Rhythmic Influence of Top–Down Perceptual Priors in the Phase of Prestimulus Occipital Alpha Oscillations

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Abstract

■ Prior expectations have a powerful influence on perception, biasing both decision and confidence. However, how this occurs at the neural level remains unclear. It has been suggested that spontaneous alpha-band neural oscillations represent rhythms of the perceptual system that periodically modulate perceptual judgments. We hypothesized that these oscillations instantiate the effects of expectations. While collecting scalp EEG, participants performed a detection task that orthogonally manipulated perceptual expectations and attention. Trial-by-trial retrospective confidence judgments were also collected. Results showed that, independent of attention, prestimulus occipital alpha phase predicted the weighting of expectations on yes/no decisions. Moreover, phase predicted the influence of expectations on confidence. Thus, expectations periodically bias objective and subjective perceptual decision-making together before stimulus onset. Our results suggest that alpha-band neural oscillations periodically transmit prior evidence to visual cortex, changing the baseline from which evidence accumulation begins. In turn, our results inform accounts of how expectations shape early visual processing. ■

INTRODUCTION

Perception is subject to powerful top–down influences. For example, a highly ambiguous figure can be easily identified following brief priming of object identity (Porter, 1954). Many believe that the feed-forward sensory input is shaped by feedback or recurrent connections from high-level cortical areas to lower-level regions (Gilbert & Li, 2013; Gilbert & Sigman, 2007; Lee, 2002) following a first pass up the sensory hierarchy (Bar, 2003). However, the neuronal mechanisms that integrate top–down and bottom–up signals remain largely unknown (Bar, 2003).

Top–down influences, including priming, context effects, and prior exposure, can be parsimoniously construed as a process that biases perceptual inference toward a plausible solution. In line with this, there has been renewed interest in framing top–down influences in terms of probabilistic prior beliefs or "expectations" (Summerfield & de Lange, 2014), which, behaviorally, bias perceptual choice (Sherman, Seth, Barrett, & Kanai, 2015; De Lange, Rahnev, Donner, & Lau, 2013). It is suggested that expectations are represented in high-level cortical regions before the perceptual event and entrain task-relevant neurons at lower levels to increase sensitivity (Engel, Fries, & Singer, 2001). Spontaneous neural oscillations are therefore a promising candidate mechanism for how expectations shape perception.

Oscillations in the alpha range are particularly relevant when considering how expectations influence perception. Theoretical models have associated top–down processes with oscillations in the 8–14 Hz range (Friston, Bastos, Pinotsis, & Litvak, 2014; Bastos et al., 2012), and recent neurophysiological findings suggest that occipital alpha oscillations primarily propagate in a top–down fashion (Van Kerkoerle et al., 2014), supporting the notion that alpha power is intimately related to top–down control (Mathewson et al., 2012; Klimesch, Sauseng, & Hanslmayr, 2007; Palva & Palva, 2007). Recent work has revealed that the phase (in addition to power) of prestimulus alpha oscillations also predicts various components of perception. These include spatial attention (Busch & VanRullen, 2010), saccadic reaction speed (Drewes & VanRullen, 2011), and perceptual awareness ratings (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). This has been interpreted as reflecting cycles in the "preparedness" of the perceptual system (Vanrullen, Busch, Drewes, & Dubois, 2011). In Bayesian terms, prior beliefs (i.e., expectations) are available before stimulus onset. Accordingly, we hypothesized that this "preparedness" should be modulated by expectations: anticipating a perceptual event should bias perceptual inference toward that event. This was tested by asking whether the extent to which decisions are biased by expectation oscillates with prestimulus occipital alpha phase.

Perceptual decisions are additionally accompanied by a subjective degree of confidence, which is associated with uncertainty arising through external (i.e., sensory) or internal noise. Recent work has shown that the decision variable and decision confidence may be encoded together (Kiani & Shadlen, 2009) and arise from the same sensory

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evidence (Fetsch, Kiani, Newsome, & Shadlen, 2014). In addition to expectations biasing decision, expected perceptual events are associated with greater subjective confidence (Sherman, Seth, et al., 2015). Following these findings, we additionally hypothesized that prestimulus alpha phase would predict the influence of perceptual priors on confidence.

These two hypotheses were tested by adopting a dual-task Gabor detection paradigm, which manipulated prior expectations while controlling for the (often conflated) influence of attention (Feldman & Friston, 2010; Summerfield & Egner, 2009). Prior expectations of target presence or absence were induced by manipulating (block-wise) the probability of Gabor appearance, presented at a contrast that yielded 70% accuracy. The probability was either 25%, such that absence was expected, or 75%, such that presence was expected. A concurrent visual search task diverted attention from the Gabor task in half of the blocks. Critically, the visual search array and Gabor were presented simultaneously following a jittered ISI (Figure 1). This allowed us to time-lock our EEG analysis to both Gabor-present and Gabor-absent trials and compute independent measures of decision threshold (bias) and detection sensitivity as a function of condition and prestimulus EEG phase.

Our first hypothesis was that prestimulus alpha phase would predict the extent to which decision threshold is biased by expectation. This would be shown if (1) decision threshold oscillates with prestimulus phase and (2) there is some phase angle that predicts "yes" responses when expecting target presence (the 75% condition) while predicting "no" responses when expecting target absence (the 25% condition).

Our second hypothesis was that prestimulus alpha phase would also predict expectancy effects on subjective confidence. This would be shown if (1) confidence oscillates with prestimulus phase and (2) the same phase that predicts high confidence when expectations are met will predict low confidence when expectations are violated.

METHODS

Participants

Participants were 20 English-speaking participants (13 women) aged between 20 and 32 years (M = 25.6, SD = 3.3) with normal or corrected-to-normal vision. One participant's data were excluded from analysis for being excessively noisy and a second for having too few trials (<500 vs. mean of ~1100). This was due to excessively slow responding. This left 18 participants' data for analysis. All participants gave informed, written consent and were reimbursed at £10.30/hr. On average, each session lasted 2.5 hr, and two sessions were completed 24 hours apart. Ethical approval was awarded by the University of Sussex ethics committee (C-REC).

Stimuli and Design

The experiment was presented on a 21-in. CRT monitor (100 Hz, 1048 × 700 resolution) using Psychtoolbox for Matlab (Natick, MA). The experiment was composed of two concurrent tasks: detection of a peripheral Gabor patch and a visual search task in the center of the screen (Figure 1).

