

# Increased Stimulus Expectancy Triggers Low-frequency Phase Reset during Restricted Vigilance

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## Abstract

■ Temporal cues can be used to selectively attend to relevant information during abundant sensory stimulation. However, such cues differ vastly in the accuracy of their temporal estimates, ranging from very predictable to very unpredictable. When cues are strongly predictable, attention may facilitate selective processing by aligning relevant incoming information to high neuronal excitability phases of ongoing low-frequency oscillations. However, top-down effects on ongoing oscillations when temporal cues have some predictability, but also contain temporal uncertainties, are unknown. Here, we experimentally created such a situation of mixed predictability and uncertainty:

A target could occur within a limited time window after cue but was always unpredictable in exact timing. Crucially to assess top-down effects in such a mixed situation, we manipulated target probability. High target likelihood, compared with low likelihood, enhanced delta oscillations more strongly as measured by evoked power and intertrial coherence. Moreover, delta phase modulated detection rates for probable targets. The delta frequency range corresponds with half-a-period to the target occurrence window and therefore suggests that low-frequency phase reset is engaged to produce a long window of high excitability when event timing is uncertain within a restricted temporal window. ■

## INTRODUCTION

Ongoing neuronal oscillations reflect fluctuations of neuronal ensembles between low and high excitable phases, during which incoming stimuli are less or more efficiently processed, respectively (Lakatos et al., 2005; Buzsáki & Draguhn, 2004). When events are highly temporally predictive, for example, in rhythms, high excitable phases can be aligned to the arrival time of incoming information, effectively changing the phase of ongoing oscillations (Kayser, Logothetis, & Panzeri, 2010; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). The strength of this phase reset increases when extra top-down resources are employed, for instance, when there is an expectancy cue about the occurrence of relevant stimuli (Stefanics et al., 2010). In contrast, during absence of any temporal predictability—for example, when a cat is waiting for a mouse to exit its mouse hole without any cues of when this will happen—Schroeder and Lakatos (2009) proposed a “vigilance mode” of processing. In this mode, increased attention enhances the amplitude of high-frequency gamma oscillations to produce many, densely distributed, high excitable phases and hereby optimizes the chance that an unpredictable stimulus will arrive during a high excitable phase.

Dichotomizing all possible temporal contexts in “predictable” versus “unpredictable” might not be sufficient

because in many natural situations there is a mixture of both regularities and uncertainties in our temporal estimates, which has been tested in variable foreperiod studies (Wright & Fitzgerald, 2004; Los, Knol, & Boers, 2001; Niemi & Näätänen, 1981). Considering the cat–mouse–hole example, when the cat briefly hears the mouse, its attention will be raised for a short while, because the mouse might come out very soon. In this example, there are temporal cues (i.e., the sound of the mouse), which indicate that an event is expected to occur soon, but their temporal precision is not very accurate, leaving the exact event timing uncertain. With these kinds of intermediate temporal cues, it seems beneficial to allocate attention continuously for a constrained time, which we will define here as “restricted vigilance.” We hypothesize that low-frequency oscillations will be reset when attending for a restricted period of time to ensure high excitability during the entire window of stimulus occurrence while not using metabolically demanding gamma oscillations (Mukamel et al., 2005; Niessing et al., 2005). These low-frequency oscillation would thereby efficiently cover the restricted vigilance window with the high excitability half of the oscillation period.

To investigate top-down influences on phase reset mechanisms during a situation of restricted vigilance, we presented a blue or yellow circle, which indicated a high (80%) or low (50%) probability of a target sound following. This probability manipulation allowed us to vary the top-down expectancy about the probability that a temporally unpredictable, but behaviorally relevant,

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event will occur while keeping the restricted vigilance window constant. After these expectancy cues, low-intensity auditory stimuli were presented in the corresponding proportion of the trials, with SOAs ranging from 0 to 450 msec, while recording EEG. Our findings reveal enhanced low-frequency oscillations (1–3 Hz) in evoked power as well as intertrial coherence (ITC) in the high-probability condition. The restricted vigilance window matches with half-a-period the revealed oscillatory frequency range, suggesting that the whole temporal attention window may be enclosed within the high-excitability phase of the low-frequency oscillations, whereas the low excitable phases fall outside the window in which stimuli are expected. This low-frequency oscillation enhancement was significantly stronger in case of high as compared to low sound likelihood, and moreover, only in the high-probability condition delta phase modulated auditory detection. This influence of probability suggests that, when event occurrence is likely, delta phase is consistent over trials, and this phase determines whether stimuli are perceived or not, whereas for unlikely events, there is less phase consistency and subsequent delta phases do not determine the percept. These results reflect that phase reset of low-frequency oscillations leads to a longer temporal attention window for likely relevant events that are presented in a restricted temporal window and underline the flexibility of phase resetting as an important mechanism underlying selective processing.

## METHODS

### Participants

Fourteen healthy volunteers took part in our study (mean age = 24 years, range = 19–35 years, seven men). All participants reported normal hearing and normal or corrected-to-normal vision. Before participating, all gave informed consent. Ethical approval was given by the ethics committee of the Faculty of Psychology and Neuroscience at the University of Maastricht. Participants received a monetary compensation. One participant was excluded from the analyses (see Data Analyses section for details).

