucidate whether the same mechanisms hold for the perception of salient but challenging visual stimuli presented for up to 1,500 ms. To this end, we presented participants with hard to distinguish but salient upright or tilted Gaussian gratings in a two-alternative forced choice task, while recording occipital electroencephalographic activity. Previous reports link alpha power to stimulus detection hit rates, and we found that low prestimulus power at the individual alpha frequency relates to higher perceptual accuracy. Contrary to recent findings, we neither found an influence of alpha power on criterion, nor an influence of alpha phase on perception or response speed. We argue that longer presentation times might attenuate a possible response bias, and increased excitability might sharpen the discrimination ability, thereby leading to increased perceptual accuracy and unaffected response criterion.
threshold and participants displayed lower alpha power for trials they correctly identified compared with trials they did not. Similarly, Van Dijk et al. (2008) examined occipital alpha activity when participants had to distinguish two shortly presented superimposed disks. Again, higher alpha power led to lower hit rates during the task. Accordingly, Klimesch et al. (2007) proposed the ‘inhibition-timing hypothesis’, which suggests that alpha activity corresponds to shifts in cortical excitability, with strong synchronized alpha activity (high power in the 8–12 Hz band) representing a state of inhibition and low cortical excitability, and desynchronized alpha activity (low power in the 8–12 Hz band) representing states of high cortical excitability. The ‘gating-by-inhibition’ hypothesis assigns alpha oscillations a more active role (Jensen & Mazaheri, 2010) and suggests that alpha band oscillations represent an active inhibition mechanism, thereby providing a temporal processing code, which gates processing resources as well as information flow (Jensen et al., 2012, 2014; Zumer et al., 2014).

Extending the finding that higher prestimulus alpha power decreased the detection rate of briefly presented stimuli, Busch and colleagues (Busch et al., 2009) showed that also the phase of the alpha oscillation differed significantly for detected and undetected stimuli (see also Vanrullen, 2016). Moreover, the alpha phase predicted performance for expected visual stimuli (Busch & Vanrullen, 2010). In a metacontrast masking paradigm, Mathewson et al. (2009) independently made the same discovery: High prestimulus alpha power reduced subsequent detection rate, and the phase of the alpha oscillation had an influence on correct detection. From these findings, the authors derived a theory of ‘pulsed inhibition’, suggesting that over the course of an alpha oscillation brain areas cycle through more and less excitable states (Mathewson et al., 2009). Instead of viewing alpha activity as a mechanism that inhibits brain areas at all times, they suggest that the phase of the alpha oscillations indicate moments of especially high or low cortical excitability (Mathewson et al., 2010). Recently, Ruhnau et al. (2014) extended this idea and proposed that neural oscillations provide windows of opportunity for stimulus processing (Dugué et al., 2011). In line with this theory, reaction times (RTs) also vary depending on the phase of the alpha oscillation at which the stimulus is presented (Callaway & Yeager, 1960; Dustman & Beck, 1965).

Thus, stimulus processing and perception should depend on the power and phase of ongoing oscillations, and inhibition can be overcome either when alpha power decreases, or when the alpha oscillations are at a certain phase.

Most of the studies on the influence of neural oscillations on perception only looked at the change in accuracy, i.e., the hit rates of correct responses, while ignoring false alarm rates. For two alternative forced choice tasks, such as the choice between having detected a stimulus versus not having seen one, signal detection theory (SDT) can be used to analyze differences in answering tendencies (Stanislaw & Todorov, 1999). In particular, increased sensitivity to a stimulus results in higher hit rates and lower false alarm rates. In contrast, a change in criterion will lead to higher hit rates and higher false alarm rates. Recent research on prestimulus alpha activity suggests that increases in hit rates are due to subjective changes in criterion. In a metacontrast paradigm, with increasing prestimulus alpha power, participants shifted their criterion to be more conservative: They responded more often that they did not see a stimulus (Limbach & Corballis, 2016). Thus, higher prestimulus alpha power led to a decrease in both hit rates and false alarm rates. In an extensive study, Iemi et al. (2017) also found a change in criterion (but not sensitivity) with increased alpha power. In a follow-up study, Iemi and Busch (2018) found that the influence of alpha activity on criterion seems to influence subjective perception instead of changing the answering strategy, both of which would impact the criterion. This hypothesis is also supported by subjective confidence measures. In an orientation detection task, participants had to rate their confidence, after making a decision. Low prestimulus alpha power led to higher confidence ratings but not higher accuracy (Samaha et al., 2017). Thus, changes in prestimulus alpha power appear to influence the decision criterion.