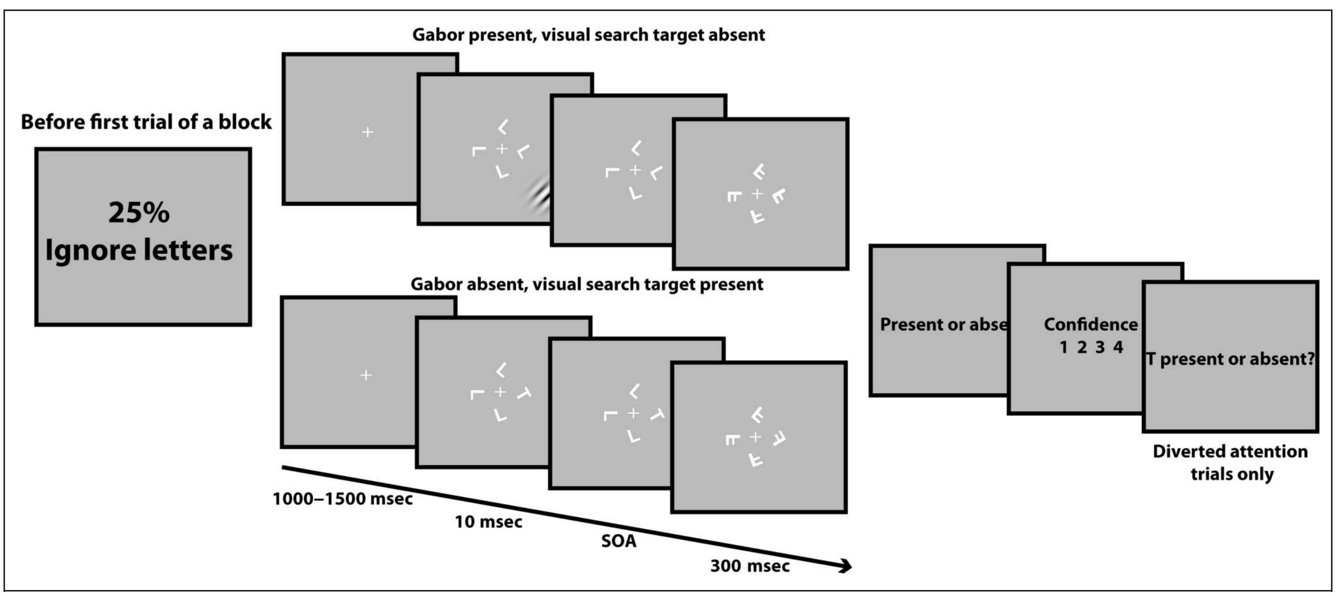

Figure 1. Trial sequence. Before the first trial of a block participants are informed of the experimental condition they are in. In this example, "25%" means that the participant is in the 25% chance of Gabor presence condition and "ignore letters" means that the participant should ignore the visual search array (i.e., they are in the full attention condition). During the trial, a target Gabor is either present (top) or absent (bottom). Similarly, a visual search target T is either present (bottom) or absent (top). Response prompts followed the offset of the masking array.

Trials began with the onset of a white fixation cross. After a jittered ISI (1000–1500 msec), the visual search array appeared. This consisted of four rotated (random orientation of 0°–359°), white, capitalized letters arranged around fixation (1.43° × 1.43°) at 0°, 90°, 180°, and 270°. On 50% of trials, the visual search target was absent and all letters were Ls. On the other 50%, one randomly designated L was replaced by a target T. To ensure that the task was sufficiently difficult to divert attention from the Gabor task, this array was backward masked by an array of Fs. The SOA between the visual search and masking array was titrated for each individual to equated detection performance to 78% across participants (see Staircases).

On Gabor "target-present" trials, a peripheral (3.85° × 4.095° visual angle) Gabor patch (*SD* 0.89°, *sf* 0.08c/d, phase 45°) was presented in the lower right quadrant of the screen. On these trials, the Gabor and the visual search array appeared simultaneously. The Gabor was presented for 10 msec at the contrast resulting in a 70% hit rate (see Staircases).

Following the offset of the visual search array, a series of response prompts appeared. Using a key press, participants made unspeeded judgments of, first, Gabor presence or absence; second, confidence that they were correct on an interval scale from 1 (*no confidence*) to 4 (*total confidence*); and finally, the presence or absence of a T in the visual search array.

The experiment had four conditions, constructed in a blocked attention (full, diverted) × expectation (expect Gabor presence, expect Gabor absence) design. Under full attention participants fixated centrally but did not perform the visual search task, thereby allocating full attention to Gabor detection (visual search responses were not requested). Under diverted attention, participants performed both tasks, prioritizing visual search. Expectation was manipulated by informing participants of the true probability of Gabor presence (as well as the attention condition) before each block began. This was either 25% (expect absence) or 75% (expect presence). After each experimental trial, a condition-specific 2 down 1 up staircase titrated the contrast of the Gabor to maintain a consistent hit rate during the long experimental sessions. Expectation-specific staircases controlled for potentially greater levels of sensory adaptation to the Gabor in the 75% condition.

Each block consisted of 12 trials from one of the conditions, and blocks were completed in sets of 8 (2 of each condition, 96 trials). Blocks were fully counterbalanced. Participants completed as many blocks as possible in each testing period (always equal numbers of each condition; 6–18 runs of each condition per session, M = 11.5). Across participants, there was considerable variation in total trials completed due to the cumulative effect of RT differences.

After explaining the task to participants, they completed a set of practice trials. Next, they completed three staircase procedures (see Staircases) and, finally, the experimental trials. Participants were encouraged to take regular breaks and were offered to leave the session early if they became too tired to continue.

Staircases

Following a set of practice trials, participants completed three interleaved 2 down 1 up psychophysical adaptive staircase procedures with eight reversals to equate task difficulty across conditions and participants. The visual display was always the same as that in the experimental trials, but the instructions and response prompts differed. In the first staircase, participants performed Gabor detection while ignoring the visual search array (full attention). Only Gabor-present/-absent responses were collected. Gabor contrast was titrated to achieve a 70% hit rate (contrast cannot be titrated in target absent trials) under full attention. In the second staircase (3 up and 1 down), the Gabor was ignored, and participants performed only visual search. Here, only responses to the visual search target were collected (T-present/-absent). The SOA between the visual search array and the masking array was titrated to achieve 78% accuracy in the visual search task. In the third staircase, participants performed both Gabor detection and visual search simultaneously, prioritizing visual search and reported both Gabor presence/absence and T presence/absence. Here, Gabor contrast was titrated to achieve a 70% hit rate under diverted attention. The SOA for the visual search display was set to that determined by the second staircase. Confidence judgments were not collected during the staircases.

EEG Acquisition

EEG data were collected on an ANT system at a sample rate of 2048 Hz with no online filtering. Activity was measured continuously from 62 active electrode channels arranged according to the 10/20 system over the scalp. The ground electrode was placed on the forehead, and data were averaged across the whole head online. Impedances were kept below 7 kΩ throughout the experimental session. Participants sat in an electrically shielded faraday cage with an external monitor viewed through shielding glass. Their head was stabilized with a chin rest.

EEG Preprocessing

EEG data were preprocessed using the EEGLAB toolbox for Matlab. During preprocessing EEG recordings were downsampled to 256 Hz and high-pass (0.1 Hz) filtered with a finite impulse response filter (EEGlab function *eegfilt*). EEG data were visually inspected for excessively noisy channels, which were manually interpolated with their two neighbors on a block-wise basis. No participant required more than three channels interpolated (five participants in total). No interpolated channels were included in analyses presented in this article. After interpolation, data were referenced to participants' average signal. Data were epoched from 1000 msec before visual search array (and Gabor target, if present) onset to 500 msec after. Manual artifact rejection was performed on saccade, eye blink, and excessively noisy trials (5% of trials removed on average). For each participant, each electrode, and each trial we computed, the time–frequency wavelet decomposition of the EEG data. Window lengths of 1 oscillatory cycle at low frequencies (starting at 2 Hz) were utilized. This length linearly increased with frequency band to a maximum of 15 cycles at 50 Hz. This decomposition method generated wavelet coefficients for 49 log-spaced frequencies and 242 time points.

Analysis

EEG: Electrode ROI

We had an a priori hypothesis that top–down influences of prior expectation would be observable over occipital regions. Initial analyses were therefore restricted to the occipital electrodes O1, Oz, and O2. Because phase at some time–frequency point will differ across electrodes, analyses were further restricted to one electrode per participant and session. To control for differences in electrode placement, electrode ROIs (eROIs) were determined on a participant-by-participant and session-by-session basis according to their sensitivity to the Gabor detection task. The grand-averaged ERP indicated a negative deflection following hits relative to misses in the 75–200 msec range. Each participant's session-specific eROI was therefore chosen as the occipital electrode (i.e., O1, Oz, or O2) that showed the greatest ERP amplitude, as defined below. To compute the ERPs, a 200-msec prestimulus baseline was subtracted from each epoch. Epochs in which hits (respectively, misses) were made were averaged together. For each response type (hit or miss), we obtained the maximal local peak amplitude (LPA) in the 75–200 msec period. LPA is defined as the greatest amplitude within a range of time points such that this peak is greater than the average amplitude of the surrounding 7 time points (Luck, 2005). This method minimizes the chance of selecting spurious spikes. The eROI for each participant was chosen as the occipital electrode that showed the greatest value for $LPA_{hit} - LPA_{miss}$. Subsequent analyses on phase were restricted to these eROIs.