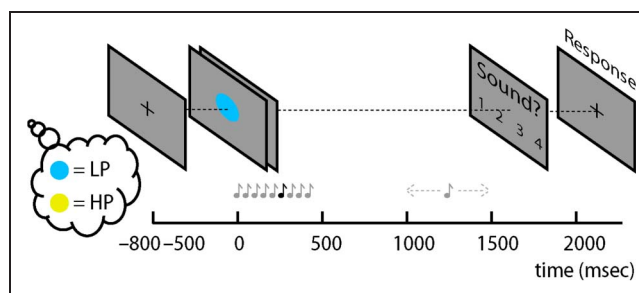
### Stimuli and Procedure

First, the individual detection threshold of participants was determined with the method of constant stimuli. Low-intensity sounds (1 kHz beeps lasting 75 msec with on and off ramp of 5 msec) varying from 27 dB up to 42 dB in steps of 1.56 dB were presented in constant white noise (46 dB), and participants had to indicate whether they detected the sounds or not. A trial was 1-sec long, and the sound onset was randomized between 300 and 800 msec after trial onset. In total, 20 stimuli were presented per intensity. Thereafter, a cumulative Gaussian was fitted using the psychometric fitting toolbox *modelfree v 1.1*

(Zchaluk & Foster, 2009), implemented in Matlab (The MathWorks, Natick, MA), and the 70% detection threshold was calculated. This intensity was used in the main experiment. During the experiment, detection rates between 30% and 85% were ensured by manually changing the intensity if the intensity was not in this range for a block.

After the threshold was determined, the EEG cap was mounted and the main experiment started. In this experiment, a trial consisted of the presentation of a visual circle (visual angle = 15°, color blue [RGB: 0, 191, 255] or yellow [RGB: 238, 238, 0], lasting 75 msec), after which the low-intensity sound was presented or not (Figure 1). The task of the participant was to indicate whether they heard a sound or not on a 4-point scale (1 = *I did not hear the sound*, 2 = *I think I did not hear the sound*, 3 = *I think I did hear the sound*, 4 = *I did hear the sound*). The auditory stimulus could be presented at the same time as the visual stimulus or up to 450 msec after the visual stimulus in steps of 50 msec (of which the order was randomized). Additionally, the sound could also be presented within the interval of 1–1.5 sec to ensure that participants were still paying attention at the end of the trial. The detection question did not appear before the end of the trial (lasting 1.8 sec), and a random delay was inserted varying between 500 and 800 msec before the onset of the next trial. The probability of sounds presented depended on the visual color. For one color, a sound was presented in 50% of the trials, in 80% for the other color. The specific colors with a low versus a high probability of sounds were counterbalanced over participants. Participants were informed about this difference by the instruction that for one color there was a high chance of the occurrence of a sound and for the other color there was a low chance of the occurrence of a sound. Hereby, we manipulated the participants' top-down expectancies of sound occurrence.

In total there were 1300 trials, resulting for the low probability in 25 trials per SOA (75 for SOA = 0) and 325 trials without a sound and for the high probability



**Figure 1.** Example of a trial. After a variable delay, a visual cue was presented. The color of the visual cue indicated high or low probability of auditory stimulus occurrence (HP or LP). One auditory stimulus (black) was presented per trial. All gray notes indicate when the auditory stimulus could occur. After 1.8 sec, the question trial appeared, in which participants had to indicate whether they detected the stimulus or not.

in 40 trials per SOA (120 for SOA = 0) and 130 trials without a sound. There were more trials of SOA 0 to ensure that participants were focusing at the beginning of the trial (see also Fiebelkorn et al., 2011). All trials were divided over 10 blocks lasting approximately 5 min each. Background color was gray (RGB: 100, 100, 100), and a black fixation cross was presented throughout the experiment. Participants were seated approximately 57 cm from the screen, and Presentation software (Neurobehavioral Systems, Inc., Albany, NY) was used for stimulus delivery. Participants were instructed to fixate the entire trial and to try to blink only after the question appeared on the screen.

### EEG Acquisition and Preprocessing

EEG data were recorded (DC-200 Hz, sampling rate 500 Hz) in a sound-attenuated and electrically shielded room with a 61-channel cap (Easycap, Montage No. 1) and two BrainAmp Standard EEG amplifiers (BrainProducts GmbH, Munich, Germany). The left mastoid was used as reference and Afz as ground. Three additional electrodes were placed to record eye movements (below the left eye and at the lateral sides of both eyes). Impedance levels were kept below 15 k $\Omega$ . Data were analyzed using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), the circular statistics toolbox (Berens, 2009), and custom Matlab scripts.

Preprocessing steps were as follows. First, data were re-referenced to the average of the left and right mastoid. This reference was kept throughout all data analyses to keep the reference of the different analyses steps the same, but therefore might differ from commonly used average reference topographies. Second, data were notch-filtered (50 Hz) to remove electrical noise. Additionally, epochs were created for all the trials ( $-1$  to  $3$  sec relative to the visual stimulus); the mean of each single epoch was subtracted for all epochs, and data were resampled to 256 Hz. Independent component analysis was performed to remove blink and muscle artifacts (fast ICA with 50 PCA components). Remaining trials with high variance were removed by visual inspection.

### Data Analyses

#### *Behavioral Analyses*

We calculated for each SOA and each condition the sensitivity and bias (Green & Swets, 1966). Hits were defined as all the trials in which there was a sound and the participants pressed button 3 or 4. Misses were trials with a sound and participants choose option 1 or 2. If there was no sound presented but participants pressed button 3 or 4, there was a false alarm. Because any false alarm cannot be associated with one specific SOA (as there is no sound), the sensitivity and bias estimates were calculated using the same false alarm rate for each SOA. A repeated-

measures ANOVA with the factors SOA (11 SOA points) and Probability (low and high probability) was conducted with Greenhouse–Geisser correction for both the sensitivity and the bias. Post hoc pairwise comparisons were conducted for significant effects, correcting for multiple comparisons via false discovery rate. One participant had a difference of 60.8% between the false alarm rates of the two conditions, indicating that the participant based his choices purely on the visual stimulus, and was therefore excluded.

