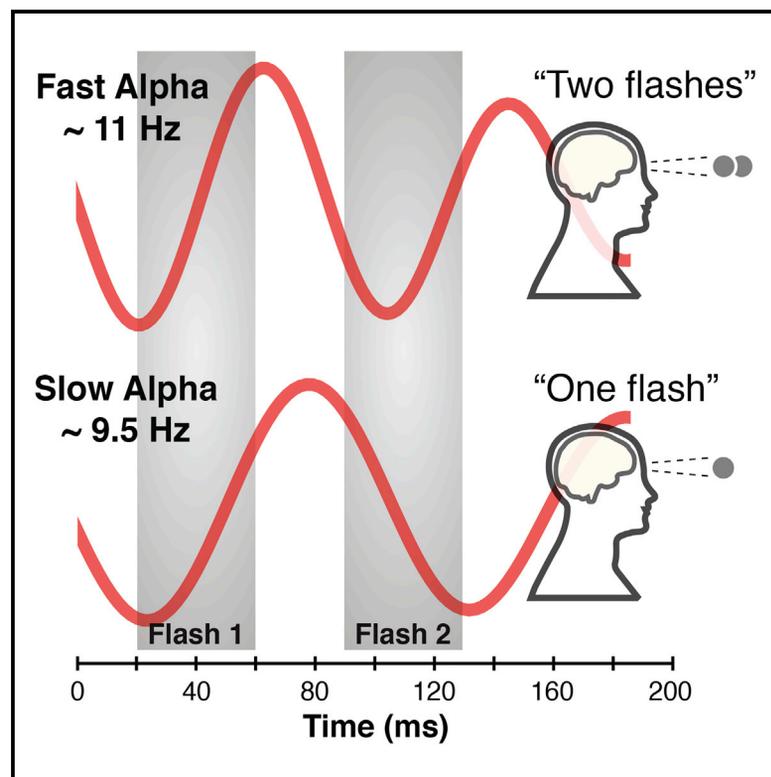# Current Biology

The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception

Graphical Abstract

Authors

Jason Samaha, Bradley R. Postle

Correspondence

jsamaha@wisc.edu

In Brief

Samaha and Postle demonstrate that individuals' temporal resolution of visual perception, as measured by two-flash fusion thresholds, can be predicted by the speed of their occipital alpha rhythm. Both within and between subjects, higher alpha frequencies correspond with a finer-grained resolution of visual processing.

Highlights

- Individuals with higher alpha frequencies have vision with finer temporal resolution

- Eyes-closed and prestimulus peak alpha frequency both show this relationship

- Within an individual, spontaneous fluctuations in alpha frequency predict perception

- Alpha oscillations may dictate the resolution of conscious visual updating

Report

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The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception

Jason Samaha[1,*] and Bradley R. Postle[1,2]
[1]Department of Psychology, University of Wisconsin-Madison, Madison, WI 53703, USA
[2]Department of Psychiatry, University of Wisconsin-Madison, Madison, WI 53703, USA
*Correspondence: jsamaha@wisc.edu
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SUMMARY

Evidence suggests that scalp-recorded occipital alpha-band (8–13 Hz) oscillations reflect phasic information transfer in thalamocortical neurons projecting from lateral geniculate nucleus to visual cortex [1–5]. In animals, the phase of ongoing alpha oscillations has been shown to modulate stimulus discrimination and neuronal spiking [6]. Human research has shown that alpha phase predicts visual perception of near-threshold stimuli [7–11] and subsequent neural activity [12–14] and that the frequency of these oscillations predicts reaction times [15], as well as the maximum temporal interval necessary for perceived simultaneity [16]. These phasic effects have led to the hypothesis that conscious perception occurs in discrete temporal windows, clocked by the frequency of alpha oscillations [17–21]. Under this hypothesis, variation in the frequency of occipital alpha oscillations should predict variation in the temporal resolution of visual perception. Specifically, when two stimuli fall within the same alpha cycle, they may be perceived as a single stimulus, resulting in perception with lower temporal resolution when alpha frequency is lower. We tested this by assessing the relationship between two-flash fusion thresholds (a measure of the temporal resolution of visual perception) and the frequency of eyes-closed and task-related alpha rhythms. We found, both between and within subjects, that faster alpha frequencies predicted more accurate flash discrimination, providing novel evidence linking alpha frequency to the temporal resolution of perception.