EEG: Phase Opposition Analysis

Next, we sought to determine if, for our eROI, spontaneous EEG phase differed at any time point and in any frequency band between "reported present" (yes) and "reported absent" (no) trials. This was done to isolate candidate time–frequency regions in which expectation might interact with the influence of EEG phase. The relationship between phase and response was quantified with the measure phase opposition (Vanrullen et al., 2011), which is defined as the mean of phase-locking values (PLVs) for yes and no responses. PLV measures the extent to which phase angle at some time–frequency point over one electrode is predicted by either (A) phase at the same time–frequency point over another electrode or (B) a behavioral response (as in the present article). Here, we used PLV as a measure of the relationship between ongoing phase and response. Because yes and no responses encompass all possible responses and because stimulus onset is unpredictable (randomized ISIs), the joint PLV across all trials is expected to be small (no different from chance). However, if EEG phases for a given behavioral response are clustered about some angle (necessarily different for yes and no), then the individual PLVs for both yes and no responses and, therefore, the resulting phase-opposition value will be high (up to 1 for perfect phase opposition; see Vanrullen et al., 2011, for additional details). High (and statistically significant) values indicate that phase predicts yes versus no responses. For a set of n trials where response R is given and where $C(R)$ is the complex coefficients of the wavelet transform, PLV_R and phase opposition (PO) for responses R_1 and R_2 are defined as follows:

$$\mathrm{PLV}_R = \left| \frac{1}{n} \sum_n \frac{C(R)}{|C(R)|} \right| \qquad \mathrm{PO}_{R_1,R_2} = \frac{\mathrm{PLV}_{R_1} + \mathrm{PLV}_{R_2}}{2}$$

This measure PO is similar to the phase bifurcation index (PBI; Busch, Dubois, & VanRullen, 2009). PBI is defined as $(\mathrm{PLV}_{R1} - \mathrm{PLV}_{ALL}) \times (\mathrm{PLV}_{R2} - \mathrm{PLV}_{ALL})$, that is, the baseline-corrected product of PLVs for Response 1 and Response 2. We preferred the additive measure PO, because PBI can give unreliable results when taking the product over very small values. Moreover, because PO is additive, it is robust to differences in trial counts between "yes" and "no" trials: any baseline correction applied to empirical PO values would be equally applied to bootstrapped PO values and cancel out.

PO between yes and no responses was separately calculated for each level of attention and expectation. Separate calculation of PO for each level of expectation was necessary because we hypothesized that the phases predicting "yes" (respectively, "no") would differ as a function of expectation. The four PO time–frequency maps corresponding to each experimental condition were averaged together.

At each time–frequency point, PO statistical significance was assessed by estimating the mean and standard deviation of the null distribution from 8000 bootstrapped samples per participant. To obtain bootstrapped samples, responses were pseudorandomly assigned to trials such that the number of yes and no responses stayed the same. PO was then recalculated. This method removed any relationship between the EEG signal and behavior. Z scores and p values were computed by comparing empirical PO values to the mean and standard deviation of the bootstrapped values. p values were false discovery rate (FDR) corrected for multiple comparisons over all frequencies and all prestimulus time points.

EEG: Phase Modulation of Perceptual Decision

The time–frequency representation of phase opposition values revealed that phase is related to the participants' response (see above and Figure 3B). However, we did not know (and aimed to determine) whether the "optimal" phase for a yes response is comparable for the different expectation conditions. To determine whether the influence of expectation on decision is predicted by prestimulus phase in some frequency band, a follow-up analysis was run in which the data were restricted to a time–frequency ROI. The time–frequency ROI was taken as the point of maximal phase opposition (PO) significance. Critically, there was no circularity in this analysis because PO values had been collapsed across levels of expectation.

For each participant, each condition, and each trial, the phase at the time–frequency ROI was binned into one of six phase bins. For each bin, we then computed within-subject signal detection theoretic (SDT) outcome variables d' (sensitivity), c (decision threshold/bias), and confidence (percentage of trials reported with high confidence). This provided values of each SDT outcome as a function of condition and phase bin. Using six bins enabled a sufficient number of trials for SDT estimates to be reliable.

SDT Outcomes

To obtain separate measures of detection sensitivity and decision bias, we used SDT (for an overview, see Sherman, Barrett, & Kanai, 2015; Green & Swets, 1966). For each experimental condition, trials were categorized into hits, misses, false alarms, and correct rejections. Hit rate and false alarm rate are then defined as

$$\text{Hit rate} = \frac{\sum \text{Hits}}{\sum \text{Hits} + \sum \text{Misses}}$$

$$\text{False alarm rate} = \frac{\sum \text{False alarms}}{\sum \text{False alarms} + \sum \text{Correct rejections}}$$

From these quantities, detection sensitivity for the Gabor target d' and decision threshold c are given by

$$d' = Z(\text{Hit rate}) - Z(\text{false alarm rate})$$

$$c = -\frac{Z(\text{Hit rate}) + Z(\text{false alarm rate})}{2}$$

where Z is the inverse normal cumulative distribution function. Note that for decision threshold c, positive values represent a conservative bias (more likely to report no) and negative values represent a liberal bias (more likely to report yes).

In computing these measures, we used the log-linear rule, which adds 0.5 to the total number of hits, misses, false alarms, and correct rejections. This ensures that SDT outcome variables can be computed for all conditions and phase bins and also acts as a Bayesian prior on a d' of zero.

Confidence

Confidence ratings were collected on a 4-point scale. To account for individual differences in how the scale was used (mean confidence = 2.92, range = 2.34–3.47), we collapsed ratings onto a binary scale. This was achieved by calculating each participant's mean confidence across all conditions and then categorizing each rating as high (greater than the mean) or low (lower than the mean). Note that we did not use a median split because, here, the median is always an integer.

Statistical Analyses

Data were collapsed over experimental session. The factor Session (1 or 2) did not significantly interact with any other factors under any behavioral dependent variable. Analyses were conducted using Matlab, CircStat toolbox for Matlab (Berens, 2009) for circular statistics, and SPSS. Where appropriate, p values were FDR-corrected. Where appropriate, circular statistics were corrected for the binning of phase angles. Unless otherwise specified, data subjected to within-subject ANOVAs met the assumption of sphericity.

RESULTS

Expectation and Attention Separately Influence Contrast Sensitivity

To determine the success of our attention manipulation, we asked whether diverting attention with the visual search task decreased contrast sensitivity (as determined by the psychophysical staircases). Mean Gabor contrast was subjected to an Attention (full, diverted) × Expectation (25%, 75%) repeated-measures ANOVA. This revealed a significant main effect of Attention, $F(1, 17) = 22.60$, $p < .001$, $\eta_p^2 = .57$, such that contrast sensitivity was significantly greater (i.e., contrast threshold decreased) in the full (19.8% ± 1.2%) than diverted (25.7% ± 1.3%) attention condition. Our manipulation of attention was therefore successful. The ANOVA also revealed a significant main effect of Expectation, $F(1, 17) = 8.50$, $p = .010$, $\eta_p^2 = .33$, whereby contrast sensitivity is significantly greater in the 75% (22.3% ± 1.1%) than the 25% (23.3% ± 1.1%) condition. This is likely to be an outcome of more Gabor exposure in the 75% than the 25% condition, which was controlled by implementing running staircases during the experimental phase (see Staircases). The interaction between Attention and Expectation was not significant,

$F(1, 17) = 1.26, p = .278, \eta_p^2 = .07$. Results are represented in Figure 2A.