### EEG Analyses

#### *ERP Analyses*

Single epochs were band-pass filtered from 0.05 to 20 Hz (second-order Butterworth filter) and corrected for the  $-200$  to  $0$  msec baseline. Only epochs in which no sound was presented and in which participants indicated that there was no sound (button 1 or 2) were used for the EEG analyses (baseline correction and epoch selection are the same for all henceforth described analyses excluding the delta phase analysis). We used only these trials because (1) the participant would stop attending after hearing a possible sound and (2) we intended to focus our analyses on trials without any auditory evoked responses. For each individual, trials were averaged per condition, and the two conditions were compared with each other using cluster analyses implemented in Fieldtrip (Maris & Oostenveld, 2007). On average for the low-probability condition, 248 trials were used ( $SD = 59.3$ ), and for the high-probability condition, 93 trials were used ( $SD = 24.5$ ). The same trials were used in the evoked and total power analyses. For the cluster analysis, first the paired samples  $t$  values are calculated for all channels and time points ( $0.05$ – $1.8$  sec after visual stimulus onset and after the question onset), then clusters are defined based on these  $t$  values, and statistical significance is determined via Monte Carlo randomizations (the following parameters were used: cluster alpha of 0.05, dependent samples  $t$  test alpha of 0.01, 10,000 randomizations, and the maximal sum of all the time and channel bins in one cluster as dependent variable; all reported  $p$  values reflect a two-sided test).

#### *Time–Frequency Analyses—Evoked Power*

Primarily, we were interested in the power spectrum directly evoked by the stimulus, that is, the stimulus phase-locked power responses. This analysis would give us an idea which frequency bands could relate to a phase reset (Makeig, Debener, Onton, & Delorme, 2004). We therefore averaged the epochs for each individual for each condition and applied *banning tapers* (time window linearly rising from two cycles at 1 Hz up to 10 cycles at 40 Hz; frequencies below 1 Hz had a time window of 2 sec) for frequency range of  $0.2$ – $40$  Hz and time range of

0–1 sec. Data were baseline-corrected for the –0.2 to 0 sec time interval. Also here a cluster analysis was performed. Because we were only interested in the frequency of the evoked response, we averaged over 0.08–0.40 sec (because it had the highest amplitudes in the ERP results) and calculated significant frequency clusters with the same analyses as before.

#### *Time–Frequency Analyses—Total Power Responses*

To all individual epochs, the same hanning tapers as for the phase-locked time–frequency analyses were applied. Thereafter, the power spectra were averaged within participants. We analyzed using channel Fz (because it had the strongest effect for the evoked power) and took the same time and frequency range as in the phase-locked time–frequency analyses (again averaging over time). Data were baseline-corrected for the –0.2 to 0 sec time interval. We used Monte Carlo simulations (10,000 repetitions) for all the frequency points separately, using the  $t$  values (of the paired  $t$  tests) as dependent variable (Maris & Oostenveld, 2007). This method creates a simulated distribution of  $t$  values by shuffling the labels of the two conditions and repeating the  $t$  test calculation for these shuffled labels. This is done 10,000 times, and the subsequently reported  $p$  values reflect the proportion of shuffled labels that have a higher  $t$  value as the original  $t$  value. We report the average  $p$  and  $t$  value of the significant frequency bins. We corrected for multiple comparison using the false discovery rate.

#### *Intertrial Coherence*

Intertrial phase coherence characterizes how consistent the phases of different frequencies are over multiple trials, independent of power (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996), and therefore provides an indication for pure phase resetting. We calculated for the single-epoch Fourier spectra for Fz using hanning tapers for 0.2–40 Hz with the same parameters as for the time–frequency analyses. Thereafter, we extracted the phases of the Fourier spectra of the single epochs and calculated for each participant and each condition the ITC. Because the ITC is inflated with fewer trials (i.e., trials with a high probability of a sound had fewer trials without a sound than trials with a low probability of a sound), we applied permutations to the low-probability trials. Therefore, we first only calculated the ITC for the high-probability trials. Then, we randomly selected an equal amount of trials for the low-probability condition and calculated the ITC. This randomized trial selection procedure and ITC calculation were repeated 500 times, and we took the mean of the repetitions as the ITC for the low-probability trials. Then we used the same averaged time interval (0.08–0.4 sec) and frequency range (0.2–40 Hz) for statistics with the same methods as for the total power time–frequency analysis.

#### *Delta Phase during Misses and Hits*

To test whether delta phase is indeed important for detecting the stimuli, we sorted all the trials containing sounds to hits and misses per probability condition. Thereafter, we filtered all the data around delta (second-order IIR Butterworth filter, using a causal bandpass filter with cutoff frequencies at 1–1.75 Hz, cutoff = –3 dB) and extracted per participant the mean angle and ITC of the Hilbert transformation at sound onset. Across participants, there were on average 104 hit trials and 132 miss trials for the low-probability condition ( $SD = 45.0$  and  $46.7$ , respectively) and 159 hit trials and 220 miss trials for the high-probability condition ( $SD = 57.4$  and  $65.7$ , respectively). A causal filter was used because we wanted to exclude any effects that could be due to differences in the evoked response between hits and misses (Zoefel & Heil, 2013). To estimate whether an interaction effect between probability condition and detection exists, we first calculated the circular distance between hits and misses for both conditions separately for each participant. Then, we used the Zar's Hotelling test to investigate whether these distances have a different mean angle for different conditions (van den Brink, Wynn, & Nieuwenhuis, 2014; Zar, 1998). This test has the advantage that it takes into account the ITC such that mean angles corresponding to a low ITC are also considered to be less consistent in phase. Because for the distance measure two ITCs need to be considered (i.e., the one from the hits and the one from the misses), we choose to incorporate the minimum ITC of the two. This seemed valid as the lowest ITC of the hits and misses determines how consistent the overall phase difference will be. Thereafter, we used the same Zar's Hotelling test to test whether the mean angle for the hits and misses are different for the two conditions separately. All trials with SOAs ranging between 0 and 100 msec were excluded because effects of phase reset are unlikely at such an early SOA considering the different transmission latencies between auditory and visual responses (see, e.g., Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008).