RESULTS

The temporal resolution of visual perception was measured as the interstimulus interval (ISI) at which two successively presented, spatially overlapping light flashes could be discriminated from a single flash (Figure 1; see Supplemental Experimental Procedures), known as the two-flash fusion threshold [22]. Individual alpha frequencies (IAFs) were derived from electroencephalographic (EEG) recordings taken before and after (eyes closed) as well as during the perceptual task. Each subject showed a posterior scalp distribution of alpha power during eyes-closed recordings (Figure 2A) as well as a clear peak in alpha-band power (Figure 2B). Two-flash fusion thresholds were estimated from a psychometric function fitted to subject's accuracy in discriminating one from two flashes at each of five "flash-event" durations, ranging from 90 to 130 ms, with ISIs on two-flash trials ranging from 10 to 50 ms, respectively (Figure 2C; see Supplemental Experimental Procedures).

In support of our hypothesis, we found that individuals with higher eyes-closed alpha frequencies showed significantly lower thresholds for two-flash fusion, indicating that they could perceive two flashes at an ISI at which subjects with a lower IAF could perceive only one (Figure 3A). This effect was maximal at occipital electrodes (Figure 3B). To assess the specificity of the effect, we analyzed nearby theta (3–7 Hz) and beta (15–30 Hz) frequency bands at the same electrode. Peaks in these bands did not predict two-flash thresholds (p = 0.21 and 0.71, respectively), suggesting that this effect may be selective to the alpha frequency. To ensure that this result was not an artifact of the thresholds extracted from our psychometric function (i.e., due to potentially poor fits), we also tested this relationship using the proportion correct from the intermediate SOA (30 ms). This, too, yielded a significant correlation (rho = 0.53; p = 0.015), indicating that individuals with higher alpha frequencies were better at discriminating one from two flashes. Further, individual differences in eyes-closed alpha *power* at any electrode did not explain fusion thresholds (all p's > 0.19).

Next, we determined whether two-flash discrimination correlated with alpha frequency during the perceptual task by deriving IAF from the 700 ms of data prior to target onset, excluding any stimulus-evoked responses. Prestimulus IAF was also found to be highly predictive of individual differences in the temporal resolution of visual perception; subjects with higher prestimulus alpha frequency had significantly lower two-flash fusion thresholds (Figure 4A). This relationship also held when the proportion of correct responses at the 30-ms SOA, rather than psychometric thresholds, was used (rho = 0.40; p = 0.044; one-tailed). Again, individual differences in prestimulus alpha power did not predict fusion thresholds (rho = −0.093; p = 0.695).