Previous studies focusing on the relationship between neural oscillations, excitability, sensitivity, and criterion used very brief stimuli, with presentation times up to 100 ms. However, it remains currently unclear how alpha oscillations influence perception of longer stimuli, which cover multiple inhibitory pulses. Therefore, in the current experiment, we present participants with a Gabor patch, and ask them to discriminate as accurate and fast as possible whether the pattern is upright or rotated. The amount of rotation applied to the Gabor patch is determined individually for each participant using a staircase procedure preceding the main experiment. Importantly, the stimuli are salient but challenging to identify. In contrast to previous studies, they are presented until the participant makes a choice. We measure RT and responses for all trials. In our analysis, we examine answering tendencies, and we treat the rotated stimulus as the signal. Numerous previous studies indicate that the alpha oscillations influencing visual perception can be recorded across occipital scalp areas (Iemi et al., 2017; Limbach & Corballis, 2016; Mathewson et al., 2009; Samaha et al., 2017; Van Dijk et al., 2008; Zumer et al., 2014). Therefore, we record electroencephalography (EEG) from three posterior and occipital electrodes. Based on the previous literature, we test hypotheses regarding the influence of alpha power and phase on accuracy, sensitivity, criterion, and RTs. Testing these hypotheses can extend previous findings using short stimuli. SDT typically assumes that decisions are based on a single sample of information (Smith & Ratcliff, 2004). Our work can help addressing questions regarding the length of this single sample of information and the duration of the
state of the brain which influences perception: If the results are same for 20 or 2,000 ms stimuli, we can deduce that the ‘single sample’ covers at least 2,000 ms. If, however, our results differ from those obtained with shorter stimuli, the ‘single sample’ is likely shorter and other processes come into play. This will allow forming hypotheses regarding the role of slow fluctuations of cortical states reflected in changes in oscillatory power and fast fluctuations reflected in the oscillatory phase. Replicating the influence of phase on the perception of long-duration stimuli would highlight the importance of processing the stimulus onset. Replicating the influence of power on stimulus discrimination would indicate the importance of slow fluctuations of cortical excitability.

We first investigate the effect of prestimulus alpha power on the accuracy (i.e., the sum of ‘hits’ and ‘correct rejections’, divided by the number of all trials), sensitivity (i.e., $d'$, the difference between the $z$-transformed ‘hits’ and ‘false alarms’), and criterion (i.e., $C$, the sum of the $z$-transformed ‘hits’ and ‘false alarms’, multiplied by $-0.5$). More specifically, we test whether there is a difference in accuracy, sensitivity, criterion, and RT between trials with low and high prestimulus alpha power.

With regard to alpha phase at onset, we explore whether alpha phase affects the discrimination of the stimulus or the RTs in correctly identified trials. Moreover, we test the difference in accuracy, sensitivity, and criterion between trials with different alpha phases at stimulus onset.

## 2 | METHODS

### 2.1 | Participants

In the current experiment, 28 participants gave informed consent and participated in the study for partial course credit. The study was conducted in accordance with the 2008 Declaration of Helsinki and approved by the ethics committee of the Charité–Universitätsmedizin Berlin (approval number: EA1/207/15). Because of malfunctions of the EEG recording system, for four of these participants no valid EEG signal could be recorded, and they were excluded from further analysis. Six additional participants were excluded because of their performance in the experiment. They showed accuracies that were either too close to chance level (<60% correct) or too high (>90% correct), not showing enough wrong answers. Therefore, analyses were performed using the data of the remaining 18 participants (12 females, 6 males; age range: 18–28).

### 2.2 | Stimuli and procedures

After filling out the consent and demographic data forms, the experimental procedure and function of the EEG recording system were explained to the participants. They had the possibility to ask questions at all times. Participants were seated in a comfortable armchair 265 cm away from a white wall. Stimuli were presented on this wall using a BenQ TH681 + projector with a resolution of $1,920 \times 1,080$ pixels and a refresh rate of 60 Hz. The experiment was programmed and presented with PsychoPy 3.1.5 (Peirce, 2007; Peirce et al., 2019). All stimuli were presented on a grey background. Each trial consisted of a black, centrally placed fixation dot ($1^\circ$ visual angle; presentation time selected randomly between 1,500 and 2,500 ms) followed by a circular Gabor patch ($8^\circ$ visual angle, $1^\circ$ spatial frequency, Gaussian mask). The Gabor patch was presented for up to 1,500 ms or until a response was made. In half of the trials, the Gabor patch was upright. For the other half of the trials, the Gabor patch was slightly rotated, either clockwise or counterclockwise (balanced across trials). The amount of rotation was individually determined for each participant using a staircase procedure preceding the main experiment (see below). Participants had to decide whether the presented Gabor patch was rotated or upright and were asked to answer as accurately and quickly as possible in all trials. Responses were given with the thumb of the right hand using two keys on a handheld game pad (Logitech Gamepad F310, Logitech, Lausanne, Switzerland). Participants were instructed to press the “A” button if the grating was upright, and the “B” button if the grating was tilted (Figure 1a). All participants completed 120 staircase trials followed by 1,000 experimental trials. For the whole experiment, this resulted in 500 upright, 250 clockwise, and 250 counterclockwise trials for each participant. After every 100 trials, participants were asked to take a self-paced break.