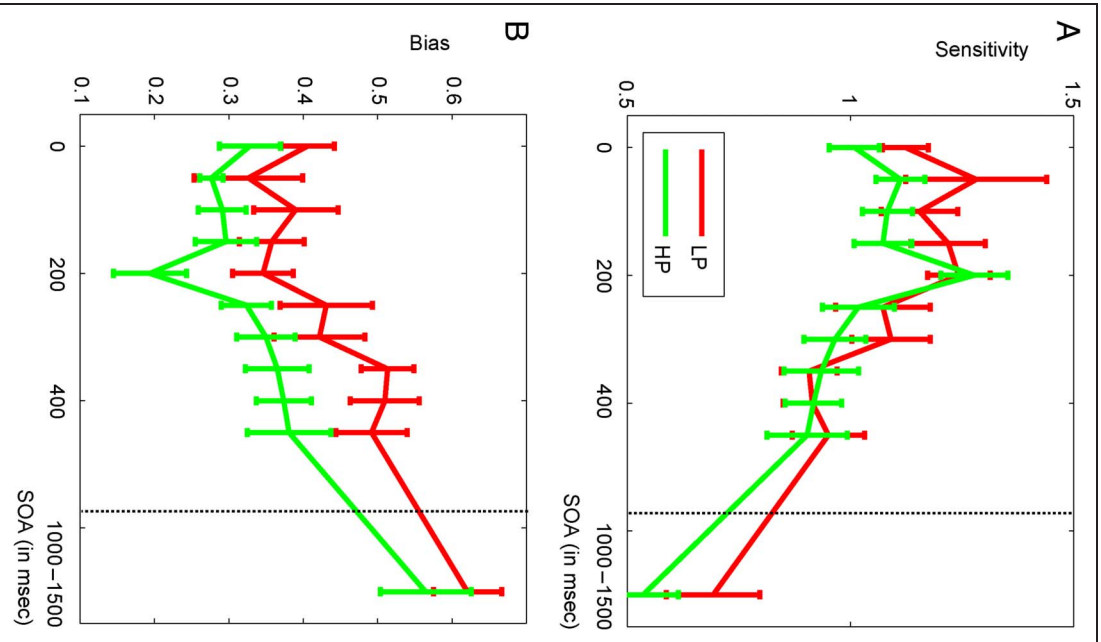
## **RESULTS**

### **Behavioral Results**

#### *Sensitivity*

The repeated-measure ANOVA showed a main effect of SOA,  $F(10, 120) = 8.647$ ,  $p < .001$  (Figure 2A). Pairwise comparison showed that all the SOA points were significantly different from the 1000–1500 msec time point (Table 1). Furthermore, it seems that the middle time points are detected best relative to earlier and later time points. This is confirmed with a significant quadratic contrast,  $F(1, 12) = 21.995$ ,  $p = .001$ . No higher-order polynomials were significant. This contrast was also significant when excluding the last time point,  $F(1, 12) = 6.534$ ,





**Figure 2.** Behavioral results. Sensitivity (A) and bias (B) for the high (green) and low (red) probability condition over SOA. Error bars indicate the *SEM*. To calculate the *SEM*, the individual data were normalized by subtracting the overall mean of the sensitivity/bias for the individual participants.

$p = .025$ . The main effects of Probability and the interaction of Probability  $\times$  SOA were not significant,  $F(1, 12) = 1.700$ ,  $p = .217$  and  $F(10, 120) = 0.478$ ,  $p = .776$ , respectively.

#### Bias

The bias estimate showed the reversed pattern of the sensitivity (Figure 2B). Again there was a main effect of SOA,  $F(10, 120) = 8.647$ ,  $p < .001$ , and a significant quadratic contrast,  $F(1, 12) = 21.995$ ,  $p = .001$ . The main effect of Probability and the interaction were not significant, although the main effect showed a slight trend of

**Table 1.** Crosstab of All the Pairwise Comparisons

	50	100	150	200	250	300	350	400	450	1000–1500
0	−1.71 (.190)	−.74 (.554)	−1.83 (.171)	−2.78 (.044)*	.21 (.894)	.50 (.706)	2.09 (.120)	2.91 (.038)*	1.74 (.184)	4.21 (.007)**
50		.75 (.554)	.62 (.628)	−.75 (.554)	1.51 (.240)	1.62 (.214)	2.65 (.053)	3.47 (.021)*	2.11 (.120)	4.95 (<.001)**
100			−.46 (.717)	−1.87 (.163)	.87 (.503)	1.17 (.336)	2.57 (.060)	4.03 (.010)**	2.34 (.084)	5.04 (<.001)**
150				−1.42 (.269)	1.21 (.327)	1.38 (.272)	2.68 (.052)	4.09 (.010)**	3.05 (.037)*	5.41 (<.001)**
200					2.33 (.084)	2.93 (.038)*	5.27 (<.001)**	5.51 (<.001)**	3.08 (.037)*	6.87 (<.001)**
250						.18 (.894)	1.38 (.272)	1.77 (.181)	1.35 (.280)	3.90 (.010)**
300							1.54 (.236)	2.03 (.128)	1.29 (.297)	4.14 (.007)**
350								.09 (.930)	−.07 (.894)	3.95 (.021)**
400									−.16 (.894)	3.44 (.038)*
450										2.96 (.038)*

All values in the table represent the results of the *t* test for the two SOAs corresponding to the SOAs of the row and column. The initial number is the *t* value and the number between brackets is the corrected *p* value. Asterisk and double asterisks correspond to significance at the .05 and the .01 level, respectively.

higher bias for the low-probability condition,  $F(1, 12) = 3.180, p = .100$  and  $F(10, 120) = 0.478, p = .776$ . As the false alarm rate does not change for different SOAs and both the bias and sensitivity are calculated as a linear transformation relative to the false alarm rate, the pairwise comparisons for the main effect of SOA are the same for the bias as for sensitivity and therefore not reported.

Although in this behavioral analyses no clear difference between the two probability conditions was present, the later EEG behavioral analyses indicates a more subtle behavioral difference between these conditions.

### EEG Results

#### ERP Results

The ERPs show two clear evoked responses, one in response to visual stimulus onset and one in response to question onset (Figure 3A). The cluster analyses (see Methods for details) showed no significant effects of condition (high vs. low probability) for the whole interval up to the question (0–1.8 sec) and after the question (1.8–2.5 sec).