Expectations Bias Decision and Increase Subjective Confidence

The main behavioral analyses presented here used SDT (for details, see Methods). To ensure that our expectation manipulation successfully biased choice, decision threshold c was calculated as a function of condition. Here, $c > 0$ represents a conservative bias (i.e., toward reporting "no"), whereas $c < 0$ represents a liberal bias (i.e., toward reporting "yes"). An Attention (full, diverted) × Expectation (25%, 75%) repeated-measures ANOVA revealed that c was significantly affected by Expectation, $F(1, 17) = 70.33, p < .001, \eta_p^2 = .80$. As predicted, c was significantly more conservative in the 25% than the 75% condition ($M_{diff} = 0.21 \pm 0.03$; Figure 2B), meaning that decisions were more biased toward absence in the "expect absent" (25%) than the "expect present" (75%) condition. There was neither a significant main effect of Attention, $F(1, 17) = 0.01, p = .952, \eta_p^2 < .01$, nor a significant interaction between factors, $F(1, 17) = 1.45, p = .244, \eta_p^2 = .08$.

To determine whether detection sensitivity had been successfully equated across conditions, an Attention × Expectation repeated-measures ANOVA under detection sensitivity d' was run. This revealed a significant main effect of Expectation, $F(1, 17) = 52.85, p < .001, \eta_p^2 = .76$, such that d' was greater in the 25% (2.60 ± 0.09) than the 75% (2.23 ± 0.09) condition. This small difference was an unavoidable consequence of liberalizing decision threshold while ensuring a constant hit rate. The main effect of Attention, $F(1, 17) = 0.46, p = .507, \eta_p^2 = .03$, and its interaction with Expectation, $F(1, 17) = 0.23, p = .655, \eta_p^2 = .01$, was not significant.

We have previously found that expectations increase subjective confidence (Sherman, Seth, et al., 2015), and on this basis, we hypothesized that prestimulus phase would modulate the influence of expectations on confidence. To address this at the behavioral level, the next analysis determined whether this finding was replicated.

Previous work has shown that confidence increases when the perceptual report (i.e., percept) is congruent relative to incongruent with prior expectations. In the 25% condition, where Gabor absence is expected, the expectation-congruent report is "no," whereas in the 75% condition, where Gabor presence is expected, the

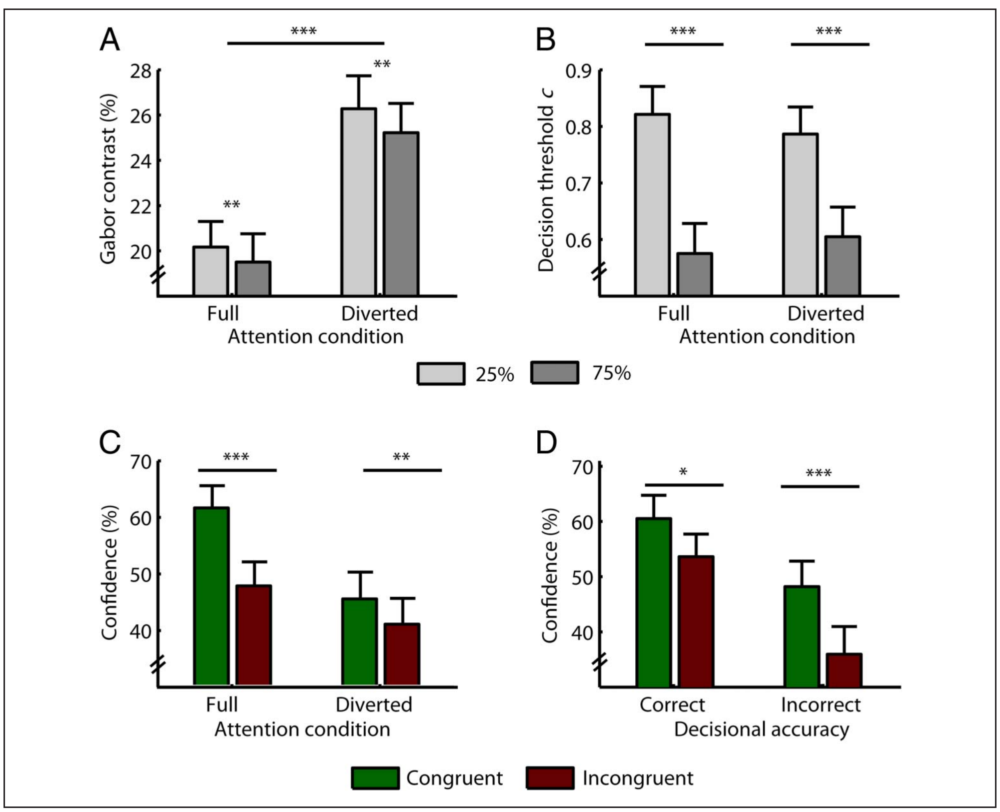

Figure 2. Behavioral results. (A) Mean contrast at which the Gabor was presented over the course of the experiment in each condition. Asterisks over levels of expectation represent significantly higher thresholds in the 75% than the 25% condition (main effect). Asterisks over levels of attention represent significantly higher thresholds under full than diverted attention (main effect). (B) Effects of attention and expectation on decision threshold c. Independent of attention, decision threshold in the 25% condition, where Gabor absence is expected, is higher than in the 75% condition, where Gabor presence is expected. Note that greater values represent stronger biases for reporting target absence. (C) Effects of attention and expectation report congruence on confidence. Congruent responses are reports of presence/absence in the 75%/25% condition and vice versa for incongruent responses. Confidence is higher for congruent than incongruent reports in both attention conditions, but the effect of congruence is greater under full attention. The main effects of both attention and congruence are also significant. (D) Effects of accuracy and expectation report congruence on confidence. Congruent responses are reports of presence/absence in the 75%/25% condition and vice versa for incongruent responses. Confidence is higher for congruent than incongruent reports for both correct and incorrect responses, but the effect of congruence is greater in the incorrect case. The main effects of both accuracy and congruence are also significant. Error bars represent within-subject *SEM*. $^*p < .05$, $^{**}p < .01$, $^{***}p \leq .001$.