#### 2.2.1 | Responses

For each trial, participants had two possible answers: They could either indicate that the stimulus was tilted (by pressing the “B” button) or that was upright (by pressing the “A” button). In classical applications of SDT, there is one condition with only noise and another with a signal added to the noise. In the current experiment, conditions only differ in rotation. Depending on individual preference, it can be argued that either the upright stimulus is the signal to look out for or that it is the tilted stimulus. To be consistent with SDT terminology, the tilt of the stimulus is defined as signal. Trials in which the stimulus is presented upright represent the noise condition, whereas trials in which the stimulus is rotated represent the signal + noise condition. Therefore, rotated trials which are identified correctly count as ‘hits’ and rotated trials which are not correctly identified count as ‘misses’. Furthermore, upright trials which are correctly classified are ‘correct rejections’, while upright trials which are incorrectly identified are ‘false alarms’ (Figure 1b).
From these responses, accuracy is computed as the sum of ‘hits’ and ‘correct rejections’, divided by the number of all trials. Importantly, accuracy takes ‘false alarms’ into account, as ‘correct rejections’ are equal to 1 minus ‘false alarms’. Following SDT (Macmillan & Creelman, 2005), the sensitivity ($d'$) is computed as the difference between the $z$-transformed ‘hits’ and ‘false alarms’, with $z$ as the inverse of the standard normal cumulative distribution function ($d' = z(H) - z(FA)$). The criterion is computed as the sum of the $z$-transformed ‘hits’ and ‘false alarms’, multiplied by $-0.5$ ($C = -0.5 \times (z(H) + z(FA))$).

### 2.2.2 | Staircase procedure

To account for varying perceptual performance between participants, a 1-up 3-down staircase procedure was used to determine the individual perceptual threshold of each participant. This procedure followed the parameter estimation by sequential testing (PEST) algorithm (Taylor & Creelman, 1967), homing in on 80% accuracy. A random performance would result in a 50% accuracy, so we opted for an accuracy goal halfway between the random performance and a perfect performance, slightly above the midpoint to foster the participants’ motivation (Kaernbach, 1991). During the staircase, the amount of rotation applied to the Gabor patches was adapted in accordance to the answers of the participant. For every three correct answers, the rotation of the tilted patches was slightly decreased, but slightly increased for every incorrect answer. Trials were chosen randomly to be either upright (50% chance), tilted clockwise (25%), or tilted counterclockwise (25%). After the staircase was completed, the average of the last six staircase reversals was computed and the resulting rotation was used for all tilted trials of the main experiment.

### 2.2.3 | Pretest

To test the functionality of the experiment, as well as the staircase procedure, a pretest was conducted with five participants, following the previously described procedure. The pretest included 100 staircase trials followed by 1,000 experimental trials. No EEG was recorded for the pretest. Participants achieved an average accuracy of 80.8% ($SD = 6.6\%$, range = 73.6%–90.8%). The performance of the staircase procedure was deemed satisfactory. As a result of the pretest, the visual stimulus was slightly decreased in size for the main experiment.

### 2.2.4 | EEG recording and analysis

EEG was recorded at a sampling rate of 512 Hz and amplified by a Nexus-32 amplifier (Mind Media). Participants wore an electrode cap using the 10/20 layout with 21 possible electrode positions (EasyCap). The current experiment focused on occipital alpha activity, and thus EEG was only recorded from three posterior, occipital Ag (silver)/AgCl (silver chloride) electrodes (O1, O2, and Pz, Figure 2a). The FCz electrode was used as ground electrode, and the signal across electrodes was used as reference signal (average reference).

EEG data were analyzed using the FIELDTRIP toolbox (Oostenveld et al., 2011) for MATLAB. Following recording, the offset from the ongoing EEG data was removed by subtracting the mean across the whole recording from each electrode, and EEG data were high-pass filtered at 0.5 Hz and low-pass filtered at 45 Hz using windowed sinc finite impulse response filters (Widmann et al., 2015). Subsequently, 2-s trials were extracted around each visual stimulus onset. For each participant, manual artifact rejection was performed. Trials that showed high variance were visually scanned for artifacts,
and trials that contained artifacts were removed from further analysis. In total, less than 1% of all trials were removed in this process. Following preprocessing, EEG data from electrodes O1 and O2 were referenced to electrode Pz to create two bipolar occipital electrodes. Finally, the individual alpha frequency (IAF) was estimated. To this end, EEG data were averaged across the two bipolar electrodes and a fast Fourier transform with a single ‘Hann’ window taper was applied to the entire trial for the frequency range of 2–30 Hz in steps of 0.5 Hz with zero padding to the maximum trial length (i.e., 2 s, ‘maxperlen’-option) (Figure 2b). It must be pointed out that the frequency resolution is artificial due to the spectral smearing across neighboring frequencies. The IAF was defined as the peak in the power spectrum between 8 and 13 Hz (Haegens et al., 2014).