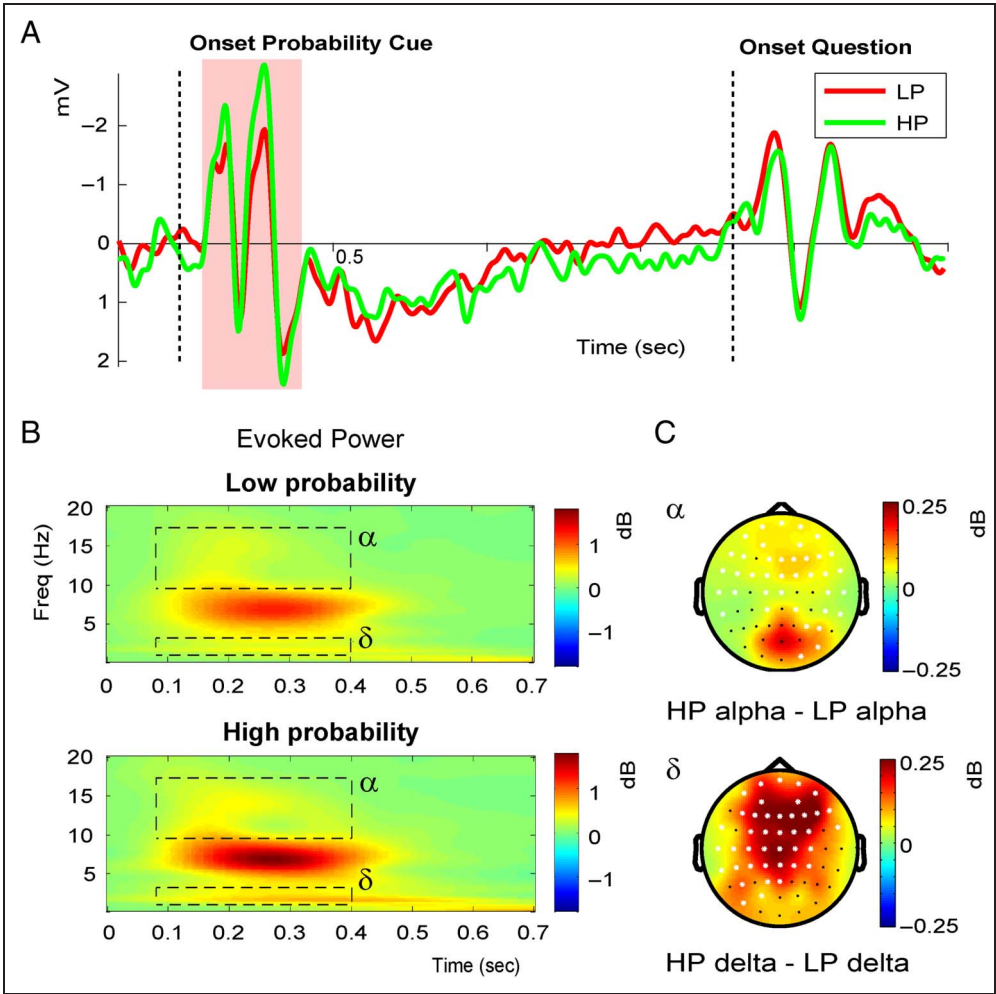
#### Time-Frequency Analyses—Evoked Power

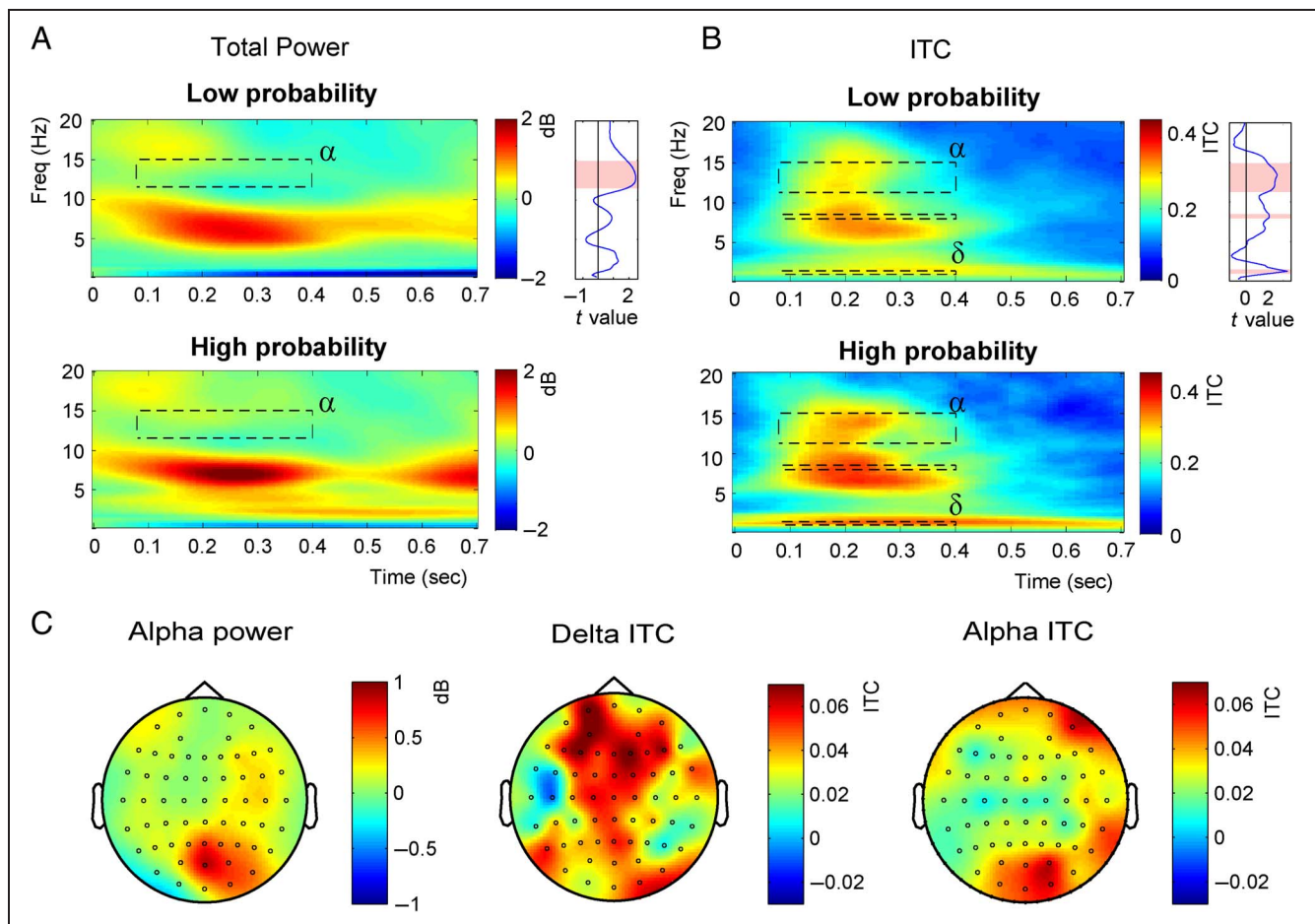
The evoked power analysis revealed a higher evoked response for low delta frequencies (Figure 3B; 1–3.25 Hz, cluster statistics = 462.19,  $p = .042$ ) during the high-probability condition that was frontal/centrally organized (Figure 3C). Also, a higher evoked alpha (9.5–17.25 Hz) response was found at occipital channels for the high-probability condition. Although the highest difference values were occipitally located, a significant frontal cluster was found for this effect (cluster statistics = 1511.1,  $p = .004$ ). This cluster likely relates to the visual evoked response. Although the figure might suggest a difference in the 5–10 Hz frequency range, no significant cluster was found.

