

Perceptual Echoes at 10 Hz in the Human Brain

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Summary

The occipital alpha rhythm (~10 Hz) is the most prominent electrophysiological activity in the awake human brain [1], yet its functional role [2–4] and relation to visual perception [5] are little understood. Transient stimuli normally elicit a short series of positive and negative deflections lasting between 300 and 500 ms [6–8]: the visual-evoked potential (VEP). Alpha oscillations, on the other hand, are generally suppressed by transient visual input [1, 8]; they only augment in response to periodic (“steady-state”) inputs around 10 Hz [9, 10]. Here, we applied reverse-correlation techniques to the visual presentation of random, nonperiodic dynamic stimulation sequences and found that the brain response to each stimulus transient was not merely a short-lived VEP but also included a strong ~10 Hz oscillation that lasted for more than 1 s. In other words, the alpha rhythm implements an “echo” or reverberation of the input sequence. These echoes are correlated in magnitude and frequency with the observer’s occipital alpha rhythm, are enhanced by visual attention, and can be rendered perceptually apparent in the form of ~10 Hz flicker. These findings suggest a role for the alpha rhythm in the maintenance of sensory representations over time.

Results

Echo Functions

To investigate the response properties of human visual cortex, we recorded 64 channel electroencephalogram (EEG) while observers ($n = 8$) viewed dynamic sequences (6.25 s duration) randomly modulated in luminance (Figure 1). The cross-correlation between the stimulus luminance sequence on each trial and the corresponding EEG was computed to reveal the average brain response to a unit luminance increment (following an approach introduced by Lalor and colleagues [11]). As expected, the early part of this response resembled a classic VEP [6, 7]; to our surprise, however, the cross-correlation functions also presented a high-amplitude oscillation at approximately 10 Hz, which persisted at delays well above 600 ms for all observers and even beyond 1 s for some of them (Figures 2A and 2D). This oscillation was visible as a strong peak around 10 Hz in the amplitude spectrum of the cross-correlation (Figures 2B and 2C). The oscillation differed in phase and peak frequency across subjects but was stable and reproducible for each subject, even at testing intervals

above 6 months (see Figure S1A available online). Topographical mapping of the ~10 Hz amplitude in the cross-correlation functions showed that the oscillation occurred principally over occipital electrodes (Figure 2E). Of course, the occipital EEG spectrum is itself dominated by a peak around 10 Hz (Figure 1, left), which raises the potential concern that the ~10 Hz oscillation in cross-correlations could have arisen as an artifactual consequence of basic EEG properties. If this were the case, however, the oscillation would be present regardless of the precise stimulus sequence used for computing the cross-correlation. Contrary to this hypothesis, we found that the oscillation vanished when the EEG recorded on a given trial was correlated with the stimulus sequence presented on a different one (Figure 2). In other words, the oscillation represents a genuine brain response to the specific visual input sequence presented in each trial. The existence of significant correlations between visual stimuli and subsequent EEG responses at delays of up to 1 s, waxing and waning at ten cycles per s or so, indicates that the visual system “echoes” or “reverberates” the stimulus sequence at this frequency. Therefore, in the remainder of the manuscript, we refer to these oscillatory cross-correlation functions as “echo functions.”

How do these echo functions relate to classic VEPs? Though both responses are triggered by visual stimulation, and must therefore share neuronal substrates in visual cortex, we also found clear evidence for a dissociation: when we contrasted cross-correlation functions obtained from peripheral versus foveal stimulation, the VEP-like response during the early part of the cross-correlation function changed drastically, both in terms of its temporal profile and its scalp topography, whereas the later and longer-lasting echo function remained essentially unchanged (Figure S1C).

The notion of an “echo” suggests that every stimulus event is reverberated in the EEG response. However, because the cross-correlation function is the average response to all stimulus events, it could be argued that the oscillatory responses we measured were only evoked by a few particularly intense events during the stimulation sequence. Contrary to this interpretation, however, we found that the 10 Hz reverberations persisted when the cross-correlation was computed after discarding the 20%, or even the 50% most extreme luminance values in the random stimulation sequence (Figure S1B). It should also be noted that in all analyses, the first 0.5 s of each EEG epoch and each stimulus sequence was excluded from the cross-correlation; therefore, echo functions cannot have been generated by any initial EEG response to stimulus sequence onset.

Relation to Spontaneous Alpha Rhythms

The frequency of maximal amplitude in the echo functions differed between subjects (Figure 2B) but remained in the range of 8–12 Hz. Because this is also the frequency range of the occipital alpha rhythm [1], we sought to compare the two oscillations on a subject-by-subject basis. For each of ten observers, we obtained echo functions and contrasted them with the alpha rhythm recorded during periods of rest with eyes closed. The two oscillations were strongly correlated