2.2.5 | Prestimulus alpha power and phase

The current analysis focused on power and phase at the IAF. For each participant, prestimulus alpha power at IAF was extracted over a time window from 500 ms before stimulus onset until stimulus onset using the fast Fourier transform with a single ‘Hann’ window taper with zero padding, separately for each electrode. The quartiles for prestimulus alpha power were then calculated for each electrode, and trials accordingly split up into four groups. For each of these groups of trials, accuracy, $d'$, criterion, and median RT of the participants were calculated. For all statistical analyses involving power, an alpha level of $p = 0.05$ was set with Holm–Bonferroni correction for multiple comparisons (Holm, 1979).

The phase of the alpha oscillation at stimulus onset was measured for both electrodes individually. To this end, the trials were cut to two cycles of the IAF prior to stimulus onset, and then Fourier transformed (IAF ± 1 Hz) using a Hanning tapering window to obtain complex-valued Fourier spectra from which the phase angle was extracted (van Elswijk et al., 2010). Similar to the analysis of power, all phase effects were analyzed separately for each electrode. Again, an alpha level of $p = 0.05$ was set with Holm–Bonferroni correction for multiple comparisons (Holm, 1979).

2.3 | Statistical analysis

The statistical analysis of the behavioral data focused on RTs and trial numbers. RTs were compared among the four response categories using a 2 × 2 repeated measures Analysis of variance (ANOVA; Trujillo-Ortiz et al., 2020) with the factors Stimulation (upright and rotated) and Response (upright and rotated) and post-hoc paired-samples $t$ tests with Holm–Bonferroni correction for multiple comparisons (Holm, 1979). Moreover, the number of ‘hits’ and ‘correct rejections’ was compared using a paired-samples $t$ test. In order to illustrate the statistical results in more detail, we computed Bayes Factors (BF10, Rouder et al., 2009) as an indicator of the relative evidence for the $H_0$ and $H_1$. BF between 1 and 3 indicate anecdotal support for the alternative hypothesis ($H_1$), while BF between 3 and 10 and above 10 indicates, respectively, moderate and strong support for $H_1$. BF = 1 indicates equal support for $H_1$ and null hypothesis ($H_0$), while BF between 1/3–1, 1/10–1/3, and below 1/10 provides, respectively, anecdotal, moderate, and strong support for $H_0$ (Aczel et al., 2017). The statistical analysis of the EEG data focused on hypotheses regarding the influence of IAF power and phase on accuracy, $d'$, criterion, and RT, derived from the literature.

First, the difference in perceptual performance between trials with high or low prestimulus IAF power (lowest and highest power quartile) was compared. To this end, we used
two-sided, paired-samples t tests comparing the difference in accuracy, $d'$ and criterion for the groups of trials in the first and fourth power quartile. Similarly, we compared the median RT for the correctly identified trials (“hits” and “correct rejections”) between trials in the first and fourth power quartile. Second, to investigate the impact of IAF phase on accuracy on each trial, we categorized all trials into those in which participants identified stimuli correctly (“hits” and “correct rejections”, coded “1”) and those participants got wrong (“misses” and “false alarms”, coded “2”) for each participant. To evaluate the relationship between phase and behavior, we used a parametric logistic regression analysis within each participant to test whether phase predicts responses at the single-trial level (Zoefel et al., 2019). As described by the authors, “Sine- and cosine-transformed phases were included in the regression model, yielding two circular predictors of the participant’s response. The full regression model (including phase) was then compared with an intercept-only model, using an F test, and yielding a p-value for each participant”. The individual p-values were subsequently combined according to Fisher’s method (see Zoefel et al., 2019, section 2.2.2. “Parametric Regression-Based Methods” for details). To investigate the impact of IAF phase on RT and to estimate the possible confounding effect of RT difference, the same approach as in the previous step was used. For each participant, we selected the correctly identified trials (“hits” and “correct rejections”) and used a parametric linear regression analysis within each participant to test whether phase predicts RT at the single-trial level (Zoefel et al., 2019). Again, the individual p-values were subsequently combined according to Fisher’s method.