#### Time-Frequency Analyses—Total Power

The total power showed no significant effect at delta range. However, a significant difference at alpha range was found (Figure 4A; 11.5–15 Hz; average  $t$  value over all significant alpha frequency bins (11) = 2.21, average  $p$  value = .026), with stronger alpha power for the high-probability condition.

**Figure 3.** ERPs and evoked power for the trials without a sound. (A) ERP of Fz for the whole trial time course. The red-shaded area indicates the interval used for subsequent analyses. (B) Phase-locked time-frequency spectra with two significant clusters ( $p < .05$ ) estimated within the 0.08–0.4 time window, indicated by the two black rectangles. (C) The corresponding topographic distributions with white dots indicating the significant channels. Topographies show the data of the high minus the low probability.





**Figure 4.** Power and ITC estimates in Fz. (A) Induced power for both conditions. Insert on the right shows  $t$  values of the low-versus high-probability comparison for the entire frequency range. (B) ITC for both conditions. Insert on the right shows  $t$  values of the low versus high-probability comparison for the entire frequency range. (C) Difference topographic distributions of three different significant clusters (alpha power, delta ITC, and alpha ITC; cluster between 11.25 and 15 Hz). Red-shaded areas and black rectangle indicate significance ( $p < .05$ ) within the 0.08–0.4 time window.

### Intertrial Phase Coherence

The ITC plot shows a significant stronger delta ITC for the high-probability conditions (Figure 4B; 1–1.75 Hz, average  $t$  value(11) = 2.89, average  $p$  value = .01). Additionally, a strong response at alpha band is again present, significantly stronger for the high-probability condition, which was separated in two different bands in alpha range (from 8 to 8.5 Hz, average  $t$  value(11) = 2.03, average  $p$  value = .037, and from 11.25 to 15.00, average  $t$  value(11) = 2.40, average  $p$  value = .019).

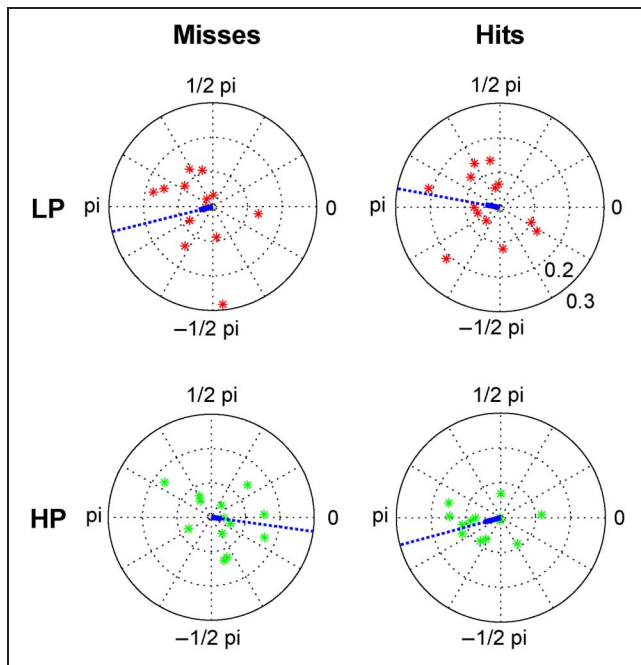
### Delta Phase during Misses and Hits

The polar plots in Figure 5 show the angle distribution separate for hits and misses and separate for the two conditions when SOAs from 150 to 450 msec were included. It seems that the mean direction between the hits and misses in the low-probability condition does not show any difference, whereas in the high-probability condition there is a phase difference. Indeed, the phase distances of the hits and misses were significantly different between

the low- and high-probability condition,  $F(2, 11) = 4.793$ ,  $p = .032$ . Additionally, the two individual Zar's Hotelling tests showed that for the low-probability condition there was no difference between mean phases,  $F(2, 11) = 0.139$ ,  $p = .872$ , whereas for the high-probability condition there was a significant difference between the mean phase of the hits and the misses,  $F(2, 11) = 5.39$ ,  $p = .023$ .

