

Making Waves in the Stream of Consciousness: Entraining Oscillations in EEG Alpha and Fluctuations in Visual Awareness with Rhythmic Visual Stimulation

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Abstract

■ Rhythmic events are common in our sensory world. Temporal regularities could be used to predict the timing of upcoming events, thus facilitating their processing. Indeed, cognitive theories have long posited the existence of internal oscillators whose timing can be entrained to ongoing periodic stimuli in the environment as a mechanism of temporal attention. Recently, recordings from primate brains have shown electrophysiological evidence for these hypothesized internal oscillations. We hypothesized that rhythmic visual stimuli can entrain ongoing neural oscillations in humans, locking the timing of the excitability cycles they represent and thus enhancing processing of subsequently predictable stimuli. Here we report evidence for entrainment of neural oscillations by predictable periodic stimuli in the alpha frequency band and show for the first time that

the phase of existing brain oscillations cannot only be modified in response to rhythmic visual stimulation but that the resulting phase-locked fluctuations in excitability lead to concomitant fluctuations in visual awareness in humans. This entrainment effect was dependent on both the amount of spontaneous alpha power before the experiment and the level of 12-Hz oscillation before each trial and could not be explained by evoked activity. Rhythmic fluctuations in awareness elicited by entrainment of ongoing neural excitability cycles support a proposed role for alpha oscillations as a pulsed inhibition of cortical activity. Furthermore, these data provide evidence for the quantized nature of our conscious experience and reveal a powerful mechanism by which temporal attention as well as perceptual snapshots can be manipulated and controlled. ■

INTRODUCTION

Rhythmic stimulation is present throughout the natural and modern world. Similarly, our brain's networks are dominated by rhythmic activity (Adrian & Matthews, 1934), measured as local field potential (LFP) or the EEG. It has long been theorized that these periodicities represent oscillations in neuronal excitability (e.g., Lindsley, 1952).

In support of this theory, recent evidence has shown optimal processing at preferential phases of ongoing oscillations, with suppression at opposite phases. For example, neurons preferentially fire during specific phases of the LFP (Lórinçz, Kékesi, Juhász, Crunelli, & Hughes, 2009; Jacobs, Kahana, Ekstrom, & Fried, 2007). Spiking activity, evoked responses, and fMRI activation to identical visual stimulation vary as a function of the phase of ongoing oscillations (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Scheeringa, Mazaheri, Bojak, Norris, & Kleinschmidt, 2011; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Barry et al., 2004; Jansen & Brandt, 1991). Furthermore, RTs (Stefanics et al., 2010; Callaway & Yeager, 1960), saccadic latency (Drews &

VanRullen, 2011; Hamm, Dyckman, Ethridge, McDowell, & Clementz, 2010), simultaneity judgments (Varela, Toro, John, & Schwartz, 1981), somatosensory detection (Monto, Palva, Voipio, & Palva, 2008), and visual awareness (Mathewson et al., 2009, 2011; Busch & VanRullen, 2010; Mathewson, Fabiani, Gratton, Beck, & Lleras, 2010; Busch, Dubois, & VanRullen, 2009) have all been shown to vary as a function of the phase of ongoing oscillations in neural activity.

Moreover, the phase of spontaneous oscillations can become locked to rhythmic environmental stimuli (Walter & Walter, 1949; Adrian & Matthews, 1934). Flicker or steady-state studies show that rhythmic visual stimuli can induce cortical oscillations at many different frequencies and harmonics (Pastor, Artieda, Arbizu, Valencia, & Masdeu, 2003; Pastor et al., 2002; Herrmann, 2001). Given that attention enhances this effect (Kim, Grabowecky, Paller, & Suzuki, 2011; Lakatos et al., 2008; Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Morgan, Hansen, & Hillyard, 1996), it has been suggested that entrained oscillations in cortical excitability represent a mechanism for temporal attention (Rohenkohl & Nobre, 2011; Lakatos et al., 2008; Buhusi & Meck, 2005; Coull, Vidal, Nazarian, & Macar, 2004; Large & Jones, 1999). In humans and nonhuman primates, low frequency (1.5-Hz) LFP oscillations can become entrained to external stimulus periodicity in an attended modality. The

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phase of these entrained oscillations then influences both the evoked response and RTs (Besle et al., 2011; Lakatos et al., 2008). Furthermore, temporal expectancies created by auditory trains shorten RTs to predicted auditory targets and lock the phase of ongoing 0.5–3 Hz delta oscillations (Stefanics et al., 2010).

The phase of ongoing 8- to 12-Hz alpha oscillations has been shown to influence awareness of visual targets (Mathewson et al., 2009), leading us to propose that alpha oscillations represent a pulsed inhibition of ongoing sensory processing (Mathewson et al., 2011). Here we tested the hypothesis that entrained EEG oscillations could similarly influence visual perception by presenting observers with rhythmic visual stimuli (at the frequency of alpha) at fixation, followed by masked visual targets with onsets at various lags with respect to the preceding stimulation phase. In previous behavioral research, we showed that visual awareness varies cyclically as a function of the phase lag between entrainment and target stimuli (Mathewson et al., 2010). Here we recorded the EEG to examine the relationship between induced oscillations in awareness and the oscillations in neural activity that may become locked to the entraining rhythmicity.

We predicted that rhythmic stimulation in the alpha range should lead to phase-locked rhythmic activity in the EEG at the same frequency. Over trials, this should manifest as a consistent phase of alpha EEG oscillations with respect to the rhythmic stimulation. Furthermore, this effect should last beyond the offset of the rhythmic sequence for several cycles into the period in which the masked visual target is presented and thus influence the subject's awareness of the target. Specifically, targets presented in-phase and out-of-phase with the preceding rhythmic stimulation should have different alpha phases at the time of their onset. Furthermore, the phase of alpha oscillations at the moment of target onset should predict detection, with stimuli in-phase with the preceding stimulation being more easily detectable than those that are out-of-phase (see Mathewson et al., 2009, 2010). Finally, we expect these effects to be graded, with maximum gains in perceptibility when the target timing is perfectly in-phase with the entraining stimuli and decreasing effects as the timing becomes more variable.

To preview the results, as predicted, the amount of EEG phase locking to the visual stimulation and specific phase of alpha predicted the magnitude of the differences in detection rate as a function of target timing. Furthermore, these effects were related to (a) the amount of resting alpha power before the experiment and (b) the EEG power at 12 Hz at the start of each trial, suggesting that ongoing oscillations in cortical activity are being entrained.

METHODS

Participants

Seventeen paid volunteers (age = 18–26 years; five men) gave informed consent before participating. Data from four

participants whose detection rate in the Rhythmic condition was less than 9% were removed from the data set, leaving 13 participants. Electrophysiological data from one of these subjects were contaminated by extensive artifacts. Therefore, all EEG analyses were restricted to data from the remaining 12 participants.