Finally, we analyzed the influence of IAF phase at stimulus onset on accuracy, $d'$ and criterion. All these parameters can only be calculated for groups of trials and not individual trials. Therefore, we grouped trials of similar phase together into four phase bins for each participant (Hussain et al., 2018). Each phase bin comprised 90° (out of the total 360° of one oscillation) of phase. The first bin contained all trials with phases from −135° to −45°, the second all trials from −45° to 45°, the third from 45° to 135°, and the fourth from 135° to −135° (Figure 2d). Since the duration of the fixation dot is randomized, we expected the phase at stimulus onset to be random as well, and all bins should contain a similar number of trials. We then calculated accuracy, $d'$, and criterion for groups of trials in the first (“trough”) and third (“peak”) bin within each participant. To test this non-directional hypothesis, we used two-sided, paired-samples t tests analyzing the difference in accuracy, $d'$, and criterion for the groups of trials in the first and third phase bin.

Previous studies showed an effect of the duration of an experiment on alpha band power (Benwell et al., 2019; Van Dijk et al., 2008). To estimate the confounding influence of the time on the task, for the two electrodes we computed two 2 × 2 repeated measures ANOVAs on the mean alpha power with the factors Time (first and fourth quartile of trials) and Power (lowest and highest power quartile), with Holm–Bonferroni correction for multiple comparisons (Holm, 1979). An interaction between the two factors would indicate a non-linear shift in alpha band power over time, which could bias our results.

3 | Results

3.1 | Behavior

In a first step, we compared the number of trials between ‘hits’ and ‘correct rejections’ to test for a response bias. The two-tailed paired-samples t test did not reveal a significant difference between both response categories ($t(17) = 1.79$, $p = 0.091, BF_{10} = 0.91$, Figure 3a). In other words, participants were equally able to correctly identify upright and rotated stimuli. Next, we compared median RT between all response categories using a 2 × 2 repeated measures ANOVA with the factors Stimulation (upright and rotated) and Response (upright and rotated) (Figure 3b). RTs varied for each participant ($M = 764$ ms; $SD = 105$ ms). We did not find a main effect of Stimulation ($F(1,16) = 0.45, p = 0.50$), but we found a main effect of Response ($F(1,16) = 16.52, p < 0.001$). We also did not find an interaction ($F(1,16) = 0.12, p = 0.73$). Post-hoc paired-samples t tests with Holm–Bonferroni correction for multiple comparisons revealed faster responses for ‘hits’ than for ‘false alarms’ ($t(17) = −4.69, p = 0.001, BF_{10} = 147.10$), faster responses for ‘correct rejections’ than for ‘misses’ ($t(17) = −3.08, p = 0.03, BF_{10} = 7.30$), and faster responses for ‘correct rejections’ than for ‘false alarms’ ($t(17) = −5.82, p < 0.001, BF_{10} = 1,152.95$). All other comparisons were not significant (‘miss’ vs ‘hit’: $t(17) = 2.10, p = 0.15, BF_{10} = 1.41$; ‘correct rejection’ vs ‘hit’: $t(17) = −0.05, p = 1.0, BF_{10} = 0.24$; ‘false alarm’ vs ‘miss’: $t(17) = 0.50, p = 1.0, BF_{10} = 0.27$). Thus, participants were overall faster to respond correctly than to make an error.

3.2 | EEG data

The analysis of EEG data focused on the influence of the IAF power and phase prior to stimulus onset on accuracy, $d'$, criterion, and RT.

First, the difference in perceptual performance between trials with high or low prestimulus IAF power (lowest and highest power quartile) was compared (Figure 4). We found that accuracy was lower in the quartile of trials with high alpha power than in low alpha power trials, but only on the right hemisphere electrode O2 ($t(17) = −3.00, p = 0.015, BF_{10} = 6.33$). On the
same electrode, we found a non-significant trend for reduced sensitivity in trials with high alpha power ($d'$, $t(17) = -2.40$, $p = 0.055$, BF10 = 2.27). Next, we compared criterion between the lowest and highest power quartile but did not find significant differences. Similarly, we did not find an influence of alpha power on RTs. Thus, IAF power influenced accuracy and sensitivity, but not the decision criterion or response speed.

Subsequently, we tested the relationship between the IAF phase estimated based on two cycles prior to stimulus onset on single-trial accuracy and RT, separately for electrodes O1 and O2. Within each participant, we computed a regression, and combined $p$-values across participants. Across the whole group, we neither found a significant relationship between the IAF phase and accuracy, nor between the IAF phase and RT (Figure 5). In other words, the IAF phase at stimulus onset had no influence on response accuracy or speed.

Finally, we split trials into four bins according to the phase angle and compared accuracy, sensitivity ($d'$) and criterion between the “peak” and “trough” phase bins, separately for electrodes O1 and O2. Using two-sided, paired-samples $t$ tests, we found no significant differences in accuracy, sensitivity, or criterion between the phase bins (Figure 6). In other words, IAF phase bin at stimulus onset had no influence on perception. Importantly, the number of trials between the “peak” and “trough” phase bins was not significantly different.