## DISCUSSION

Attention is thought to optimize selective information processing by orchestrating the synchronization between incoming temporally predictive information and high-excitability phases of ongoing low-frequency neuronal oscillations (Buzsáki & Draguhn, 2004; VanRullen & Koch, 2003). In many situations, temporal cues are not highly predictive, containing some predictability as well as uncertainties. We hypothesized that in one of such situations, that is to say when attention has to be allocated continuously but within a restricted window



**Figure 5.** Delta phase effects. Circular histogram plots for all trials with a sound, sorted for hits and misses for both conditions (LP = low probability, HP = high probability). Blue arrows indicate the mean direction. For the LP, the mean direction is the same for both hits and misses, whereas for the HP it differs.

of time (“restricted vigilance”), a longer, but not excessively long period, of high neuronal excitability should provide optimal processing. An efficient way to accomplish this is phase resetting of low-frequency oscillations; this provides high excitability over longer periods but does not excessively use metabolically demanding gamma oscillations (Mukamel et al., 2005; Niessing et al., 2005). To investigate whether top-down expectancy of stimulus occurrence during a restricted period of vigilance results in a stronger reset of low-frequency oscillations, we manipulated the probability that a low-intensity, temporally nonpredictive, auditory target would be presented in a given time window (450 msec) following a visual cue. We indeed found stronger representations of low frequencies (1–3 Hz) in the evoked power and phase coherence for the high-probability condition. Moreover, delta phase determined hits and misses in the high-probability condition, but not in the low-probability condition. These findings indicate that, during restricted vigilance, low-frequency phase reset increases the window of enhanced excitability, with the strength of this mechanism being amplified with greater stimulus probability.

#### Attention Window Created through Low-frequency Phase Reset

Our current paradigm of restricted vigilance, in which attention has to be allocated for a constrained time

window, seems to bridge two attention modes that have been suggested in the literature to operate for unpredictable versus predictable inputs (see also Niemi & Näätänen, 1981). Specifically, in the absence of any temporal predictability, Schroeder and Lakatos (2009) proposed a “vigilance mode,” in which primarily high-frequency gamma oscillations are amplified. Boosting gamma oscillations may improve stimulus detection because they produce many, densely distributed, high-excitability phases, and this increases the chance that a temporally unpredictable input will arrive during a state of high neuronal excitability (Fries, Nikolic, & Singer, 2007; Fries, 2005). This mechanism is complementary to the “rhythmic mode,” which employs low-frequency oscillations to selectively process temporally predictable stimuli. During “rhythmic mode” processing, the amplitude of gamma oscillations is phase coupled to lower frequencies, providing limited temporal windows during which processing is enhanced. Restricted vigilance requires parsing for a constrained time window, and low-frequency oscillations seem a plausible candidate, as these produce a high-excitability phase for a longer period of time. Because in our paradigm the restricted vigilance window is 450 msec, an oscillation of approximately 1 Hz will fit this vigilance window with half-a-cycle (i.e., the high-excitability phase of the oscillation). We indeed find effects of stimulus probability (high vs. low probability) on phase consistency to be pronounced at low frequencies (around 1 Hz) that were related to the participants’ behavior. This means that, when relevant information can only occur within a limited time interval, processing is specifically enhanced by aligning high excitable phases to this interval via phase reset of low-frequency oscillations. In future studies, it will be interesting to investigate whether for longer time intervals restricted vigilance will still operate and what will happen if the vigilance window occurs not right after the expectancy cue onset but later in the trial.

The expectancy cue modulated the low-frequency effect by changing the strength of the phase reset. A similar effect has been shown in another EEG study (Stefanics et al., 2010), in which rhythmic stimuli provided a predictable temporal structure. The pitch of the stimuli indicated the chance of the next stimulus being a target. Similar as in the current study, the strength of the phase reset depended on the likelihood of stimulus occurrence indicated by the expectancy cue. It thus seems that a rhythmic processing mode is strengthened by expectancy cues. It is an open question whether these effects can be purely attributed to changes in expectations or are modulated by changes in attention to the time window of the target stimulus occurrence (Summerfield & Egner, 2009). Although expectancies are created by changing the probability of stimulus occurrence, attention guides perception via goal-directed amplification of responses. As in the current experimental setting, stimulus probabilities of task-relevant features are manipulated; the effect of attention



is difficult to dissociate from expectations (Summerfield & de Lange, 2014). Whereas increases in stimulus expectancy often lead to decreases in neuronal responses (Näätänen, Paavilainen, Rinne, & Alho, 2007), increases in attention are associated with increased responses (Maunsell & Treue, 2006). Therefore, our results seem more compatible with the latter view, but studies separately controlling for attention and expectancy have to be conducted to verify this view.

### **Implicit versus Explicit Timing**

In our paradigm, it seems that the temporal structure of the task is implicitly acquired and consequently influences perception (Coull & Nobre, 2008). This is in contrast with explicit timing during which an overt estimate of temporal information has to be made, for example, when participants have to discriminate between the lengths of two intervals. During a task with implicit timing, participants are required to make a motor or perceptual judgment while using the knowledge of when stimuli are more likely to occur (Wright & Fitzgerald, 2004; Niemi & Näätänen, 1981). Therefore, the task is not temporal. There is evidence that the neuronal substrates of the two timing mechanisms are different (Coull & Nobre, 2008). Implicit timing uses mechanisms of the brain to temporally predict arriving targets (Schubotz, 2007). One such mechanism is the use of slow ongoing oscillations to align phases at a high excitable phase at the arrival time of a target (Lakatos et al., 2008). The current results indeed show that delta phase modulates perception when events are more likely to occur. Additionally, there seems to be a difference whether implicit rhythmic temporal cues or single temporal cues (as in the current study) are guided via different mechanisms (Wilsch, Henry, Herrmann, Maess, & Obleser, 2015; Triviño, Arnedo, Lupiáñez, Chirivella, & Correa, 2011). Our study highlights that oscillatory phase reset mechanisms seem to play a role also with single temporally predictive cues, but it is still unclear whether the exact mechanism is the same as with a predictive input stream.