Stimuli

A metacontrast paradigm was used. Figure 1 shows the stimulus dimensions for target and mask (Figure 1A) and trial timeline (Figure 1B). Participants sat 57 cm from a 17-in. monitor that refreshed every 11.7 msec. The subject's task was to detect the presence of an 11.7 msec circular target (1° diameter) at fixation. The target was always backward-masked by a 23.4-msec annulus (2° diameter; 1° center cutout), with a 45.6-msec mask SOA. Participants had 1500 msec from the onset of the target to indicate whether or not they had detected the target. On 20% of the trials, the target was omitted (catch trials) to measure false alarms and to ensure that we were measuring changes in detection and not in response criterion.

Each trial began with a 247-msec fixation cross followed by a 459-msec blank screen. Then, one of the three randomly chosen target sequences was presented at fixation. In the Rhythmic condition, eight annuli identical to the mask were presented for 23.4 msec each, one every 82.3 msec (~12 Hz). In the Variable condition, the gap between each annulus was varied between 11.7 and 257.4 msec, such that the overall duration from first to last annulus onset was identical to that in the Rhythmic condition. Ten different randomly chosen Variable sequences were used in this condition, which varied in the degree to which they differed from the Rhythmic sequences. In the Control condition, only two annuli were presented with a SOA of 576.5 msec, such that the pretarget periods of all three conditions had the same overall length. This type of sequence controlled for the possible forward-masking effects of the final entrainer (Mathewson et al., 2010).

Following the final pretarget annulus entrainer, the target was presented after one of seven lags, sampling various phases with respect to the preceding entrainment. On each trial, this lag (i.e., the SOA between the final entrainer and the target [tSOA]) was randomly chosen from 36, 60, 83, 106, 130, 154, or 177 msec, with 83 and 177 msec being in-phase with the preceding stimulation and 36 and 130 msec being out-of-phase. These SOAs were fully counterbalanced with respect to the three pretarget conditions, providing 21 stimulus variations. Subjects completed 24 blocks consisting of 54 trials each, providing an average of 62 trials for each of the entrainment-by-lag combinations.

EEG Recording

The EEG was recorded at 200 Hz from 20 scalp locations referenced on-line to the left mastoid and rereferenced

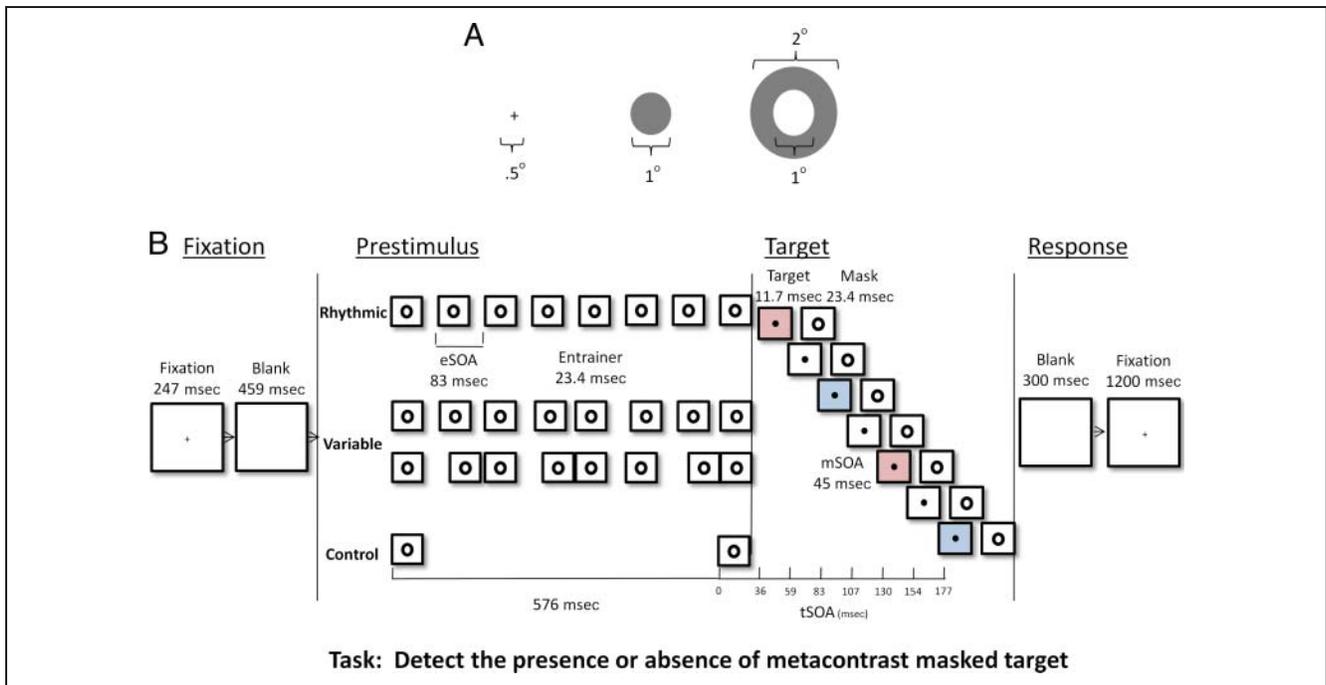


Figure 1. (A) Stimulus dimensions. (B) Trial timeline. e = entrainer; t = target; m = mask.

off-line to the left and right mastoid average. The EOG was recorded from two bipolar electrode pairs placed above and below the left eye and on the outer canthus of each eye. Data were filtered on-line with a half-amplitude band-pass from 0.01 to 30 Hz, rejecting common mode noise.

Preprocessing

The EEG data were divided into 3500-msec segments locked to the onset of the initial fixation cross, including a 1000-msec baseline period. Trials with voltage fluctuations larger than 750 μ V, RTs shorter than 200 msec, or trials with no responses were discarded. Eye movement artifacts were then corrected with a regression procedure, removing all variance in the EEG channels that could be accounted for by either horizontal or vertical eye movements (Gratton, Coles, & Donchin, 1983). Trials with voltage deflections greater than 125 μ V after eye movement correction were also removed.

Entrainment-evoked Activity

As an initial test of the effects of rhythmic entrainment on EEG oscillations, we computed the average broadband EEG waveform time-locked to the onset of each rhythmic entrainer. Data were processed as described above. The segments were locked to the onset of each entrainer, and the average in the 200 msec baseline before the onset of the entrainer was subtracted from each waveform. For comparison, the waveforms locked to the first entrainer were compared against the waveforms locked to the re-

maining entrainers in the sequence, averaged over all trials in each condition.

EEG Power and Phase

A wavelet analysis of the segmented data was computed using the *newtimef()* function of the EEGLAB toolbox (Delorme & Makeig, 2004). A group of complex Morlet tapered wavelets were computed with parameters set to obtain an optimal balance of temporal and frequency resolution at all frequencies ($m = 3.15$; $\sigma_t = 0.20$; $\sigma_f = 3.13$). Tapered wavelets had three cycles at the lowest frequency (4.7 Hz) and increased by a factor of 0.01 up to 19 cycles at the highest frequency (30 Hz; cutoff of on-line filter), with 7.5 cycles at the 12-Hz entrainment frequency. These parameters provide estimates of power and phase every 0.8 Hz from 4.7 Hz up to 30 Hz and from -642 to 2137 msec around the event of interest.