To examine a possible shift in alpha power over the course of the experiment, we used separate repeated measures ANOVAs on the mean alpha power, accuracy, sensitivity, criterion, and RTs with the factors Time (first and fourth quartile of trials) and Power (lowest and highest power quartile). As expected, for the analysis of mean alpha power, we found a trivial main effect of Power, indicating higher power in the highest power quartile than in the lowest power quartile (O1: $F(1,16) = 15.42$, $p_{holm} = 0.0022$; O2: $F(1,16) = 15.05$, $p_{holm} = 0.0022$). Moreover, in line with previous reports (Benwell et al., 2019), we found a trend for a main effect of Time with higher power in later trials at electrode O1 (O1: $F(1,16) = 5.07$, $p_{holm} = 0.0757$; O2: $F(1,16) = 2.22$, $p_{holm} = 0.1546$). For the analysis of RTs, we found a main effect of Time, indicating faster reactions in later trials at electrode O1 (O1: $F(1,16) = 5.51$, $p_{holm} = 0.0313$; O2: $F(1,16) = 7.61$, $p_{holm} = 0.0269$). All other comparisons were not significant. Importantly, we did not find any interaction between Time and Power (Table S1). The absence of an interaction between Time and Power speaks against a confounding effect of experimental duration on our findings.

4 DISCUSSION

A number of reports show an influence of ongoing neural oscillations on visual (e.g., Van Dijk et al., 2008), auditory (e.g.,
FIGURE 4  Comparison of perceptual performance between trials with low (Q1) and high (Q4) alpha power for electrodes O1 (a) and O2 (b). (a) No effects were found for electrode O1. (b) High alpha power reduced perception accuracy (first panel) and sensitivity (second panel) for electrode O2. However, no influence on criterion (third panel) or reaction times (fourth panel) was found (Holm–Bonferroni corrected paired-sample t tests, *p < 0.05)

FIGURE 5  Single-trial analysis of perceptual performance for electrodes O1 (a) and O2 (b). Within each participant, the relationship between accuracy and phase (a) and between RT and phase (b) was estimated on a single-trial level. Points indicate the individual p-values of the within-participant comparison between the full regression model (including phase) and an intercept-only model. Horizontal bars indicate the average p-value across individuals and “pcomb” the combined p-values across the group
Leske et al., 2015), and tactile perception (e.g., Baumgarten et al., 2016), but also on the neural effects induced by magnetic stimulation (e.g., Keil et al., 2014). Moreover, ongoing alpha oscillations can influence the perception of a multitude of visual, auditory, and multisensory illusions (Lange et al., 2014). However, these findings are usually reported for very brief stimuli at the perceptual threshold. Here, we aimed at extending these findings to visual stimuli that are salient but challenging to distinguish and presented until participants made a response choice. To this end, we created high-contrast visual stimuli, in which participants were asked to discriminate a clockwise or counterclockwise rotation. Importantly, the degree of rotation was adjusted individually to ascertain an 80% accuracy. Our data analysis focused on the individual alpha band power and phase prior to stimulus onset. Using these long-duration stimuli, we found that IAF power had an influence on accuracy, but not on criterion or RTs, and an inconclusive effect on sensitivity. Moreover, the phase at stimulus onset did not influence perception or response speed.

In the current experiment, we found that participants were significantly more accurate at identifying the stimuli, when alpha power was lower prior to stimulus onset. This finding supports theories connecting alpha activity with changes in cortical excitability (e.g., Klimesch et al., 2007). Also, it is partly in line with previous studies showing reduced alpha power prior to “hits” compared to “misses” of briefly presented stimuli (e.g., Ergenoglu et al., 2004; Mathewson et al., 2009; Van Dijk et al., 2008). However, without accounting for the false alarm rate, it is not clear whether excitability affects the bias to report a stimulus or the accuracy (Iemi & Busch, 2018). Therefore, the present analyses of accuracy, sensitivity, and criterion accounted for false alarm rates in addition to hit rates. We, thus, extend previous results by showing that the effect of alpha power on perception holds true when integrating hit rates and false alarm rates in the estimation of accuracy, for a new type of discrimination task (rotated vs upright), and for drastically longer stimulus presentation times. By examining salient visual stimuli that were presented for up to 1.5 s, we show that shifts in cortical

**FIGURE 6**  Comparison of perceptual performance between stimulus onset in peak and trough phases for electrodes O1 (a) and O2 (b).
Within each participant, trials were grouped into four phase bins according to the phase at stimulus onset. Accuracy (left panels), sensitivity (middle panels), and criterion (right panels) were compared between the ‘peak’ and ‘trough’ bins, separately for electrodes O1 (a) and O2 (b). No significant differences between performances in different phase bins were detected (Holm-Bonferroni corrected paired-sample t tests)
excitability are relevant on larger time scales than previously examined.