Because recent work suggests that peak oscillatory frequency can also vary within an individual during visual perception [23], we analyzed time-resolved changes in prestimulus alpha frequency on each trial. We computed the first temporal derivative of the phase angle time series (see Experimental Procedures), which corresponds to the instantaneous frequency of
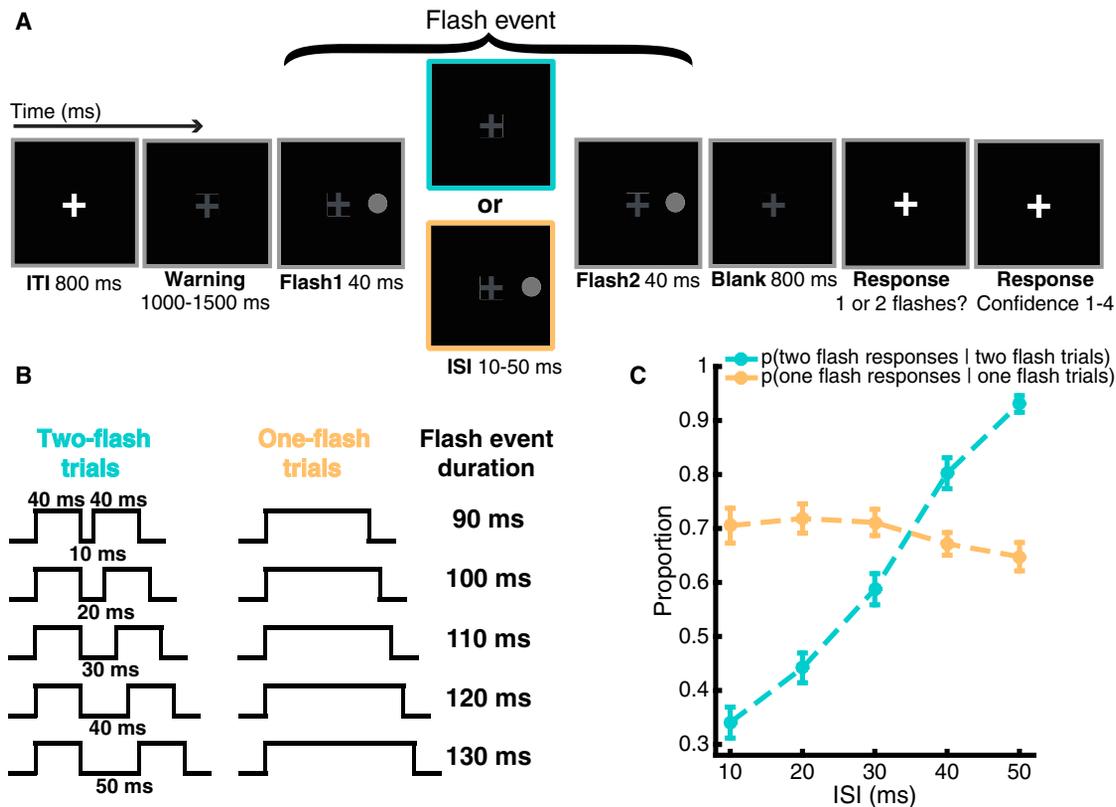
Figure 1. Stimulus Conditions and Behavior

(A) Each trial started with a bright fixation that signaled the start of the trial by dimming. On half of the trials, the "flash event" was composed of two flashes presented either to the left or the right of fixation with equal probability, with each flash separated by an ISI varying from 10 to 50 ms in 10-ms steps. On the other half of trials, only a single flash was presented.

(B) The duration of stimuli in the single-flash condition were varied to match the total duration of both stimuli in the two-flash conditions, so that total target duration did not covary with the number of flashes.

(C) Group-level proportion correct for each condition, showing that accuracy improves as a function of ISI on two-flash trials only. Error bars represent ±1 SEM. Colors are not present on actual display

a signal within a band-limited range [23]. If a higher alpha frequency allows for finer temporal resolution, then prestimulus alpha frequency should be higher prior to correctly as compared with incorrectly discriminated stimuli. The group average across-trial SD of 1.09 Hz confirmed that there was appreciable variation in trial-to-trial alpha frequency, and Figure 4B illustrates that higher prestimulus alpha frequency did, indeed, predict perceptual accuracy (Figure 4B), with this effect persisting until stimulus onset. This suggests that, although IAF is often thought to be a stable neurophysiological trait [24], "peaks" may actually reflect the average of a small range of frequencies, within which subtle spontaneous fluctuations are perceptually relevant [11, 23].

To rule out some confounding individual differences that may explain the correlation between IAF and fusion thresholds, we administered a post-experiment questionnaire aimed at assessing fatigue, food and caffeine intake, basic demographic information, and several other variables (see Supplemental Experimental Procedures). Of these measures, age was weakly, although non-significantly, correlated with eyes-closed IAF ($r = -0.26$; $p = 0.24$) and self-reported fatigue was highly correlated with two-flash fusion thresholds ($r = 0.62$;

$p = 0.003$). These variables did not, however, explain the IAF-threshold correlation; a regression model accounting for age and fatigue revealed a significant effect of IAF on fusion thresholds ($F(1,16) = 11.45$; $p = 0.003$). Further, that we observed a within-subjects effect of alpha frequency on accuracy (Figure 4B) suggests that confounding individual differences are not responsible for the relationship between alpha frequency and perception.