Phase-locking Index

We measured the phase-locking index (PLI) or the consistency of the phase at any given frequency and time across trials (i.e., *newtimef()*'s intertrial coherence), with respect to the onset of the entrainment sequence. This measure is a function of the consistency of the EEG phase over trials for a given time and frequency. The PLI is computed as the length of the vector representing the average of all trials' phases and has bounds of 0 (random phase over trials) and 1 (same phase on every trial). To minimize multiple comparisons, all analyses were

computed at electrode Pz, the site of maximal phase–awareness interactions in Mathewson et al. (2009), as well as the site of maximal phase locking in the current study (see Figures 3B and 4B). This is also the site of maximal steady-state response in the alpha range (Johnson, Hamidi, & Postle, 2010).

Single Trial 12-Hz Phase

To test whether the phase of alpha oscillations at target onset differed depending on lag with respect to the previous entrainers, additional segments were taken from –1000 to 2500 msec around the onset of each target. These were preprocessed and analyzed using the same wavelet analysis described above. The phase of the 12-Hz activity at 100 msec before the onset of the target was recorded for each trial, given that Busch et al. (2009) and Mathewson et al. (2009) found maximal effects of phase on awareness at –100 msec. For each subject, the average phase was then computed separately for targets presented in-phase and out-of-phase with the preceding rhythmic stimulation. The difference between these average phases was then computed and tested against a zero-phase difference using a Hotelling’s bivariate F test on the sine and cosine components. To test for the influence of alpha phase on awareness, this same analysis was used to compare the 12-Hz phase at the onset of targets that were either detected or undetected. For this analysis, we used a single bin at 12 Hz to get an accurate measure of single trial phase over time. Averaging of multiple phase measurements would add artifacts.

Pretrial Alpha Power

To understand the relationship between induced oscillations in neural activity and spontaneous alpha oscillations, we re-sorted the trials based on the amount of 12-Hz power at the start of each trial. For each participant, the average power between 10 and 14 Hz in the 200 msec before each trial was computed. The detection performance across conditions was then calculated separately for trials in the top and bottom quartiles of alpha power. We used a wider window centered on 12-Hz to maximize signal-to-noise ratio for this single trial analysis and allow for minor changes in the entrained frequency.

Resting Alpha Power

Before and after the set of 24 blocks, 1 min of spontaneous EEG was recorded from participants while their eyes were closed. We predicted that if we are entraining ongoing alpha oscillations, the entrainment effects on EEG and awareness should be dependent on the level of spontaneous alpha power. To understand the relationship between induced oscillations in neural activity and spontaneous alpha oscillations, we took 30 consecutive 2000-msec segments of data from the eyes-closed EEG

recordings of 10 subjects for whom we had available data from the period immediately preceding the experimental task. Although 1-min of eyes-closed EEG recording is not ideal to measure spontaneous alpha power because of long-term fluctuations in power (e.g., Linkenkaer-Hansen, Nikouline, Plava, & Ilmoniemi, 2001), we found strong reliability between our estimates of alpha power when comparing the EEG recorded before and after the experimental blocks for the nine participants for which we had postsession estimates ($r = .90$; $p < .001$). We submitted these 2000-msec segments to a stationary fast Fourier transform, averaged the log-transformed spectra across each subject’s segments, and measured the peak power and frequency within a broad alpha range (7–15 Hz). This even broader range was used to get the most accurate possible measurement of individual resting alpha power.

RESULTS

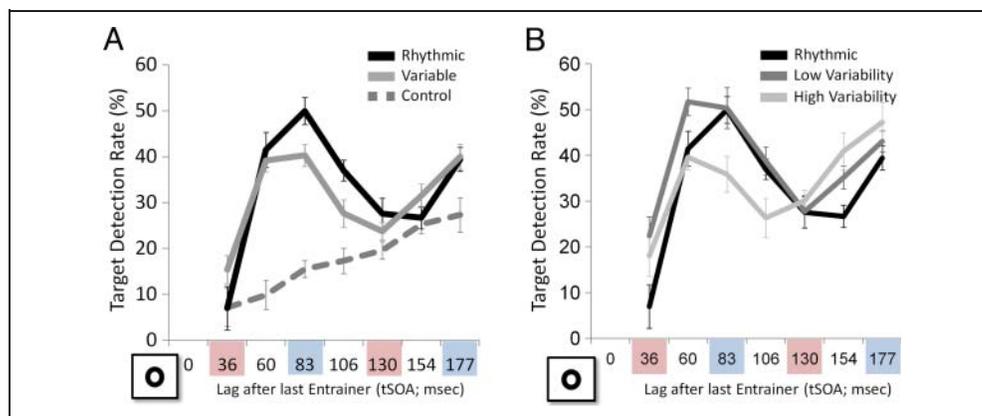
Entrainment of Visual Awareness

Figure 2A plots detection rates for three pretarget conditions as a function of the lag between the last entrainer and target (tSOA). A repeated-measures ANOVA with a Greenhouse–Geisser correction for lack of sphericity revealed significant main effects of Pretarget Entrainment Type, $F(1.12, 13.40) = 7.87$, $p < .05$, $\epsilon = .56$, and of Target Lag, $F(2.56, 30.76) = 15.94$; $p < .00001$, $\epsilon = .43$, as well as an interaction such that the effect of lag differed as a function of the type of entrainment, $F(2.93, 35.16) = 7.88$, $p < .001$, $\epsilon = .24$.

Figure 2A shows increased detection for in-phase targets (83 and 177 msec) compared with targets out-of-phase (36 and 130 msec) with the preceding entrainment for the Rhythmic and Variable conditions. Overall, there was a significant difference in detection rate for in-phase ($M = 0.45$) compared with out-of-phase targets ($M = 0.17$; $t(12) = 5.71$, $p < .0001$). At 83 msec (in-phase), detection was higher in the Rhythmic ($M = 0.50$) than in the Variable ($M = 0.40$; $t(12) = 4.11$, $p < .01$) and Control conditions ($M = 0.16$; $t(12) = 5.50$, $p < .001$). Detection was also higher in the Variable than in the Control condition ($M = 0.40$ vs. $M = 0.16$; $t(12) = 5.01$, $p < .001$). Detection rate at 177 msec (in-phase) was higher for Rhythmic ($M = 0.39$; one-tailed $t(12) = 2.20$, $p < .05$) and Variable conditions ($M = 0.40$; one-tailed $t(12) = 2.58$, $p < .05$) than the Control condition ($M = 0.27$), with no difference between Rhythmic and Variable conditions ($t(12) = .15$, ns).