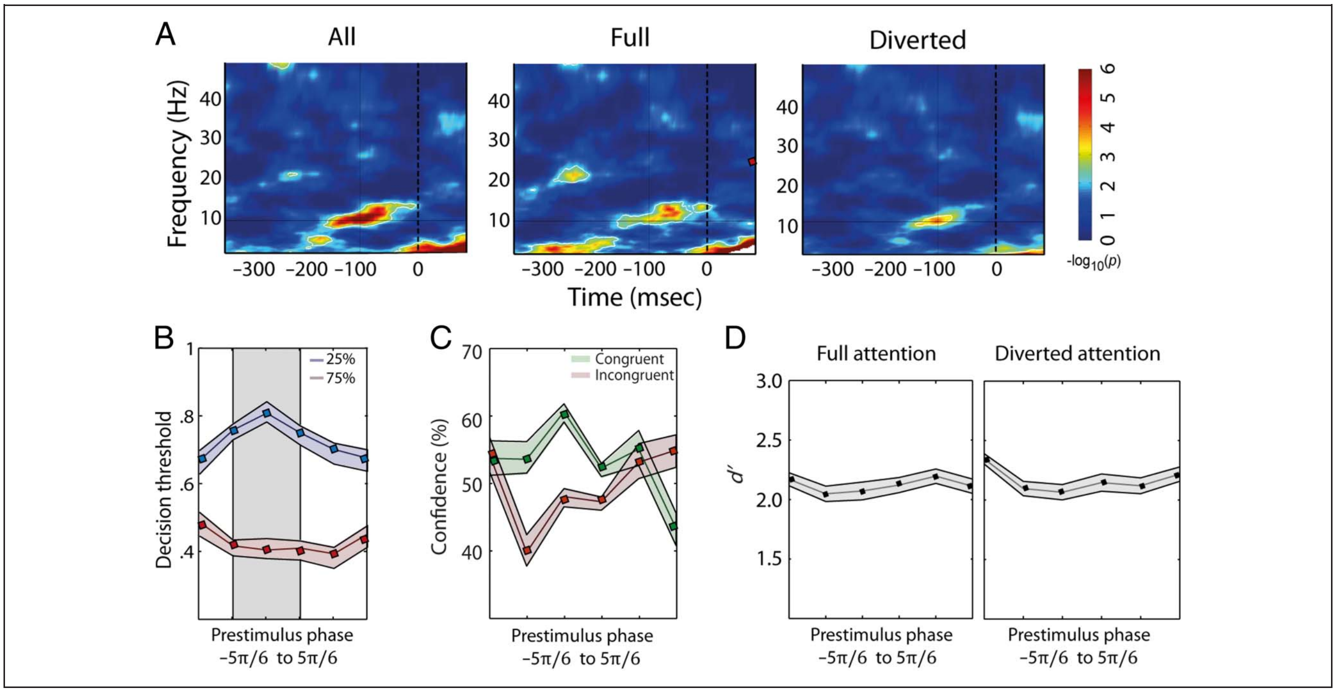

Figure 3. EEG results. (A) Time–frequency representation of phase opposition between yes and no reports over the eROI for (top) all trials, (middle) full attention, and (right) diverted attention. The vertical dashed line represents stimulus onset. The color scale represents log-transformed p values. Regions that survive FDR correction are outlined in white. (B) Relationship between decision threshold c and binned occipital 10 Hz phase at −119 msec. The blue phase criterion-function represents results from the 25% (expect absent) condition, and the red phase-criterion function represents results from the 75% (expect present) condition. Gray shading indicates the phase values that maximally predict the influence of expectation on decision: Decisions are maximally biased toward reporting "no" in the expect 25% condition, but toward "yes" in the 75% condition. Shaded outlines represent within-subject *SEM*. (C) Relationship between confidence and prestimulus 10 Hz phase at −119 msec. Congruent responses are reports of presence/absence in the 75%/25% conditions and vice versa for incongruent responses. Confidence significantly fluctuates with phase for both congruent (green) and incongruent (red) reports. Shaded regions represent within-subject *SEM*. (D) Relationship between detection sensitivity d' and prestimulus 10 Hz phase at −119 msec for the full (left) and diverted attention (right) conditions. Sensitivity does not fluctuate with phase in either condition. Shaded regions represent within-subject *SEM*.

expectation-congruent report is "yes." The reverse defines expectation-incongruent reports.

This hypothesis was tested with a within-subject Attention (full, diverted) × Accuracy (correct, incorrect) × Congruence (expectation-congruent, incongruent) repeated-measures ANOVA under confidence. Results showed that confidence was higher under full than diverted attention, $F(1, 17) = 17.67$, $p = .001$, $\eta_p^2 = .51$, for correct than incorrect responses, $F(1, 17) = 42.22$, $p < .001$, $\eta_p^2 = .71$, and for congruent than incongruent decisions, $F(1, 17) = 19.07$, $p < .001$, $\eta_p^2 = .53$.

As shown in Figure 3C, a significant Attention × Congruence interaction, $F(1, 17) = 14.83$, $p = .001$, $\eta_p^2 = .47$, revealed that diverting attention reduced the effect of congruence on confidence ($M_{diff} = 4.6\%$, $SE_{diff} = 1.4\%$) relative to full attention ($M_{diff} = 14.1\%$, $SE_{diff} = 3.2\%$). Congruence still increased confidence in both attention conditions (diverted: $t(17) = 3.25$, bootstrapped $p = .006$; full: $t(17) = 4.41$, bootstrapped $p = .001$).

As shown in Figure 3D, a significant Accuracy × Congruence interaction, $F(1, 17) = 8.48$, $p = .010$, $\eta_p^2 = .33$, revealed that the influence of congruence on confidence was greater for incorrect ($M_{diff} = 12.0\%$, $SE_{diff} = 2.6\%$) than correct ($M_{diff} = 6.7\%$, $SE_{diff} = 2.1\%$) responses. Crucially, congruence increased confidence in both cases (incorrect: $t(17) = 4.67$, bootstrapped $p = .001$; correct: $t(17) = 3.29$, bootstrapped $p = .014$), indicating that the influence of congruence on confidence is not confounded by differences in decisional accuracy.

No other significant effects were found (Attention × Accuracy, $p = .102$, $\eta_p^2 = .15$; Attention × Accuracy × Congruence, $p = .975$, $\eta_p^2 < .01$). Thus, effects under confidence reported in Sherman, Seth, et al. (2015) were replicated: expectations liberalize confidence, and the effect was weaker (but present) under diverted than full attention.

In summary, our paradigm successfully manipulated attention and expectation: contrast sensitivity increased in the presence of full attention, and expectation biased perceptual decisions. There was a small difference in d' across levels of expectation but not across levels of attention. Expectation further increased confidence, such that participants were more confident in their Gabor detection reports when that report had been congruent with their prior expectations.

Although these effects of expectation were present at the behavioral level, they are not necessarily modulated by prestimulus brain oscillations. The next analyses first determined whether oscillatory phase predicts perceptual decision irrespective of expectation and then determined whether the predictive value of oscillatory phase reflects prior expectations.

Perceptual Decision Is Predicted by Occipital Alpha Phase

Before addressing the question of whether the effect of expectation on decision is modulated by prestimulus phase over visual regions, we checked that prestimulus phase predicted perceptual choice, irrespective of expectation. Analyses were restricted to the occipital electrode (O1, Oz, or O2) that showed the greatest poststimulus response to the Gabor task. This method gave, for each participant and for each of the two sessions, a single electrode (eROI) that was involved in early poststimulus processing. eROIs were extracted by selecting the occipital electrode with the greatest ERP amplitude for hit relative to miss trials ($M_{\text{diff}} = 0.75$ μV, $SD_{diff} = 0.64$ μV; see Methods for details).

The predictive value of phase in perceptual decision was assessed using the measure phase opposition (PO). PO is the average of PLVs for two responses—here, yes and no (Vanrullen et al., 2011)—and therefore reflects the extent to which prestimulus phase predicts subsequent choice (see Methods for details). For response R and complex wavelet coefficients C, PLV and PO are defined as

$$\mathrm{PLV}_R = \left| \frac{1}{n} \sum_n \frac{C(R)}{|C(R)|} \right| \qquad \mathrm{PO}_{R_1,R_2} = \frac{\mathrm{PLV}_{R_1} + \mathrm{PLV}_{R_2}}{2}$$

PO values for each time–frequency point were calculated separately for each level of attention and expectation and subsequently collapsed across expectation conditions. This was done because for this initial analysis we were seeking time–frequency regions in which EEG phase predicted decision, but not explicitly seeking time–frequency regions in which the influence of phase depended on expectation. Averaging over conditions means phase effects are still detectable if expectation changes (or even reverses) the preferred phase for yes or no responses. Interactions between phase and expectation were run in a separate follow-up analysis, thereby avoiding "double-dipping."

To obtain p values, PO values were compared with the null distribution by pseudorandomly allocating a behavioral response to each phase angle at each time–frequency point. This process was repeated for each session and each condition 2000 times (8000 in total), giving 1.8×10^{70} bootstrapped samples over all participants. The p values were FDR-corrected over the entire prestimulus region (−1000 msec to stimulus onset) and over all frequencies.

This analysis revealed a region of significant phase opposition in the prestimulus alpha range over all trials, which reached maximum significance at 10 Hz, 119 msec before stimulus onset ($p = 10^{-7}$, $\alpha_{\text{FDR}} = 10^{-2.6}$; Figure 3A, left). This means that prestimulus occipital alpha phase predicts yes versus no responses. Given that phase-modulation of perceptual hit rate has been shown to be dependent on attention (Busch & VanRullen, 2010), we then split phase opposition values into two separate maps, one for each level of attention. Significant phase opposition was present under full attention ($p_{-119 \text{ msec, } 10 \text{ Hz}} = 10^{-4}$, $\alpha_{\text{FDR}} = 10^{-2}$; Figure 3A, center) and was indeed reduced in extent (but present) under diverted attention ($p_{-119 \text{ msec, } 10 \text{ Hz}} = 10^{-5}$, $\alpha_{\text{FDR}} = 10^{-3}$; Figure 3A, right), consistent with previous work.