Previous results show that shifts in cortical activity bias perception, which have been interpreted as changes in criterion in detection tasks (Iemi & Busch, 2018; Iemi et al., 2017). Based on this, Samaha and colleagues proposed the baseline sensory excitability model (BSEM, Samaha et al., 2020), which predicts different effects of alpha power on accuracy, sensitivity, and criterion for detection and discrimination tasks. For our discrimination task, the BSEM predicts that a change in alpha power globally changes the cortical excitability for detectors tuned to rotated and upright stimuli, thereby increasing the hit rate, but also the false alarm rate, leading to a more liberal criterion. This increase in hit and false alarm rates would also leave the accuracy of the discrimination of the different stimuli unchanged.

This, however, was not the case in our experiment: Prestimulus alpha power did not significantly influence the discrimination criterion. Instead, alpha power influenced accuracy and appeared to modulate sensitivity when participants had more time to inspect the stimuli, but the latter effect did not survive the correction for multiple comparisons. However, compared to accuracy, sensitivity is more precise, as the former can be influenced by the criterion, and multiple combinations of sensitivity and criterion can produce the same accuracy (Lynn & Barrett, 2014). The inconsistency between sensitivity and accuracy might be the result of a more liberal criterion in low compared to high alpha power in some participants that influenced the accuracy estimates. Our results could also indicate that decreased alpha power marks a state of cortical excitability, which could have sharpened the discriminability of rotated and upright stimuli, leading to more “hits” and “correct rejections” without changing the discrimination criterion itself. Importantly, more “correct rejections” translate to fewer “false alarms”. The increased cortical excitability in combination with the longer duration of the presented stimuli, thus, might allow a more accurate discrimination compared to shortly presented stimuli, which likely rely on an internal representation of the perceived stimuli. Notably, it is assumed that a more liberal criterion under low alpha power is a result of non-specific enhanced activation of neuronal ensembles encoding the sensory representations of both stimulus alternatives (i.e., a perceptual bias) and not a result of a biased decision process (Iemi & Busch, 2018; Samaha et al., 2020). Therefore, the longer presentation time could reduce the influence of the subjective perceptual bias reflected in the criterion, as the stimuli can be inspected in greater detail and across multiple perceptual cycles. Yet, the support for this idea is weak and the relationship between stimulus presentation time, shifts in cortical activity, and perception needs to be examined in more detail. One interesting question here concerns the effect of stimulus duration: It would be interesting to see, if the influence of criterion and accuracy change with increasing viewing time.

In the current experiment, participants had up to 1,500 ms to decide, whether the presented stimulus was upright or rotated. As intended, this task was challenging for the participants, but the difficulty of the task did not differ between rotated and upright stimuli. However, participants took on average 764 ms to respond, which is considerably longer than in other studies on the role of neural oscillations and visual perception. Early reports on the relationship between alpha phase and perception report RTs in the range of 129–262 ms (Callaway & Yeager, 1960; Dustman & Beck, 1965). More recent experiments using masked target detection tasks report RTs around 600 ms (Van Dijk et al., 2008) or between 652 and 674 ms (Limbach & Corballis, 2016). Thus, in the current experiment, we can assume that participants took more time to visually inspect the stimuli prior to their response. Interestingly, studies using drift-diffusion modelling (DDM) to examine RTs and neural oscillations in detection and discrimination tasks found that changes in theta and alpha band power relate to the accumulation of evidence toward a decision (Kloosterman et al., 2019; Van Vuigt et al., 2012). Here, we found that participants took longer to report a decision compared to studies using short stimulus presentation times. Moreover, we found that participants were significantly faster in the correct compared to the incorrect responses. Future studies could, therefore, compare the parameters of the DDM (e.g., the starting point or the decision boundaries) between trials with low and high alpha band power and different onset phases to examine the influence on stimulus discrimination. Moreover, future studies could examine stimuli covering one, two, or multiple phases of the IAF to estimate the influence of examining the stimuli across multiple excitatory and inhibitory phases.

A number of studies found a negative relationship between alpha power and the amplitude of the early visual evoked responses (Becker et al., 2008; Ruhn & Başar, 2009; Roberts et al., 2014). Similarly, Iemi et al. (2019) found a reduction of the visual C1 component following strong prestimulus power. Moreover, previous studies report an influence of prestimulus alpha power on RTs, especially in lateralized detection tasks (e.g., Thut et al., 2006). We did not find such an effect, but we only considered correct responses in our analyses of RTs, to avoid biasing the analysis by random button presses. Future studies could, therefore, examine the influence of oscillatory activity on correct as well as incorrect responses.