To determine whether the effect of entrainment condition on target detection represented a change in sensitivity and not a change in threshold, we considered the false alarm rate for each tSOA and entrainment condition. Many of the participants had few or no false alarms in most of the conditions, so we pooled across tSOAs and substituted the across-subject minimum false alarm rate of 0.01 for estimation when needed, because d' is undefined

Figure 2. (A) Target detection percentage as a function of presentation lag. (B) Shows the same detection profile as in (A), but now with the Variable condition divided into random sequences that had lower or higher variability of SOAs in the beginning of the sequence. Error bars represent within-subject SEMs (Masson & Loftus, 2003).



when the false alarms rate is 0. In fact, across all conditions and tSOAs, participants' average false alarm rate was low ($M = 0.08$, $SD = .08$). Averaging over all tSOAs, the average d' in the Rhythmic condition was $d' = 1.09$, indicating sensitivity to the target. This was not significantly different from the average d' in the Variable condition ($d' = 1.11$; $t(12) = 0.21$, ns). There was, however, a lower d' in the control condition indicating significantly more masking of the target ($d' = .78$; $t(12) = 2.30$ and 2.51 for Rhythmic and Variable, respectively; $p < .05$). Furthermore, an inspection of the average false alarm rate as a function of tSOA revealed a flat function in all three conditions. As a result, only target detection is considered from hereon.

To evaluate the significance of fluctuations in visual awareness as a function of target timing, we fit linear and cubic functions across tSOAs for each participant. We normalized the detection rate across all lags and pre-target conditions for each subject and multiplied these normalized scores by their respective linear or cubic weights. A better cubic than linear fit was found in both

the Rhythmic ($t(12) = 5.86$, $p < .0001$) and Variable conditions ($t(12) = 3.53$, $p < .01$) but not in the Control condition ($t(12) = 1.60$; ns).

Figure 2B shows target detection rate as a function of lag after the final entrainer (tSOA) for the Variable sequences with high- and low-variability, which are less and more similar, respectively, to the Rhythmic sequence. For low-variability sequences (i.e., more similar to the Rhythmic sequences), the data show a peak in detection equal to that of Rhythmic trials ($t(12) = .13$, ns), although at an earlier (60-msec) target lag, indicating slightly faster preferential processing for these sequences. Importantly, the high-variability sequences had lower detection than both the low-variability ($t(12) = 3.11$, $p < .01$) and Rhythmic sequences ($t(12) = 2.92$, $p < .05$).

Entrainer-evoked Activity

Next we sought to examine the buildup of oscillatory activity in the EEG elicited by the rhythmic entrainers.

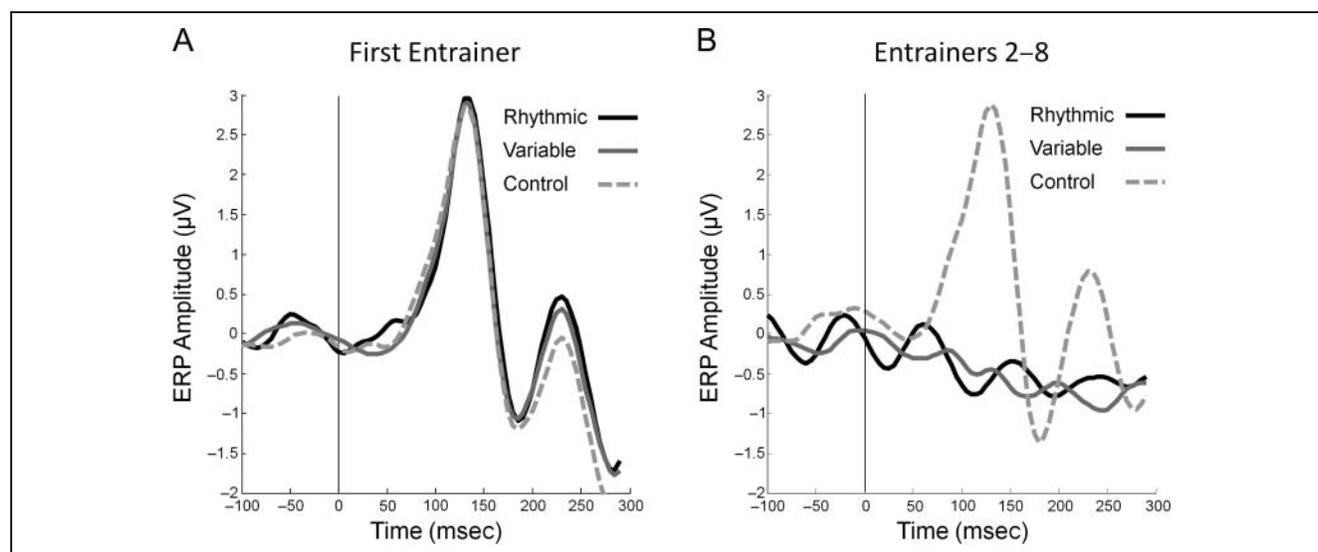


Figure 3. Average ERPs at electrode Pz evoked by the entraining stimuli for the first entrainer in the sequence (A) and all subsequent entrainer onsets (B) for each of the three pre-target stimulation conditions. Note that, in the Control condition, this only represents the evoked activity from the second annulus.