DISCUSSION

Our findings add correlational evidence to the growing body of research suggesting that alpha-band oscillations may neurally instantiate the discrete nature of conscious visual processing [2, 4, 6–11, 13, 16–19, 21]. Importantly, in visual cortex, a causal link between IAF and perceptual integration windows was demonstrated in an experiment that employed transcranial alternating current stimulation at different frequencies within the alpha band [21]. The authors found that stimulation at higher and lower alpha frequencies had the effect of shortening or lengthening, respectively, the temporal window of the sound-induced double-flash illusion. The direction of that
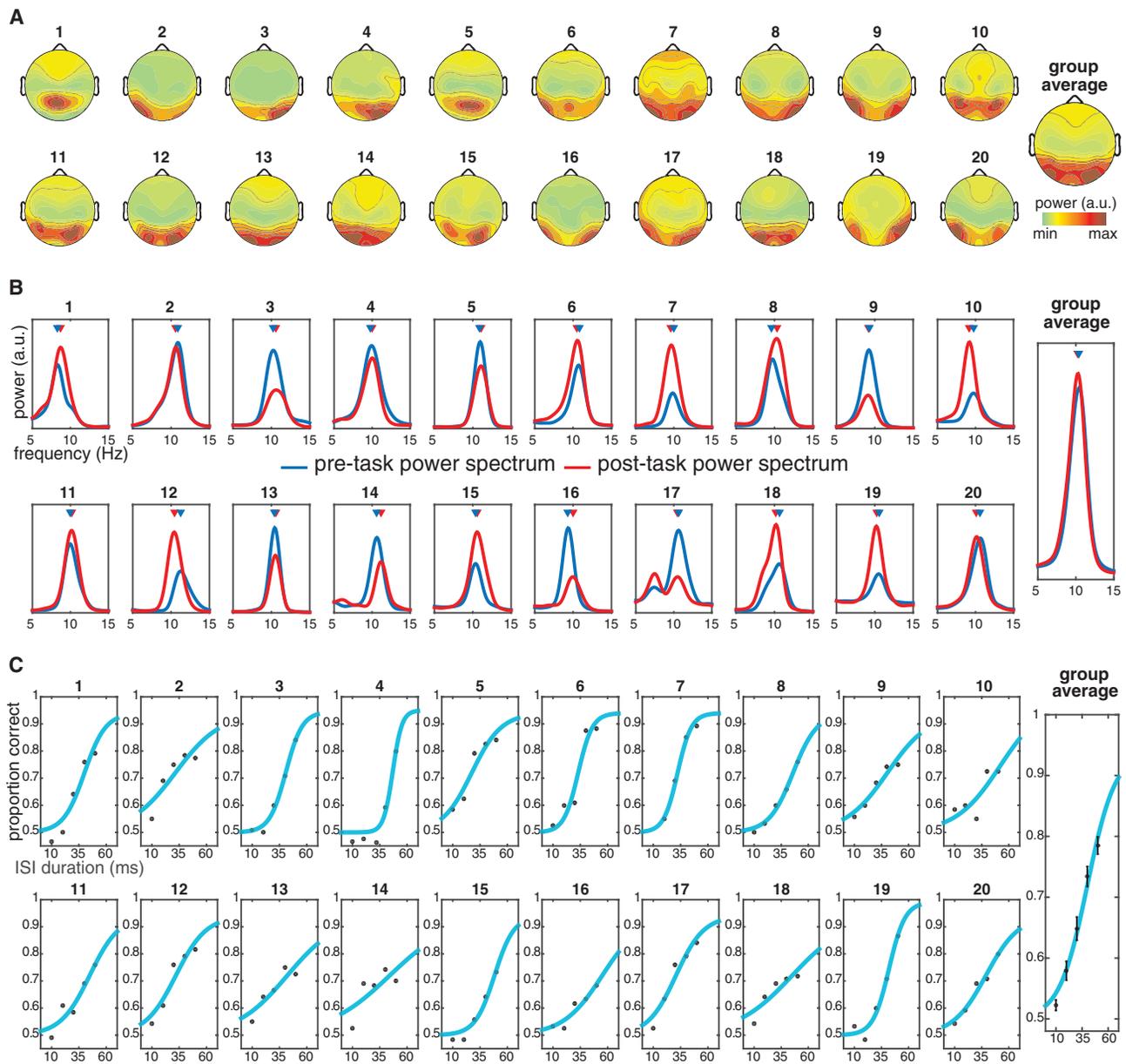
Figure 2. Brain and Behavioral Data from Each Subject