This result shows that prestimulus occipital alpha phase predicted decision, but we do not yet know whether decision bias or detection sensitivity was fluctuating. This question was addressed in the next section.

Prestimulus Occipital Alpha Phase Predicts Decision Thresholds

Previous studies on prestimulus phase have not been able to separate sensitivity from decision bias because phase analyses have only time-locked to target-present trials. Whereas target-absent trials usually have no obvious reference point for the phase analysis (when using a randomized intertrial interval), here the onset of the search array served as a reference point for both Gabor-present and Gabor-absent phase determination. This allowed us to calculate the theoretically independent measures c (decision threshold) and d' (detection sensitivity).

Computing these values required binning phase angles from each trial. We needed data from just one time point, because pooling phase angles over time points results in associating multiple, systematically rotating phase angles with a single behavioral response. Similarly, phase angles from differing frequency bands cannot be compared in terms of their position in an oscillation. We extracted phase angles from each epoch from the eROIs at the −119 msec, 10 Hz time–frequency point: the point of maximal PO significance. Each phase angle was then binned into one of six phase bins.

By considering responses on those trials, this gave, for each participant, an associated set of hits, misses, false alarms, and correct rejections as a function of phase bin. Trials were further categorized according to experimental condition. In turn, for each participant, we could calculate d' and c as a function of phase bin, attention, and expectation. Note that in splitting trials according to phase bin, the resulting six values of c per condition will not average exactly to the single value of c per condition when computed irrespective of phase bin.

First, we asked whether prestimulus phase predicts decision threshold by running an Attention (full, diverted) × Expectation (25%, 75%) × Phase bin (1 to 6) repeated-measures ANOVA on decision threshold c. Only interactions with phase bin are reported. This analysis revealed no significant main effect of Phase, $F(5, 85) = 0.66$, $p = .670$, $\eta_p^2 = .04$, no significant Attention by Phase bin interaction, $F(5, 85) = 0.38$, $p = .862$, $\eta_p^2 = .02$, and no significant three-way interaction, $F(5, 85) = 0.66$, $p = .650$, $\eta_p^2 = .04$. Critically, there was a significant two-way interaction between Expectation and Phase bin, $F(5, 85) = 2.64$, $p = .029$, $\eta_p^2 = .13$.

This interaction is depicted in Figure 3B and is such that, as hypothesized, (1) c appears to oscillate with phase in both expectation conditions and (2) the two phase-criterion functions appear to be in antiphase. These curves being in antiphase mean that the range of phase values related to highest c in the 25% condition (conservative, expectation-congruent) are similar to the minimum values for c in the 75% condition (liberal, expectation-congruent). This range is consistent with what we would expect from the optimal phase for perceptual priors to influence perceptual decision. At π rad away from this range, phase predicted the most liberal responses in the 25% condition (incongruent) and the most conservative responses in the 75% condition (incongruent). This suggests that in *this* range of phase the top–down priors exert their weakest influence and that the relative effect of perceptual priors is minimal. We assume that, here, the influence of bottom–up signals is therefore maximal.

Supporting part of our first hypothesis, this indicates that, independent of attention, the extent to which prestimulus occipital alpha phase predicted decision threshold differed in the 25% (expect absent) and 75% (expect present) conditions.

Figure 3B suggests that c oscillates in both conditions (both functions are sinusoids), but that the same phases predict opposing responses (the functions are in antiphase). However, we have not yet determined this statistically. This was the aim of our next two analyses.

Prior Expectations Change the Response Predicted by Prestimulus Alpha Phase

Does phase predict c in both expectation conditions? To check whether the phase criterion function were sinusoids, we tested whether the distance between the peak and trough of each function was π rad. We used a circular v test, which tests the hypothesis that a set of angles (here, the peak-to-trough distance) is significantly clustered about some specified angle (here, π rad). This analysis revealed that, indeed, the peak-to-trough distance was approximately π rad in both the 25% ($v = 43.98$, $p < .001$) and 75% ($v = 12.56$, $p = .044$) conditions. This means that both functions are sinusoids and, therefore, that phase predicts criterion in both the 25% and 75% conditions.

Next we asked whether the two phase criterion functions were in antiphase. This was the final, key step in testing whether expectations were reflected in prestimulus phase. A circular v test, testing whether the peak-to-peak difference between the two phase criterion functions was significantly clustered about π rad, revealed this to be the case, $v = 43.98$, $p < .001$. Thus, the two functions are in antiphase and the same phases that predict "yes" when expecting target presence predict "no" when expecting target absence. These phases are therefore those at which expectations exert their greatest effect on decision.

In summary, we have supported our first hypothesis: that the influence of expectations on decision is oscillating with prestimulus alpha phase. We do not claim that a decision threshold is set at or before stimulus onset, because clearly, sensory evidence is not yet available to the visual system. Rather, our data show that, before stimulus onset, ongoing alpha phase biases the position of a decision threshold that is set later in time.

Rhythmic Fluctuations in Confidence

Our second hypothesis was that prestimulus alpha phase would also predict the influence of expectations on confidence. Behaviorally, confidence increases for expected percepts. Consistent with this, our behavioral analyses showed that confidence for expectation-congruent reports (i.e., reporting "yes" in the 75% condition or reporting "no" in the 25% condition) was higher than for incongruent reports (i.e., reporting "no" in the 75% condition or reporting "yes" in the 75% condition). Therefore, if phase predicts the influence of expectations on confidence, then there should be a range of phase angles, which predict high confidence when congruent reports were made but low confidence when incongruent reports were made. This set of phases would be the optimal phases for expectations to shape confidence.

The 4-point scale was collapsed into a binary confident/guess report by performing a mean split on individual participants' reports. Next, we computed participants' percentage of decisions reported with high confidence, as a function of phase bin, attention, and expectation-response congruence.

An Attention × Congruence × Phase bin repeated-measures ANOVA under confidence revealed a significant main effect of Phase bin ($p < .001$), but the phase-confidence function was not sinusoidal and therefore does not reflect the existence of an optimal phase for high confidence. The three-way interaction was also nonsignificant ($p = .198$, $\eta_p^2 = .08$). Crucially, the analysis did reveal a significant two-way Congruence × Phase bin interaction, $F(5, 85) = 4.10$, $p = .002$, $\eta_p^2 = .19$.

To break down this interaction, we tested whether confidence oscillated with phase at either level of congruence. As in the analysis under decision threshold, circular v tests tested the peak-to-trough difference of the two phase-confidence functions against π. These revealed that subjective confidence oscillated with prestimulus alpha phase for both expectation-incongruent, $v = 34.56$, $p < .0001$, and expectation-congruent, $v = 25.13$, $p < .001$, responses (Figure 3C).

As was the case for the decision threshold analysis, visual inspection of the figure suggests that the two functions are in antiphase: Phases associated with relatively high confidence for congruent reports are associated with relatively low confidence for incongruent reports. This was confirmed statistically with a circular v test that showed the peak-to-peak distance between the two phase-confidence functions to be significantly clustered about π rad, $v = 43.98$, $p < .0001$. In turn, this analysis indicates that the two functions are in antiphase.

Interestingly, the phase at which congruent yes/no responses are most likely appears similar to that at which congruence maximally predicts confidence (see Figure 3C and B, respectively): the peak of the phase expectation function (the 25% minus the 75% sinusoid) appears associated with high confidence for congruent reports, but low confidence for guess reports.