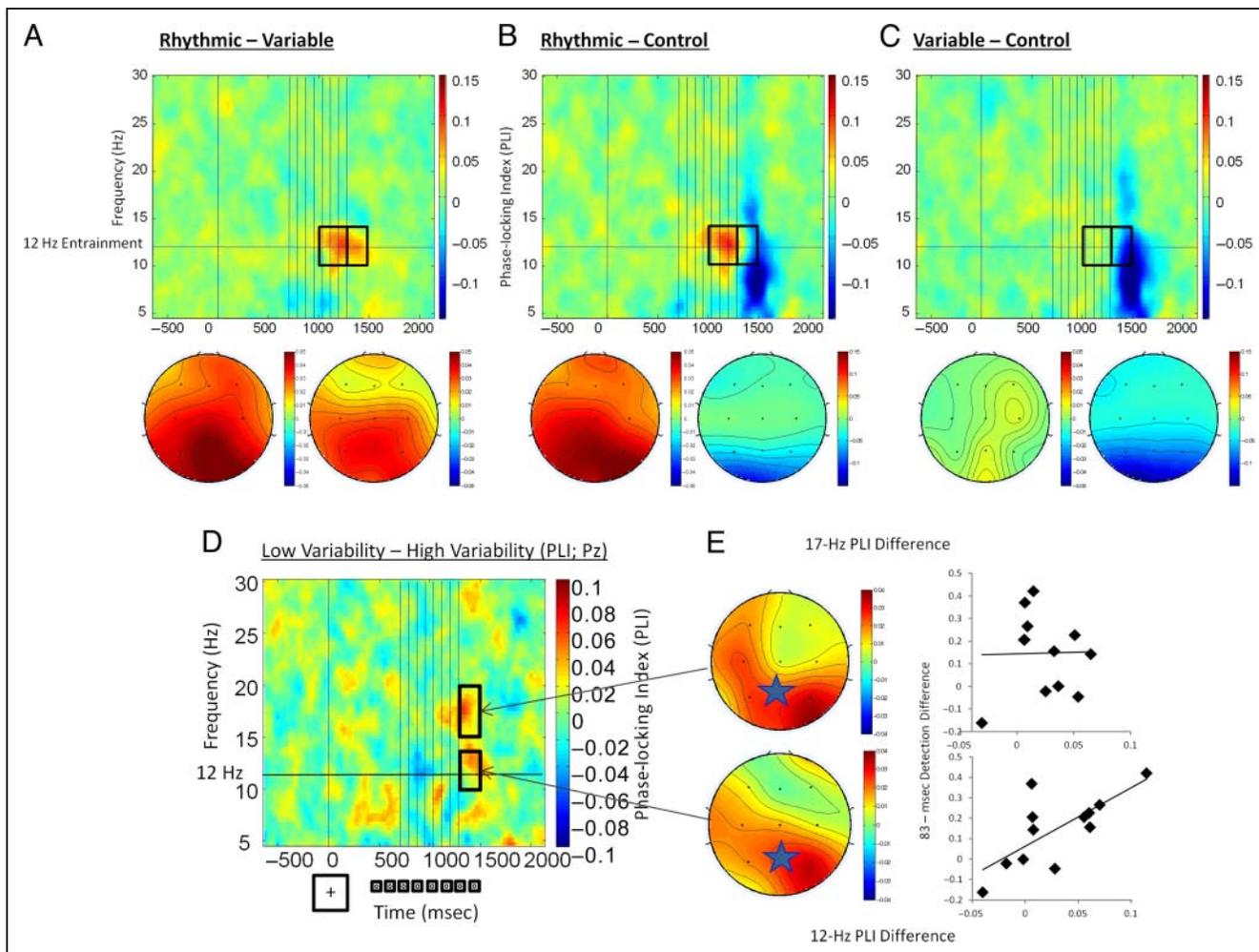


Figure 4. Average PLI, locked to the onset of the entrainment sequence, displayed over time and frequency for the entire trial period for each sequence type, including a baseline period before the fixation onset. The plots display the difference in PLI between conditions: (A) Rhythmic and Variable conditions, (B) Rhythmic and Control conditions, and (C) Variable and Control conditions. Two windows of interest ranging from 10 to 14 Hz are marked: the 300 msec before the end of the sequence and the 200 msec after the end of the entrainment sequence. Fixation onset and the onset of each pretarget annulus entrainer are indicated by vertical lines. A horizontal line indicates the rate of 12-Hz entrainment in the Rhythmic condition. All time–frequency plots refer to electrode Pz. The scalp maps presented below each plot indicate the topographic distribution of the differences in each window. (D) Variability of entrainment analysis. Difference in PLI between low- and high-variability irregular pre-target sequences. (E) Scalp maps showing the topographic distribution of the differences in each window. The accompanying scatter plots show the average difference between high- and low-variability PLI in each of the two windows, plotted against the difference in detection in these conditions at 83 msec.

Figure 3A shows ERPs locked to the onset of the first entrainer for each of the three pretarget conditions. Evident is a large evoked activity that is equal in amplitude and latency in all three conditions. Figure 3B shows, in contrast, the average evoked activity of all subsequent entrainers (only one in the control condition). Evident is a large evoked response only for the control condition, equal to that elicited by the first entrainers. This increased evoked activity is because of the more distinct stimulus onset in this pretarget condition, given the long interstimulus gap in this condition.

In the Rhythmic and Variable conditions, no evoked activity is evident; the response to the entrainers becomes attenuated over repeated presentations. Importantly, in the rhythmic condition, a clear oscillation is evident with a period

of ~ 80 msec and preferred phase of $\sim 90^\circ$. The oscillatory activity is much diminished and less consistent in the Variable condition.

Phase Locking

Figure 4A shows the difference in PLI between the Rhythmic and Variable conditions. The increase in PLI is centered around the 12-Hz entrainment frequency and larger following the rhythmic entrainment stimuli. This phase locking extends 200–300 msec after the entrainment stimuli end, matching the stimulus-related analysis presented earlier and indicating that this does not merely reflect the visual-evoked potential elicited by the annuli. The average PLI for

each subject between 10 and 14 Hz in the 200-msec interval following the final entrainer onset (late window) was greater in the Rhythmic condition ($M = 0.11$) than the Variable condition ($M = 0.07$; $t(11) = 2.94, p < .05$). The average PLI activity in an additional window during the last 300 msec of the entrainment sequence (early window) also showed significant differences between the Rhythmic and Variable conditions ($t(11) = 4.30, p < .005$). Figure 4A (bottom) includes maps of the scalp distribution of the average difference in PLI in the two measurement windows (last 300 msec of entrainment sequence and first 200 msec following the end of entrainment). The difference in PLI between Rhythmic and Variable conditions was maximal over posterior visual areas in both cases. Importantly, a test of the difference in evoked alpha power after the final entrainer between the two conditions found no difference ($t(11) = .41, ns$), suggesting that entrainment is not increasing the power of alpha activity but rather is realigning the phase of existing oscillations. Although increases in amplitude at the fundamental frequency are observed in steady-state visual evoked potential studies, they take multiple seconds to build up. Here our brief series of entrainers seems to have been enough to coordinate the alpha activity, but not to increase the local coherence sufficiently to observe an increase in power.

Figure 4B shows the difference in PLI between the Rhythmic and Control conditions, indicating the same increase in phase locking during the early window ($t(11) = 4.45, p < .005$). In the late window, this effect is overshadowed by the evoked activity in the Control condition also evident in the stimulus-locked average presented in Figure 3B. The topographic extent of this evoked activity is clearly distinct from that of the entrained 12-Hz activity. Figure 4C shows the difference in PLI between the Variable and Control conditions. Here no difference was found in PLI in the last 300 msec of the entrainment sequence (early window: $t(11) = 1.25, ns$), and again any later difference was obscured by the broadband PLI in the Control condition because of the evoked ERP components. Given this high phase consistency in a broad frequency band including 12 Hz, all further analyses of single trial phase were constrained to the Rhythmic and Variable conditions.

The amount of 12-Hz phase locking after the pretarget period was correlated with the average detection rate for the Rhythmic condition ($r = .55$; directional $p < .05$).¹ In the Variable condition this correlation was slightly reduced ($r = .44$; directional $p = .07$). However, in the Control condition, the correlation between alpha PLI and detection was negligible ($r = -.12, ns$), although there was a high level of phase locking because of the visual evoked activity from the final pretarget annulus.

These data corroborate the analyses presented in Figure 3 and suggest that the 12-Hz phase locking can be differentiated from the overlapping evoked activity elicited by the repetitive stimulus onset on the basis of a number of criteria, including scalp distribution, time course, and frequency band. Specifically, the evoked ac-

tivity is only large in response to the first entrainer and is not sustained throughout the whole entrainment interval. Furthermore, this broad-frequency evoked activity has a different spatial distribution than the 12-Hz specific sustained activity. Lastly, the temporal extent of this 12-Hz phase locking outlasts the entrainment sequence considerably.