(A) Topography of absolute alpha-band power (8–13 Hz) recorded from 60-channel EEG, averaged over pre- and post-task eyes-closed recordings. Each subject showed a clear occipital scalp distribution.

(B) Eyes-closed power spectrum from pre- and post-task recordings at the electrode where alpha power was maximal at the group level (occipital electrode O2). Individual alpha frequencies (IAF) from each recording (indicated with triangles) were highly correlated ($r = 0.83$) and were averaged to define each subject's IAF.

(C) Psychometric functions relating discrimination accuracy to the interval between flashes. Two-flash fusion thresholds were defined as the ISI corresponding to the mean of the psychometric curve. Error bars are ±1 SEM.

effect is congruent with the direction of our correlations and supports the notion that occipital alpha rhythms reflect cyclic perceptual processes. More generally, this is congruent with recent proposals that many aspects of cognition in addition to perception—including attention, control, and action selection—unfold via the coordination of multiple (and often multiplexed) discrete computations, orchestrated by neural oscillations [25].

What mechanism may account for these findings? In our experiment, an important factor could be whether or not the two stimuli fall within the same cycle of the ongoing alpha oscillation. Using our intermediate SOA of 30 ms and an individual with a period of 110 ms (~9 Hz) as an example, both 40-ms flashes would occur within the same cycle and at near-opposite phases. For an individual with a higher frequency oscillation, however (say, with a period of 85 ms; ~11.5 Hz),
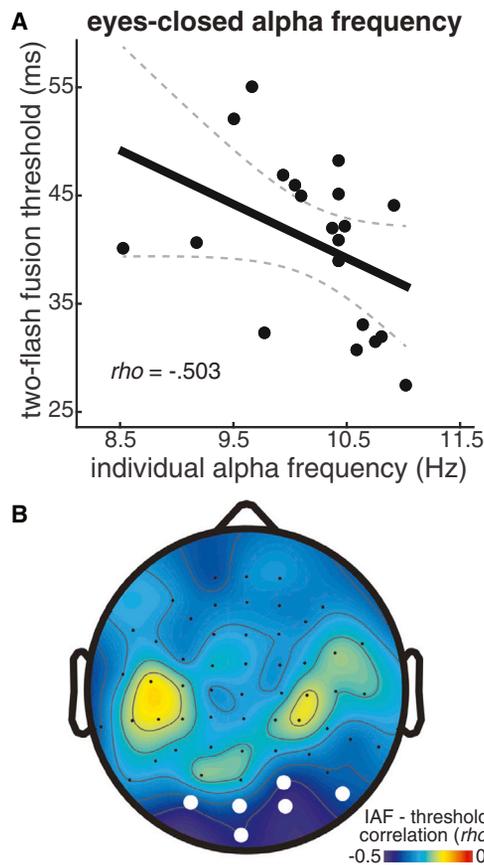
Figure 3. Relationship between Eyes-Closed IAF and Two-Flash Fusion Thresholds

(A) A significant Spearman's correlation between IAF and two-flash fusion thresholds (rho = −0.503; p = 0.023; electrode O2) indicates that individuals with faster alpha oscillations have finer temporal resolution. Dashed lines indicate 95% confidence intervals around the linear fit.

(B) The topography of this correlation was maximal over occipital sensors. White circles denote electrodes with significant rank correlations (p < 0.05; one tailed; cluster corrected).