In summary, our results suggest that, at phases where prior expectations exerted stronger influences on decision, confidence was high for the expectation congruent report, but low for expectation-incongruent reports. This means that when the influence of priors was strong, confidence increased for predicted perceptual events but decreased when expectations were violated. Together with the results under decision threshold, these data suggest a 10-Hz alternation in the extent to which perceptual priors bias both objective and subjective decision-making.

Alpha Phase Does Not Predict Perceptual Sensitivity

Confidence is typically correlated with accuracy, such that participants are more confident when they are correct than when they are incorrect. Previous work has implicated prestimulus alpha phase in the detection of perceptual stimuli (Mathewson et al., 2012; Dugué, Marque, & VanRullen, 2011; Rohenkohl & Nobre, 2011); however, previous studies have not been able to time-lock the phase analysis to target-absent as well as target-present trials. In turn, it is unclear whether these results reflect alternations in decision biases or in perceptual sensitivity. If sensitivity is predicted by prestimulus alpha phase, our results under confidence may simply reflect fluctuations in d'.

Our results under c implicate alpha phase in decisional biases; however, to ascertain whether alpha phase is also implicated in sensitivity, we ran an Attention × Expectation × Phase bin rmANOVA under d'. This revealed no significant main effect of Phase bin, $F(5, 85) = 1.65$, $p = .156$, $\eta_p^2 = .09$, nor any significant interactions (Attention × Phase: $F(5, 85) = 0.86$, $p = .507$, $\eta_p^2 = .05$, Figure 3D; Expectation × Phase $F(5, 85) = 0.37$, $p = .868$, $\eta_p^2 = .02$; Attention × Expectation × Phase, $F(5, 85) = 0.88$, $p = .499$, $\eta_p^2 = .05$). The relationship between d', Phase, and Attention is depicted in Figure 3D.

An analogous Bayesian repeated-measures Attention × Expectation × Phase bin ANOVA was run on JASP using a Cauchy prior of 0.8 HWHM. This revealed evidence for the null hypothesis of no main predictive effect of Phase (BF = 0.025) as well as no predictive effect of Phase that depended on Attention (BF = 0.003), expectation (BF = 0.001), or both Attention and Expectation (BF < .0001).

Previous studies have found that it was useful to realign each participant's phase-hit rate function to correct for individual differences in optimal phases for perceptual sensitivity (Busch & VanRullen, 2010). Even using this method, however, we found no evidence for Phase predicting d' under either full ($p = .787$) or diverted ($p = .407$) attention.

Together, these data robustly show that prestimulus alpha phase does not predict detection sensitivity. Rather, the data support the interpretation that alpha phase reflects fluctuations in objective and subjective decisional biases.

DISCUSSION

The present experiment implemented a paradigm that both separated the influences of expectation from those of attention and allowed prestimulus oscillations to be time-locked to both target-absent and -present trials. Critically, this design enabled us to compute SDT measures as a function of phase and condition and, in turn, separate phase modulation of detection sensitivity from phase modulation of decision threshold.

Our results show that top–down expectations rhythmically bias perceptual decision-making in the prestimulus period, such that the extent to which expectations biased decision was predicted by the phase of prestimulus occipital alpha oscillations. The data revealed that decision threshold was predicted by phase both when expecting target presence and when expecting target absence. However, expectation flipped the relationship between phase and criterion (decision threshold), that is, the phase criterion functions were in antiphase: the same phases that predicted biases toward reporting "no" when expecting target absence predicted biases toward reporting "yes" when expecting target presence. These phases correspond to the optimal phases for expectations to influence perception.

Importantly, we do not claim that perceptual priors entrained alpha oscillations, as is the case for temporal predictions (e.g., Samaha, Bauer, Cimaroli, & Postle, 2015; Rohenkohl & Nobre 2011). Rather, priors determined whether a specific phase angle facilitated a "yes" or a "no" judgment. This effect of prestimulus alpha phase is interpreted as evidence for fluctuations in state of the visual system before stimulus onset affecting the propensity to use prior evidence poststimulus at the decision stage. Speculatively, this could occur if prior evidence for or against target presence is periodically transmitted to visual areas, in turn resulting in periodic changes in the baseline from which evidence accumulation begins (Summerfield & Egner, 2009).

Fluctuations in the influence of expectation on objective decisions were accompanied by fluctuations in subjective confidence. For incongruent reports, subjective violations of expectation were associated with degrees of confidence that tracked the influence of the prior expectation: when perceptual priors exerted greater effects on decision, subjective violations of expectation were associated with greater subjective uncertainty. Moreover, the phase–confidences function for congruent and incongruent responses were in antiphase: The phase that predicted greatest uncertainty for incongruent reports also predicted highest confidence for congruent reports. Together, these results extend previous work, demonstrating that confidence evolves with the decision variable at early processing stages (Fetsch et al., 2014; Kiani & Shadlen, 2009) by showing that decision and confidence are jointly shaped by top–down influences. As is the case for yes/no decisions, we interpret these results as evidence for biases in the early processing of sensory signals (e.g., changes in starting point of evidence accumulation) modulating reported subjective confidence at late stages of the decision-making stream.

Consistent with previous work, we found that alpha phase modulation of perception is greater with attention than without (Landau & Fries, 2012; Busch & VanRullen, 2010), though here, still present under diverted attention. Critically, although previous evidence has demonstrated alpha modulation of perceptual hit rate (Landau & Fries, 2012; Dugué et al., 2011; Busch et al., 2009; Mathewson et al., 2009), it has not been possible to ascertain whether changes in hit rate have been driven by changes in sensitivity or bias. Here we implicate alpha oscillations in biasing perceptual decisions, but not increasing sensitivity. Critically, the influence of alpha phase on decision is modulated by expectations. Our data also extend previous research that has revealed that the influence of expectation on decision is predicted by prestimulus beta-band power over both motor (De Lange et al., 2013) and somatosensory (Van Ede, Jensen, & Maris, 2010) cortices, as well as by BOLD responses in a range of cortical areas (Rahnev, Bahdo, de Lange, & Lau, 2012; Hesselmann, Sadaghiani, Friston, & Kleinschmidt, 2010; Hesselmann, Kell, & Kleinschmidt, 2008; Summerfield & Koechlin, 2008). Prestimulus signals biasing decision at early stages of visual processing (i.e., in sensory cortices) has not, to our knowledge, been shown before. Our results therefore support an early and critically rhythmic influence of expectations on decision.

Top–down influences are increasingly modeled within Bayesian perspectives frameworks (Mathys et al., 2014; Clark, 2013; Hohwy, 2013; Daunizeau et al., 2010; Ma, Beck, Latham, & Pouget, 2006; Kersten, Mamassian, & Yuille, 2004). Here, perception is described as a Bayesian inference on sensory causes. A core tenet of these frameworks is that the prior probability of sensory causes will constrain inference accordingly, and so probable or "expected" sensory causes are more likely to be chosen and thus perceived (Yuille & Kersten, 2011; Spratling, 2008; Knill & Pouget, 2004; Lee & Mumford, 2003). A plausible implication of this view is that such prior probabilities should be reflected in the state of the brain in the prestimulus period. Consistent with this, we have shown that the influence of priors on decision oscillates with prestimulus alpha phase.

One possible explanation for these findings is that alpha oscillations orchestrate the communication of prior expectations to visual cortex. On this view, rhythmic influences of expectation on decision threshold would reflect fluctuations in the prior probability of the reported perceptual decision. However, an alternative view is that our results reflect fluctuations in the weighting of priors on decision, rather than the prior probability itself. On this alternative view, alpha phase reflects the attentional state of the system, consistent with previous theoretical work (Jensen, Bonnefond, & VanRullen, 2012; Palva & Palva, 2007), so that priors are assigned a greater weight on perceptual decision when sensory signals are expected to be unreliable. Here, perceptual expectations would increase or decrease the excitability of relevant neural populations or gain according to whether a target is expected to appear or not. In both cases, prestimulus occipital alpha phase modulates the relative weighting of prior expectations and sensory data; however, our data cannot discriminate between these two views, and we leave this question open to future research.