Sequence Variability

Figure 4C reveals no apparent phase-locking difference between the Variable and Control conditions. The random variability in entrainer onsets likely caused too much phase jitter for any phase locking to be observed. Figure 4D shows the difference in PLI with respect to the start of the sequence between the low- and the high-variability sequences. As predicted, there was greater phase locking in the 200 msec following the Variable sequence for the low-variability than high-variability sequences. In the 10- to 14-Hz frequency band, the difference was significant ($t(11) = 2.31; p < .05$) and strongly predicted, across subjects, the increase in detection at 83 msec for low- as compared with high-variability sequences ($r = .72; t(11) = 3.28; p < .01$). The maximal extent of this difference was also posterior over occipito-parietal brain areas. An additional peak PLI difference was observed at 17 Hz, indicating phase locking at a higher frequency than alpha. The faster entrained brain oscillation may correspond to the earlier peak in detection shown in Figure 2A for the low-variability condition at 60 msec. Indeed, there was a shorter average eSOA for the final three entrainers of low-variability sequences (73 msec) compared with the high-variability ones (79 msec). Thus, this low-variability condition ended with faster paced entrainers and showed a higher frequency of phase locking, coincident with an earlier entrained peak in visual awareness. However, the correlations between the difference in PLI in a 17-Hz centered window and the increase in detection rate at both 60 and 83 msec were negligible ($r = .02$ and $r = .02; ns$). Together, these results reveal that the effects of entrainment on detection and phase-locking scale with the regularity and frequency of the rhythmic sequence and are relatively robust to sequence noise.

Single-trial 12-Hz Phase

Figure 5A shows circular histograms of the single-trial phase of 12-Hz EEG oscillations at electrode Pz with respect to target onset, pooled over all trials and subjects. We compared the average 12-Hz phase between in-phase (tSOA of 83 and 177 msec; circular grand mean [CGM] = 76.2°) and out-of-phase targets (tSOA of 36 and 130 msec; CGM = 246.9°). These phases differed significantly (mean difference = 135° ; Hotelling's $F(2, 11) = 20.3, p < .005$), indicating a difference in alpha phase as a function of target timing. Importantly, the difference in average phase between the 130 and 177 tSOA (out-of-phase and

in-phase, respectively) was predictive of the difference in detection for these same targets (circular-linear correlation, Fisher, 1993; Zar, 1999; $r = .72$; $\chi^2(2) = 6.18$, $p < .05$).

Figure 5B shows these same effects for the Variable condition. Here we still consider the same in-phase and out-of-phase targets, given that the average eSOA between the entrainers is still 83 msec. Targets in-phase with the stimulation (CGM = 121.3°) again had a significantly different average 12-Hz phase than those out-of-phase with the entrainment (CGM = 241.2°; mean difference = 140°; Hotelling's $F(2, 11) = 17.1$, $p < .005$). In this case, the correlation between the difference in 12-Hz phase and the difference in detection between 130 and 177 msec did not reach significance (circular-linear correlation $r = .25$; $\chi^2(2) = 1.5$, ns), in agreement with the weaker effects of the phase seen here than in the Rhythmic condition. To test for a difference in correlation between the two conditions, we utilized a jackknife procedure, holding out one subject at a time and computing the two correlations on the remaining subjects. In all cases, the correlation was larger in the Rhythmic than in the Variable condition, and there was a marginal difference in the Fisher-transformed correlations between the two conditions ($t(11) = 1.37$; $p = .09$).

12-Hz Phase Predicts Detection

We next tested if the phase of 12-Hz EEG activity on each trial could predict detection (Mathewson et al., 2009). For homogeneity of stimulus conditions and to achieve an adequate numbers of trials per condition, as well as to minimize the effects of any evoked activity and maximize the influence of sustained entrained activity, we considered only targets appearing at the 130-, 154-, or 177-msec lags. We computed the average phase separately for detected and undetected targets averaged over all lags. Figure 5C shows histograms of the 12-Hz phase pooled over all subjects and trials, separately for detected and undetected targets, along with the grand average phase (arrows). Figure 5D shows the difference in average 12-Hz phase for each subject (black arrows). A test of these differences in the Rhythmic condition against zero indicated a significant difference in the phase of 12-Hz activity between trials in which the targets were detected (CGM = 55°) and undetected (CGM = 283°; mean difference = 243°; Hotelling's $F(2, 11) = 13.74$, $p < .05$). In the Variable condition, the 12-Hz phase also differed between detected (CGM = 200°) and undetected targets (CGM = 93°; mean difference 218°; Hotelling's $F(2, 11) = 17.42$, $p < .005$).

Figure 5. Single trial 12-Hz phase analysis and detection. (A) Circular histograms of the single-trial 12-Hz phase 100 msec before the onset of the target, for both out-of-phase (red hues) and in-phase (blue hues) targets, pooled for all trials and all participants. The thick black arrows represent the CGM phases, computed as the grand average of each participant's average phase. Also shown underneath are the differences in 12-Hz phase between in-phase and out-of-phase targets for each participant. The green arrow represents the average of these phase differences. (B) Analogous plots as in A for the Variable condition. (C) Two circular histograms of the phase of 12-Hz oscillations 100 msec before target onset, for detected and undetected targets presented at 130, 155, or 177 msec after entrainment. Arrows indicate the CGM. Also shown is the difference in average phase between detected and undetected targets for each subject (black arrows) as well as the mean of these differences (green arrow). (D) Analogous plots for trials preceded by variable entrainment.