While in previous research much focus was put on prestimulus alpha power, the impact of alpha phase has subsequently been examined more closely. For instance, the findings of Mathewson and colleagues (Mathewson et al., 2009) suggest that shifts in perceptual accuracy that were previously attributed to alpha power can be explained as phase effects of the alpha oscillation. For stimuli with a longer duration, none
of the measured behavioral variables (accuracy, sensitivity, criterion, and RT) depended on alpha phase, neither on the single-trial level nor when categorized into phase bins. Thus, for long salient visual stimuli, we do not find evidence of alpha oscillations acting out pulsed inhibition. It is conceivable that the phase at stimulus onset was less relevant for perception in the current experiment, as participants had ample time to examine the stimuli in close detail before responding. Alternatively, it is possible that our longer stimuli covered multiple inhibition and excitation pulses, thereby reducing the influence of the phase at stimulus onset. In order to understand the functional role of alpha activity in perceptual processes, it is vital to examine these effects in greater detail, with a focus on stimulus processing beyond primary sensory areas.

One caveat to our study is that it is not completely clear how participants interpreted the task and the possible responses. Participants had to differentiate between upright and rotated stimuli. The task could, therefore, have been interpreted as trying to identify ‘rotation’ as signal or it could have been interpreted as trying to find upright targets as the signal. For each of these interpretations, deciding according to a more conservative criterion has opposite effects: If ‘rotation’ is seen as the signal, a conservative answering approach (i.e., rarely responding “rotated”, often responding “upright”) with low hit rates and low false alarm rates would result in a higher criterion value. However, if a participant interprets ‘uprightness’ as the signal to look out for, a more conservative answering approach (i.e., rarely responding “upright”, often responding “rotated”) would result in a lower criterion value due to high hit rates and high false alarm rates according to our definition. If we take a look at the individual criteria for high and low pre-stimulus power quartiles (see Figure 4), we can see that most participants have positive criteria, but a few show the opposite pattern. To examine the possible influence of a subjective interpretation of the task, we repeated the analyses of prestimulus power after defining the signal based on the individual response bias. However, we found qualitatively identical results with respect to the criterion. Without explicit information regarding participants’ response strategy, we cannot differentiate between a low criterion due to the subjective perception of a rotated stimulus or a strategy to focus on the upright stimuli. Thus, future studies should pay close attention to explicitly instructing participants regarding the target condition or ask for the participants’ response strategies.

A second caveat to our study is our a priori selection of electrodes. Numerous previous studies indicate that the alpha oscillations influencing visual perception can be recorded across occipital scalp areas (Iemi et al., 2017; Limbach & Corballis, 2016; Mathewson et al., 2009; Samaha et al., 2017; Van Dijk et al., 2008; Zumer et al., 2014). However, a number of studies also found that perceptual decisions are related to prestimulus neural oscillations over frontal electrodes, which we did not include in the EEG recording (Achim et al., 2013; Busch et al., 2009; Iemi et al., 2017). Notably, alpha power and phase effects on visual perception might have different cortical generators, with power effects originating from occipital–temporal areas, and phase effects involving frontal areas (Zazio et al., 2021). Therefore, the null results found in the current experiment may be due to the omission of effects outside the two occipital electrodes. Future studies should, thus, include a whole-head coverage to allow for further data exploration.

5 | CONCLUSION

In the current experiment, we examined the influence of neural oscillations at the IAF on perception of salient but challenging visual stimuli presented for up to 1,500 ms. Contrary to previous reports, we found that prestimulus alpha power influenced perceptual accuracy and—to a lesser extend—sensitivity. Moreover, we neither found an influence of alpha power on criterion or response speed nor an influence of alpha phase on perception or response speed. Thus, we conclude that the influence of phase on perception is only relevant for briefly presented stimuli. If stimuli remain visible across multiple cycles of the alpha oscillation, participants can likely integrate information across optimal and suboptimal phases. Increased cortical excitability—indicated by low alpha band power—might then sharpen the discrimination ability leading to more accurate perception. However, if the cortical excitability is low—indicated by high alpha power—even a longer viewing time does not lead to accurate perception.

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CONFLICT OF INTEREST

The authors declare the absence of any relationships that could be construed as a potential source of conflict of interest.

AUTHOR CONTRIBUTIONS

LTJ conceived the study, LTJ and JK designed the experiment, LTJ collected the data, LTJ and GM analyzed the data, LTJ, GM, and JK drafted the manuscript, GM and JK prepared the figures.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ejn.15169.
DATA AVAILABILITY STATEMENT
Experimental scripts, preprocessed data, and analysis scripts can be found at the Center for Open Science repository “Prestimulus alpha power but not phase influences visual discrimination of long-duration visual stimuli” (https://osf.io/x5mzw/).

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