In summary, we have described evidence indicating a periodic influence of perceptual priors on both objective (detection) and subjective (confidence) decisions, predicted by the phase of prestimulus occipital alpha oscillations. This rapid and periodic alternation between top–down and bottom–up influences in visual areas extends existing data implicating alpha oscillations in top–down processing (Von Stein, Chiang, & König, 2000). Together, our data suggest that alpha oscillations may periodically transmit perceptual priors and, in turn, reveal a plausible neural mechanism by which prior information may subserve top–down modulation of early visual processing: alpha oscillations may orchestrate the reciprocal exchange of predictions and prediction errors.

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REFERENCES

Bar, M. (2003). A cortical mechanism for triggering top–down facilitation in visual object recognition. *Journal of Cognitive Neuroscience, 15,* 600–609.

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical microcircuits for predictive coding. *Neuron, 76,* 695–711.

Berens, P. (2009). CircStat: A MATLAB toolbox for circular statistics. *Journal of Statistical Software, 31,* 1–21.
Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience, 29,* 7869–7876.
Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences, U.S.A., 107,* 16048–16053.
Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences, 36,* 181–204.
Daunizeau, J., den Ouden, H. E. M., Pessiglione, M., Kiebel, S. J., Stephan, K. E., & Friston, K. J. (2010). Observing the observer (I): Meta-Bayesian models of learning and decision-making. *PLoS One, 5,* e15554.
De Lange, F. P., Rahnev, D. A., Donner, T. H., & Lau, H. (2013). Prestimulus oscillatory activity over motor cortex reflects perceptual expectations. *Journal of Neuroscience, 33,* 1400–1410.
Drewes, J., & VanRullen, R. (2011). This is the rhythm of your eyes: The phase of ongoing electroencephalogram oscillations modulates saccadic reaction time. *Journal of Neuroscience, 31,* 4698–4708.
Dugué, L., Marque, P., & VanRullen, R. (2011). The phase of ongoing oscillations mediates the causal relation between brain excitation and visual perception. *Journal of Neuroscience, 31,* 11889–11893.
Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top–down processing. *Nature Reviews Neuroscience, 2,* 704–716.
Feldman, H., & Friston, K. J. (2010). Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience, 4,* 215.
Fetsch, C. R., Kiani, R., Newsome, W. T., & Shadlen, M. N. (2014). Effects of cortical microstimulation on confidence in a perceptual decision. *Neuron, 83,* 797–804.
Friston, K. J., Bastos, A. M., Pinotsis, D., & Litvak, V. (2014). LFP and oscillations—What do they tell us? *Current Opinion in Neurobiology, 31C,* 1–6.
Gilbert, C. D., & Li, W. (2013). Top–down influences on visual processing. *Nature Reviews Neuroscience, 14,* 350–363.
Gilbert, C. D., & Sigman, M. (2007). Brain states: Top–down influences in sensory processing. *Neuron, 54,* 677–696.
Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics* (*Vol. 1*). New York: Wiley.
Hesselmann, G., Kell, C. A., & Kleinschmidt, A. (2008). Ongoing activity fluctuations in hMT+ bias the perception of coherent visual motion. *Journal of Neuroscience, 28,* 14481–14485.
Hesselmann, G., Sadaghiani, S., Friston, K. J., & Kleinschmidt, A. (2010). Predictive coding or evidence accumulation? False inference and neuronal fluctuations. *PloS One, 5,* e9926.
Hohwy, J. (2013). *The predictive mind*. Oxford: Oxford University Press.
Jensen, O., Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends in Cognitive Sciences, 16,* 200–206.
Kersten, D., Mamassian, P., & Yuille, A. (2004). Object perception as Bayesian inference. *Annual Review of Psychology, 55,* 271–304.
Kiani, R., & Shadlen, M. N. (2009). Representation of confidence associated with a decision by neurons in the parietal cortex. *Science, 324,* 759–764.
Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews, 53,* 63–88.
Knill, D. C., & Pouget, A. (2004). The Bayesian brain: The role of uncertainty in neural coding and computation. *Trends in Neurosciences, 27,* 712–719.
Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology, 22,* 1000–1004.
Lee, T. S. (2002). Top–down influence in early visual processing: A Bayesian perspective. *Physiology & Behavior, 77,* 645–650.
Lee, T. S., & Mumford, D. (2003). Hierarchical Bayesian inference in the visual cortex. *Journal of the Optical Society of America A, 20,* 1434.
Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.
Ma, W. J., Beck, J. M., Latham, P. E., & Pouget, A. (2006). Bayesian inference with probabilistic population codes. *Nature Neuroscience, 9,* 1432–1438.
Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. *Journal of Neuroscience, 29,* 2725–2732.
Mathewson, K. E., Prudhomme, C., Fabiani, M., Beck, D. M., Lleras, A., & Gratton, G. (2012). Making waves in the stream of consciousness: Entraining oscillations in EEG alpha and fluctuations in visual awareness with rhythmic visual stimulation. *Journal of Cognitive Neuroscience, 24,* 2321–2333.
Mathys, C. D., Lomakina, E. I., Daunizeau, J., Iglesias, S., Brodersen, K. H., Friston, K. J., et al. (2014). Uncertainty in perception and the Hierarchical Gaussian Filter. *Frontiers in Human Neuroscience, 8,* 1–24.
Palva, S., & Palva, J. M. (2007). New vistas for alpha-frequency band oscillations. *Trends in Neurosciences, 30,* 150–158.
Porter, P. (1954). Another picture-puzzle. *American Journal of Psychology, 67,* 550–551.
Rahnev, D. A., Bahdo, L., de Lange, F. P., & Lau, H. (2012). Prestimulus hemodynamic activity in dorsal attention network is negatively associated with decision confidence in visual perception. *Journal of Neurophysiology, 108,* 1529–1536.
Rohenkohl, G., & Nobre, A. C. (2011). α oscillations related to anticipatory attention follow temporal expectations. *Journal of Neuroscience, 31,* 14076–14084.
Samaha, J., Bauer, P., Cimaroli, S., & Postle, B. R. (2015). Top–down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proceedings of the National Academy of Sciences, U.S.A., 112,* 8439–8444.
Sherman, M. T., Barrett, A. B., & Kanai, R. (2015). Inferences about consciousness using subjective reports of confidence. In M. Overgaard (Ed.), *Behavioral methods in consciousness research* (pp. 87–106). New York: Oxford University Press.
Sherman, M. T., Seth, A. K., Barrett, A. B., & Kanai, R. (2015). Prior expectations facilitate metacognition for perceptual decision. *Consciousness and Cognition, 35,* 53–65.
Spratling, M. W. (2008). Predictive coding as a model of biased competition in visual attention. *Vision Research, 48,* 1391–1408.
Summerfield, C., & de Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience, 15,* 745–756.
Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences, 13,* 403–409.
Summerfield, C., & Koechlin, E. (2008). A neural representation of prior information during perceptual inference. *Neuron, 59,* 336–347.

Van Ede, F., Jensen, O., & Maris, E. (2010). Tactile expectation modulates prestimulus beta-band oscillations in human sensorimotor cortex. *Neuroimage, 51,* 867–876.
Van Kerkoerle, T., Self, M. W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., van der Togt, C., et al. (2014). Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proceedings of the National Academy of Sciences, U.S.A., 111,* 14332–14341.
Vanrullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Frontiers in Psychology, 2,* 60.
Von Stein, A., Chiang, C., & König, P. (2000). Top–down processing mediated by interareal synchronization. *Proceedings of the National Academy of Sciences, U.S.A., 97,* 14748–14753.
Yuille, A., & Kersten, D. (2006). Vision as Bayesian inference: Analysis by synthesis? *Trends in Cognitive Sciences, 10,* 301–308.