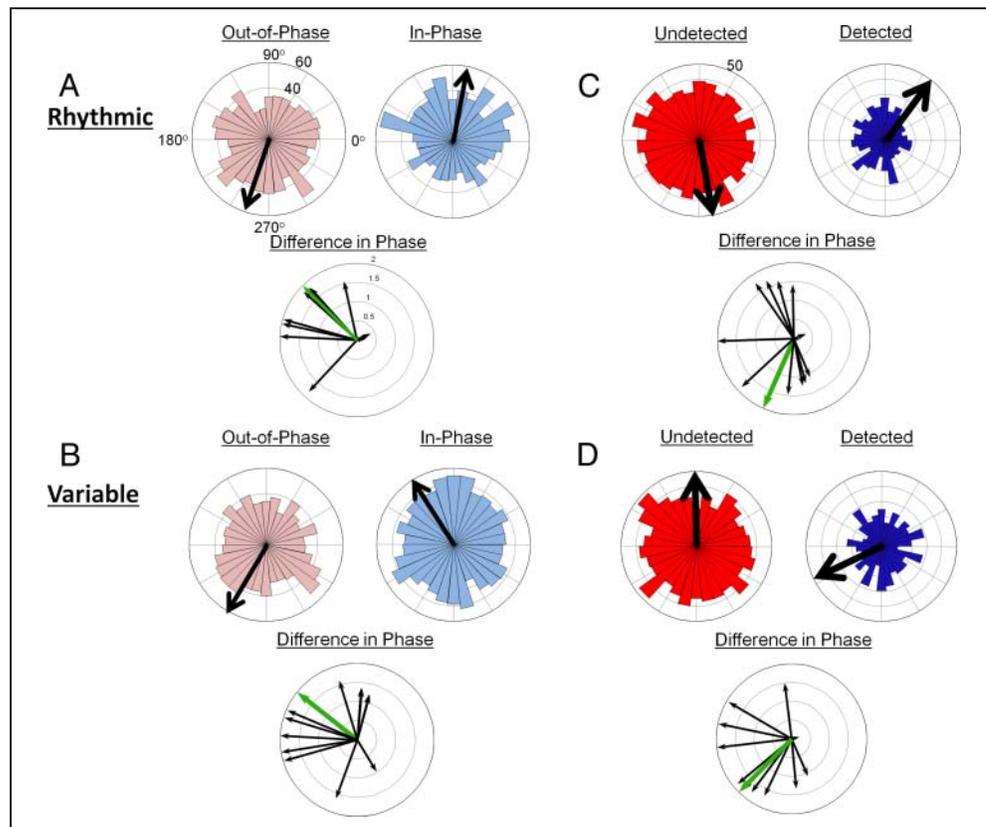
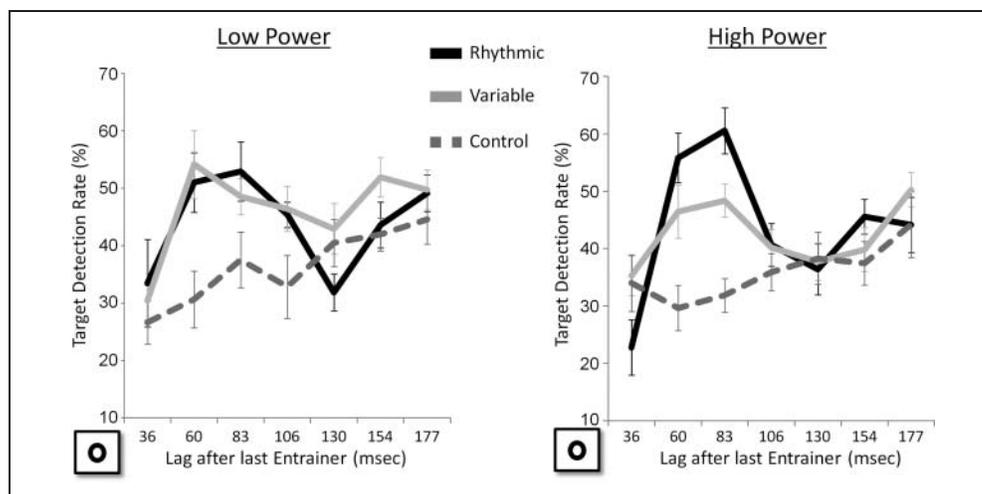


Figure 6. Plots of target detection rate as a function of tSOA, separately for trials with low (left) and high (right) 12-Hz EEG power before fixation onset. Error bars represent within-subject SEMs.



Alpha Power Predicts Entrainment

We next tested if participants' spontaneous alpha at the start of each trial and before the experiment could predict the degree to which their awareness and neural oscillations were entrained. We first sorted our trials based on the average of 10–14 Hz power in the 200 msec before fixation. We then computed the detection performance separately for trials in the top and bottom quartiles of 10–14 Hz power (Figure 6). Evident in the Rhythmic condition is a larger peak at 83-msec lag for trials beginning during high alpha power ($M = 0.605$) than during low alpha power ($M = 0.529$; directional $t(11) = 1.99, p = .07$). Furthermore, there was a larger difference between the Rhythmic and Variable conditions (directional $t(11) = 1.87, p = .08$) and between the Rhythmic and Control conditions (directional $t(11) = 3.70, p < .005$) at the 83-msec lag for high alpha power.

We also sought to understand the relationship between individuals' resting levels of alpha oscillations and the observed effects. Interestingly, the peak frequency of participants' resting alpha oscillations was not significantly correlated with any of these measures. This is perhaps because of the low variability in the peak frequency in our sample or possibly because this entrainment has influence irrespective of the peak alpha frequency of resting alpha and only depends on power. However, participants with more resting alpha power had larger differences in detection between in-phase and out-of-phase targets in the Rhythmic ($r = .55, p < .05$) and Variable conditions ($r = .53$, directional; $p = .05$). Furthermore, the amount of resting alpha power predicted the entrainment of neural oscillations, as measured by either the average PLI after entrainment in the Variable condition ($r = .54$, directional, $p = .05$), the difference in 12-Hz PLI between the high- and low-variability entrainers ($r = .56$, directional, $p < .05$), or the difference in 12-Hz phase at the onset of in-phase and out-of-phase targets (circular-linear correlation $r = .62, p = .05$). This indicates that the amount of spontaneous alpha power can predict the degree to which both participants'

awareness and their alpha oscillations are entrained by rhythmic 12-Hz stimulation.

DISCUSSION

We identified a clear increase in visual awareness for targets presented in-phase with preceding 12-Hz visual stimulation. This effect was found to scale with the regularity of the entrainment sequence and was not present at all when the pretarget period and forward masking effects of the preceding stimuli were controlled for but no rhythmicity was present. Furthermore, an overall increase in phase locking was observed following the Rhythmic sequence, which was maximal over parietal and occipital visual areas. The amplitude of this phase locking predicted the increase in visual awareness due to entrainment across subjects and could be separated from the evoked activity due to the entrainers.

The increase in target detection for in-phase targets was also predicted by the separation in the phase of ongoing 12-Hz EEG oscillations at the onset of in-phase and out-of-phase targets. Detection was particularly likely when targets are presented during one phase of the alpha EEG oscillations and conversely low when the stimuli are presented during the opposite phase. Furthermore, background levels of EEG oscillations could predict the size of the effects. Trials with higher 12 Hz power were associated with increased detection for targets in-phase with the entrainment. In addition, participants with more alpha power before the experiment showed more effectively entrained oscillations in awareness and brain activity, revealing a correspondence between the experimental effects and spontaneous, as opposed to induced, neural oscillations. We show for the first time that the phase of ongoing alpha oscillations and their effect on visual processing and awareness can be harnessed and controlled.

It may be argued that, because of the use of the annulus as both the entrainer and the mask, the impact of

entrainment on target detection may be due to either changes in target processing, changes in the efficacy of the mask, or both. Indeed, the timing of the mask may also play a role: When the targets in our study were best detected in-phase with the entrainment, their masks consistently followed at 45 msec such that they were always out-of-phase. The observed effects may thus be due to influences on mask processing, target processing, or both. However, a number of other related studies have shown that, even without a mask, detection of a visual target is modulated as a function of alpha phase (Busch & VanRullen, 2010; Busch et al., 2009). The excitability of the visual cortex as measured by the ability of a TMS pulse to induce phosphenes has also been shown to fluctuate as a function of both the ongoing alpha phase (Dugué, Marque, & VanRullen, 2011) as well as sound-induced phase resetting of alpha oscillations (Romei, Gross, & Thut, 2012). Further research manipulating the type of entrainment and the relative timing of the mask and entrainer period is needed to tease apart these possibly complementary effects on fluctuations in awareness.