Figure 4. Between- and Within-Subjects Analysis of Prestimulus Alpha Frequency

(A) IAF derived from alpha activity prior to stimulus onset was also highly correlated with two-flash fusion thresholds (rho = 0.605; p = 0.004), indicating, again, that subjects with higher frequency alpha oscillations perceived two flashes at shorter ISIs.

(B) A within-subjects analysis of the instantaneous alpha frequency prior to stimulus onset reveals significantly higher alpha frequency preceding correctly discriminated trials. Significant time points are indicated with black squares (p < 0.05; permutation test; cluster corrected). Shaded regions denote ± within-subjects SEM.

presentation of the second flash stimulus would partially overlap with a different alpha cycle, perhaps allowing for above chance discrimination. On this account, when two stimuli fall within the same alpha cycle, they are more likely perceived as one. In this manner, subtle fluctuations in the frequency of alpha may bias perception, on average (Figure 4B), by modulating the proportion of overlap the second flash has with the next cycle.

What happens when two stimuli are perceived as one? We can think of at least two possibilities. The first is that stimuli occurring within the same cycle could be fused or bound together into a single percept that incorporates features of both stimuli. An alternative explanation, consistent with prior findings demonstrating perceptual modulation within a single alpha cycle [6–11], is that because, on near- and below-threshold trials, each flash occurs during near-opposite phase angles, one flash may be processed suboptimally by the visual system and simply missed. Because both flash stimuli were identical in our experiment, we cannot adjudicate between
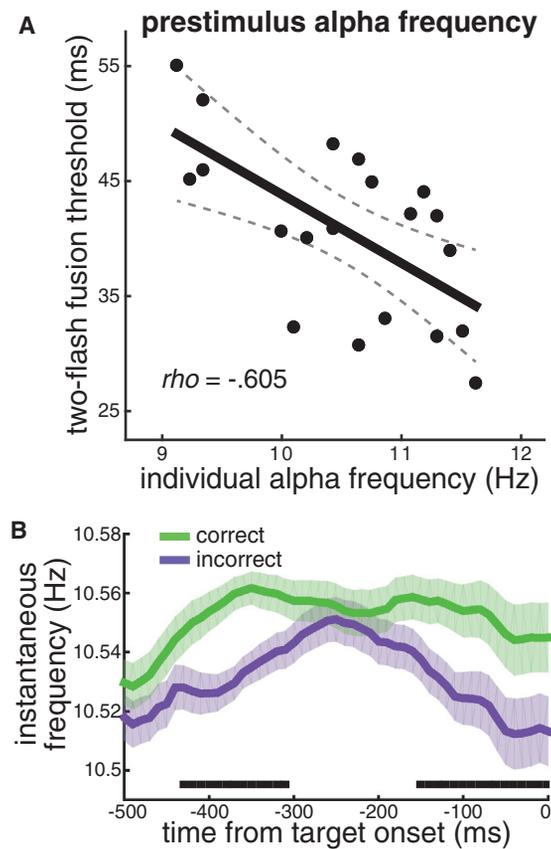
these mechanisms. Future research using two different stimuli (gratings of a different orientation, for example) could reveal whether stimuli occurring within the same alpha cycle are fused (a grid) or whether one is simply not perceived (a single orientation).

Our results demonstrate that higher frequency alpha rhythms are associated with finer temporal resolution in visual perception. IAF was highly correlated across recordings within the same individual, but small fluctuations in prestimulus alpha frequency predicted perceptual accuracy. Although this effect was small, it is consistent with prior results demonstrating significant alpha frequency modulations of ∼0.04 Hz [23] and may result from the fact that EEG averages alpha frequency from task-varying and task-invariant neural populations, making task-varying effects appear smaller. These results support the notion that the occipital alpha rhythm may dictate the resolution at which visual information can be consciously sampled.

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EXPERIMENTAL PROCEDURES

Subjects

Twenty-three subjects (11 female; age range: 19–33 years) from the University of Wisconsin-Madison community participated in the experiment for monetary compensation. All subjects provided written consent and reported normal or corrected-to-normal visual acuity and color vision. The University of Wisconsin-Madison Institutional Review Board approved the study. Three subjects were excluded from analysis because psychometric function fits failed due to near-chance performance at all ISIs.