### **Alpha versus Delta Effects: Evoked Response versus Phase Reset**

In addition to the low-frequency effects in the delta range, the evoked response in the time–frequency analyses showed significantly stronger alpha band oscillations when events were more likely to occur. This effect likely reflects differences in the visual evoked response caused by increased likelihood. As mentioned above, the direction of the effect depends on the mechanism in place (i.e., attention or expectancy). Both increases (Yamagishi et al., 2003; Näätänen, Gaillard, & Mäntysalo, 1978; Hillyard, Hink, Schwent, & Picton, 1973) and decreases (Näätänen et al., 2007) in evoked responses have been reported.

The evoked delta band modulation, however, cannot easily be explained as a difference in the visual evoked response. First, the topographic distribution does not include any occipital channels. Second, this low-frequency band generally does not emerge for simple visual evoked responses. Moreover, we could show that the mechanism behind the modulation of evoked power in the delta band is different from the alpha band evoked power by looking at the induced power and ITC: Whereas the induced power as well as the ITC showed modulations in the alpha band, only the ITC showed significant changes for the delta band. It has been shown that when power changes are absent, ITC increases can be explained via a phase reset mechanism that aligns the phases of ongoing oscillations without changing the amplitude (Makeig et al., 2004). Therefore, we believe that alpha oscillations drive visual evoked responses, whereas delta oscillations have a modulatory role, and the collective delta effects found here reflect a phase reset of which the frequency is likely influenced by the temporal predictions (i.e., 1-Hz frequencies are used to cover the restricted vigilance window of 450 msec with half-a-cycle). The neuronal origin of this effect could reflect a change in auditory cortex excitability at the predicted arrival time of the auditory stimulus, as has been reported before (Lakatos et al., 2008). However, the topography could also fit with an origin in the ACC. This brain structure has been related to the monitoring and guidance of attentional selection (Womelsdorf, Ardid, Everling, & Valiante, 2014; Buckley et al., 2009) and could therefore guide the temporal attention network to attend to relevant moments in time in the current task.

### **Delta Phase Determines Percept**

We found that, especially in the high-probability condition, hits and misses depended systematically on delta phase because there was a significant phase difference between hits and misses for this condition. For the low-probability conditions, this was not the case and therefore suggests that the delta phase modulation is primarily present when expectations are high, thus reflecting a top–down mechanism. These results add to a growing set of findings showing that delta phase is important for auditory detection (Henry & Obleser, 2012; Rohenkohl, Cravo, Wyart, & Nobre, 2012; Lakatos et al., 2008). As has been shown in a recent study, it is vital to ensure that no poststimulus portions of the data are included in the phase estimation (Zoefel & Heil, 2013), which can be avoided by using causal filters.

### **Implications for Multisensory Research**

The use of low-frequency phase reset in multisensory settings is becoming increasingly evident (Van Atteveldt, Murray, Thut, & Schroeder, 2014; Schroeder et al., 2008). Thus far, influences of low-frequency oscillations

on multisensory perception have been associated with cross-modal phase resetting, which results in subsequent periodic increases in detection thresholds or RTs (Thorne & Debener, 2013; Romei, Gross, & Thut, 2012; Naue et al., 2011; Thorne, De Vos, Viola, & Debener, 2011; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007). However, these studies have a different emphasis than classical multisensory integration studies, which generally do not have a main focus on unisensory detection or RTs but on integration and unity of multisensory information (Calvert, Campbell, & Brammer, 2000). For example, temporal unity is created when two stimuli are presented in temporal proximity (Van Wassenhove, Grant, & Poeppel, 2007; Spence & Squire, 2003). If reset frequency is modulated by the width of the restricted vigilance window, as our findings seem to suggest, integration of multisensory information might be confined in a similar framework. Specifically, an ambiguity in the requirement of temporal unity is that more complex stimuli, as well as stimuli that naturally belong together, seem to tolerate more variation in their temporal relation to still be integrated, compared to simple flashes and beeps (Vatakis & Spence, 2007; Van Wassenhove, Grant, & Poeppel, 2005; Zampini, Shore, & Spence, 2003). If integration occurs only when cross-modal stimuli fall within the same oscillation period (see e.g., Fries, 2005; VanRullen & Koch, 2003), resetting of lower-frequency oscillations for stimuli that naturally occur together (i.e., they predict each other) would result in wider temporal integration windows, because there is a longer temporal window in which the two stimuli will fall in the same period. Supporting the idea that oscillation period is vital for temporal integration is the finding that when two visual stimuli are presented with a specific delay, they are only judged as synchronous when they fall within the same visual alpha cycle (Gho & Varela, 1988; Valera, Toro, Roy John, & Schwartz, 1981). In brief, interplay between the likelihood that cross-modal stimuli can occur together and reset frequency might be related to the width of the temporal integration window. However, this prediction needs to be verified in future studies.

## Conclusion

Selective information processing is crucial to our survival considering the constant presence of abundant sensory information. Therefore, it seems beneficial to exploit temporal cues in our environment, as this enables proactive mechanisms for selective processing. When events are highly predictable, low-frequency phase reset appears to guide selective processing (Cravo, Rohenkohl, Wyart, & Nobre, 2013; Schroeder & Lakatos, 2009; Lakatos et al., 2008). Here, we show that also in the absence of a fully predictable temporal structure, low-frequency phase reset is employed to attend to a time window in which events are more likely (also see Fiebelkorn et al., 2011), revealing the full flexibility of this neural mechanism supporting selective processing. These results shed light

on the adaptive nature of phase reset to optimally sample the incoming information depending on top-down expectancies of stimulus occurrence and timing (Ten Oever, Schroeder, Poeppel, Van Atteveldt, & Zion Golumbic, 2014; Van Atteveldt et al., 2014; Zion Golumbic, Poeppel, & Schroeder, 2012). Future research should confirm that phase reset frequency is flexibly used to modify the temporal attention window, which could subsequently inform us about the functioning of other cognitive mechanisms, for example, the variable temporal integration windows for multisensory inputs, or the flexible use of different timescales during verbal communication.

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