Alpha Oscillations as a Pulsed Inhibition

Our data extend previous findings of phase-dependent effects of 12-Hz oscillations on visual awareness. We have proposed an account of alpha oscillations as a pulsed inhibition of visual processing (Mathewson et al., 2009; see Mathewson et al., 2011, for a review; see Mazaheri & Jensen, 2010, and Klimesch, Sauseng, & Hanslmayr, 2007, for a related account). Alpha acts as a sensory inhibition mechanism that can reduce the processing of information, but only at particular phases in its cycle. In the opposite phase, processing is relatively intact such that information from the environment can be readily detected. We relate this to the pulsing brake of an automobile that, like alpha's periodic sampling of the environment, intermittently releases the brake to maintain contact with the road. Here the entrainment effects were related to the pre-experiment and pre-trial 12 Hz power, supporting our proposal that this pulsating brake only acts when alpha is of sufficient power (Mathewson et al., 2009). When alpha is high, its phase can be entrained to influence visual processing and awareness.

Recently, Busch and VanRullen (2010) have shown evidence that the attentional spotlight in a continuous attention task is oscillatory. In particular, periodic fluctuations in the enhancing effects of attention appear to depend on the phase of ~7-Hz fronto-central neural activity. Importantly, they show that this effect is strongest at previously cued locations. They argue that this dissociation calls into question a central assertion of our pulsed inhibition model, namely that the phase effects should only be observed when there are high levels of alpha power, because with focused attention alpha should be low. Here we show that this periodicity in perceptual sampling and its susceptibility to entrainment are dependent on the amplitude of an individual's spontaneous brain activity

at the same frequency, showing that the influence of entrained alpha phase on EEG processing indeed has a relation to alpha power.

Entrained Excitability Cycles

Here we show that alpha oscillations can be entrained to analogous rhythmicities in the environment, such that their preferential processing phase can be aligned to relevant and predicted visual events. These data are in accordance with previous behavioral investigations that found increased visual awareness and sensitivity for targets presented in-phase with preceding entrainment (Mathewson et al., 2010) and suggest that alpha entrainment may underlie those effects. Similar effects on evoked neural responses and RTs have been found from intracranial electrodes in monkeys and humans, but at much lower frequencies (1.5 Hz) and dependent on visual attention (Besle et al., 2011; Lakatos et al., 2008). Humans have recently been shown to develop temporal expectancies about auditory sequences that influence the RTs to embedded targets as a function of the phase of the target onset with respect to that of the larger sequence (Stefanics et al., 2010).

In the current article, we demonstrated that entrained excitability cycles can induce oscillations in visual awareness and are dependent on individual's spontaneous alpha power, suggesting that ongoing brain oscillations are being entrained. Other recent work has shown that much higher frequency oscillations (40 Hz) can be controlled by visual entrainment, leading to phase-independent attention increases at the stimulated location, even when observers were unaware of the entrainment (Bauer, Cheadle, Parton, Müller, & Usher, 2009; Elliott & Müller, 1998). Furthermore, repetitive TMS at alpha frequencies (10 Hz) has been shown to induce retinotopic decrements in visual awareness, irrespective of phase, by modulating alpha power (Romei, Gross, & Thut, 2010). Recent work has shown that this rhythmic electrical and magnetic stimulation can entrain ongoing oscillations at the same frequency (Thut et al., 2011) as well as bias visual processing based on the location of entrainment (Romei, Driver, Schyns, & Thut, 2011).

Is anything special about the particular frequency (12 Hz) used in the current study? Whereas some previous work (Bauer et al., 2009; Cardin et al., 2009; Pogosyan, Gaynor, Eusebio, & Brown, 2009; Lakatos et al., 2008; Elliott & Müller, 1998) indicate that other frequencies may be entrained, other studies (Romei et al., 2012; Dugué et al., 2011; Mathewson et al., 2009, 2010; Busch et al., 2009) as well as the current article indicate that "spontaneous" EEG oscillations within the alpha band appear particularly relevant to visual perception and awareness. It is noteworthy that our study does not explicitly manipulate attention conditions, whereas this manipulation was important for those showing effects at other oscillatory frequencies (e.g., Busch & VanRullen, 2010; Stefanics et al.,

2010; Lakatos et al., 2008; but see Haegens et al., 2011). It is possible that, although cortical oscillatory activity may be generally critical for sustaining or controlling information processing, different brain regions and different experimental conditions may utilize oscillations occurring at different frequencies. Within this framework, it is possible that alpha band oscillations may be particularly important for modulating early visual processing and therefore be critical for simple detection tasks, whereas other frequency bands may be important in other areas and for other tasks. Further research is needed to test the specificity of these effects to certain frequencies of visual stimulation.

Temporal Attention

Could the purpose of these entrainable excitability cycles be to provide a mechanism of temporal attention? A cognitive theory has posited the existence of internal oscillators whose pulses of attentional energy can become entrained to rhythmicities in the environment to best process stimuli occurring at predictable times (Mathewson et al., 2010; Jones, Moynihan, MacKenzie, & Puente, 2002; Large & Jones, 1999). This proposal is strongly supported by recent neural recordings in monkeys and humans (Besle et al., 2011; Stefanics et al., 2010; Lakatos et al., 2008). Here we find that temporal expectancies create phase locking in ongoing brain oscillations, allowing for maximal processing of targets occurring at predictable moments in time. The entrainment of internal attention oscillators by rhythmic stimuli may be a mechanism supporting temporal attention in the brain (e.g., Schroeder & Lakatos, 2009) and may explain many common perceptual effects, such as those observed during rapid serial visual presentation sequences in which target detection has been shown to increase as a function of the number of intervening distracters presented around 10 Hz (Ambinder & Lleras, 2009; Ariga & Yokosawa, 2008). A further distinction has been put forward between rhythmic and continuous mode of attention (Schroeder & Lakatos, 2009). Here attention was likely operating in the rhythmic mode given the regularity of the stimuli. This rhythmic attention system seems to be robust to variability in the temporal sequence (Figures 2 and 4; Stefanics et al., 2010). The ability to harness these internal oscillations in attention has the promise of providing important practical applications, for example, in the design of attention-capturing displays (Skelly, Jones, Goodyear, & Roe, 2003).

Waves in the Stream of Consciousness

The fluctuations in awareness that we have observed locked to the timing of rhythmic visual stimuli provide support for a proposal that our perceptual awareness of the visual world is not the continuous unfolding stream that it has long been thought of (James, 1890) but instead consists of discrete snapshots (Busch & VanRullen, 2010; Van Rullen & Koch, 2003; Dehaene, 1993). The data pre-

sented here suggest that these snapshots may be due to oscillations in neural excitability in the alpha band frequency. The pulsed inhibition of ongoing cortical activity represented by alpha oscillations may create these fluctuations in awareness, making waves in the ongoing conscious stream. Here we provide a powerful technique to control these waves of consciousness, indicating that the brain is able to harness these perceptual snapshots of high excitability and optimal processing and align them with external events, a highly adaptive feature given the rhythmicity of our sensory world.

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Note

1. For these and all further correlations, we first tested the assumption of bivariate normality with a Lilliefors test (Lilliefors, 1967). In all cases, the null hypothesis that the observed values came from a normal distribution with a sample estimated mean and variance could not be rejected ($p > .05$ adjusted for multiple comparisons), indicating little departure from normality.

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