EEG Recording and Analysis

EEG was recorded from 60 Ag/AgCl electrodes with electrode positions conforming to the international 10-20 system and a subset of intermediate 10% positions. Recordings were made using a forehead reference electrode and were re-referenced to the average of all 60 electrodes offline. EEG was amplified by an Eximia 60-channel amplifier (Nextim) with a sampling rate of 1,450 Hz. Data were down sampled to 250 Hz offline using the EEGLAB toolbox [26] in MATLAB.

Eyes-closed recordings were taken just prior to, and after, the perceptual task. Subjects were asked to close their eyes and sit still for 2 min. The continuous recordings were cut into non-overlapping, 1-s epochs that were visually screened for eye and muscle artifacts and for electrodes with poor contact. An average of 2.9% of electrodes were spherically interpolated and an average of two epochs were rejected, leaving approximately 238 epochs of eyes-closed data per subject. Data epochs were then linearly detrended, multiplied by a Hamming window, zero padded and fast Fourier transformed (frequency resolution: 0.1086 Hz), and converted to power (μV^2). IAF was defined as the local maximum within the frequency range 8–13 Hz. Each subject showed a clear peak within this range at all electrodes.

Task EEG data were epoched from −700 to 0 ms relative to target onset, prior to any filtering, so that stimulus-evoked responses were not included. These epochs were also visually inspected for muscle and eye artifacts (average of 31 trials removed) and were transformed into power spectra following the same procedure described above. Peaks in the alpha band were not present at all electrodes during the eyes-open task data (i.e., no local maxima between 8 and 13 Hz), and no single electrode contained a peak for every subject. For this reason, we chose the electrode where 8–13 Hz power was maximal for each subject to identify IAF. This routine identified the following subject-specific occipital and parietal sensors that were then used to identify prestimulus IAF for each subject, respectively (Figure 3A): POz; O1; O2; O2; POz; P9; POz; P7; O1; PO4; O1; Oz; O1; O1; P9; P9; Oz; POz; P10; and O2.

Prestimulus instantaneous frequency was analyzed using methods and code developed by Cohen [23]. First, data from the electrode showing greatest alpha power at the group level, electrode O2, were epoched from −700 to 0 ms relative to target onset. Then, epochs were reflected about 0 ms; that is, data from each trial were copied and flipped from left to right and appended to the right side of the original data. This was done to avoid edge artifacts at target onset due to filtering. Epochs were then filtered between 8 and 13 Hz with a zero-phase, plateau-shaped, band-pass filter with 15% transition zones (Matlab function *filtfilt.m*). Phase angle time series were extracted from the filtered data with a Hilbert transform. The temporal derivative of the phase angle time series describes how phase changes over time and thus corresponds to the instantaneous frequency in Hz (when scaled by the sampling rate and 2π). Noise in the phase angle time series can cause sharp, non-physiological responses in the derivative, so the instantaneous frequency was filtered with a median filter using the parameters suggested by Cohen [23]; data were median filtered ten times with ten windows ranging from 10 to 400 ms prior to averaging across trials. Because this analysis considers changes only in the instantaneous phase of the data, it is mathematically independent from the power of the oscillation, except where power is equal to zero and phase is undefined.

Statistical Analysis

Unless otherwise noted, correlations were assessed using a two-tailed Spearman's rank coefficient, which tests for monotonic relationships and is less sensitive to outliers than a Pearson's correlation. Permutation-based cluster correction was applied when multiple electrodes (Figure 2B) or multiple time points (Figure 3B) were tested. First, randomly shuffled data were tested 5,000 times; each time the largest spatial or temporal cluster was saved into a distribution of cluster sizes expected under the null hypothesis. Only significant clusters in the real data that exceeded the size of the 95th percentile of the null distribution of clusters were considered statistically significant at $\alpha = 0.05$.

See Supplemental Experimental Procedures for details on the psychophysical task, psychometric function fitting, and post-experiment questionnaire.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.10.007.

AUTHOR CONTRIBUTIONS

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