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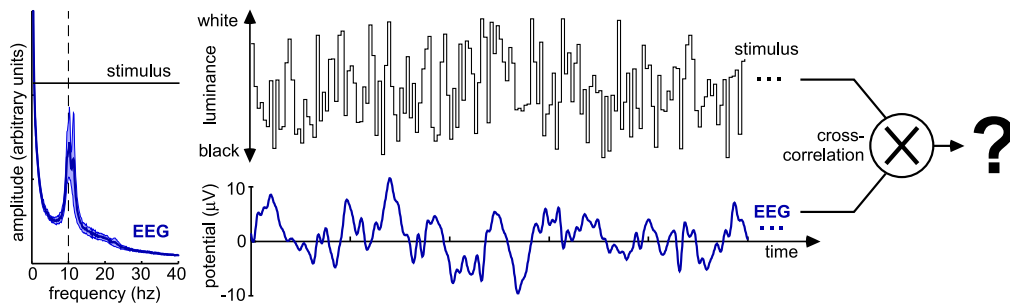


Figure 1. Illustration of the Paradigm

A random sequence of luminance values (black line, top right) was displayed at a rate of 160 frames per second within a peripheral disc stimulus above the fixation point. The sequence was designed to have equal power at all temporal frequencies (black line, left). To keep observers alert, we instructed them to monitor the sequence for the appearance of a target square inside the disc (25% probability). EEG was recorded simultaneously (blue line, bottom right). The power spectrum of the EEG during stimulus presentation (averaged over eight observers) is also shown on the left (blue line, shaded area represents SEM). The cross-correlation between the stimulus and EEG sequences recorded on each trial provides an estimation of the brain's average response function to each unit increment of stimulus luminance. It is computed by moving the visual input function point-by-point along the EEG response and multiplying the two signals (see [Experimental Procedures](#)), thereby identifying the lags where input and output are related (i.e., signal) or not (i.e., noise).

both in magnitude (Figure 3B, $r = 0.674$, $p < 0.05$) and frequency (Figure 3A, $r = 0.81$, $p < 0.005$). In fact, the peak frequency of the echo function for each observer was nearly identical to that observer's alpha frequency (the slope of the linear regression line was 1.13). Thus, echo functions are intimately linked to occipital alpha rhythms.

Because the EEG response to a random input sequence appears to be governed by a ~ 10 Hz oscillation, it is natural

to ask whether stimulus components at frequencies other than 10 Hz are processed to the same extent. To test this idea, we presented observers ($n = 5$) with full-spectrum random sequences (i.e., containing equal power at all temporal frequencies), as previously, or (in alternate trials) with a band-stop filtered sequence in which there were no stimulus fluctuations between 8 and 12 Hz (Figure 3C). In both cases, the raw EEG amplitude spectrum displayed a characteristic shape

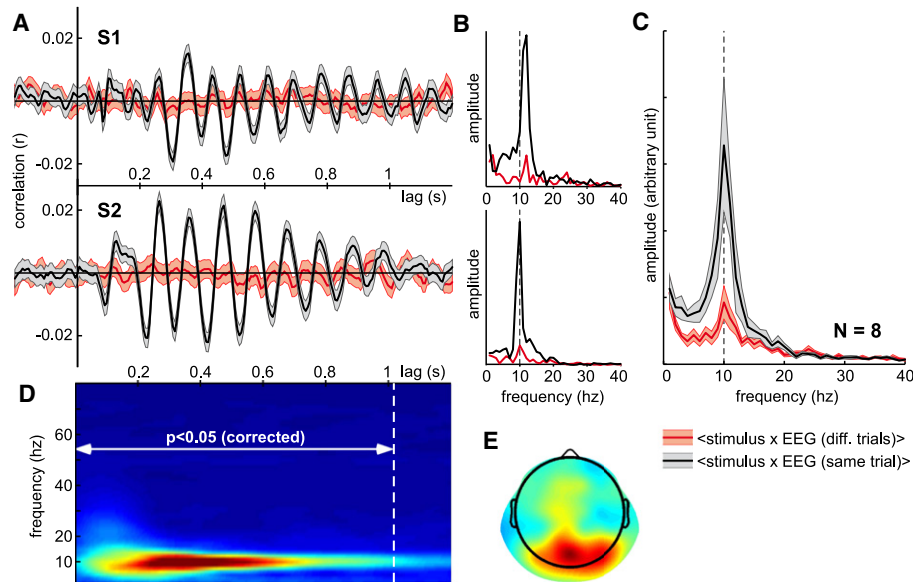


Figure 2. Echo Functions

(A) Two individual examples of response functions obtained by cross-correlating the stimulus and corresponding EEG sequences (averaged over trials for each subject, shaded areas represent SEM across trials). Corresponding surrogate functions obtained by cross-correlating stimulus and EEG sequences recorded on different trials are also represented in red. The presence of a long-lasting oscillation in the actual but not surrogate functions indicates that the oscillation is a direct consequence (an “echo”) of the visual input.

(B) Amplitude spectra of the surrogate (red) and actual (black) “echo” functions for the two observers.

(C) Amplitude spectra averaged over eight observers. The echo function is characterized by a strong peak around 10 Hz.

(D) Average duration of echo functions. Time-frequency representation of the echo function ($n = 13$, also including participants to the experiment described in Figure 4B). Direct comparison of the 10 Hz amplitude at each delay between the echo function and its surrogate (paired t test, false discovery rate-corrected for multiple comparisons, $p < 0.05$) reveals that echoes remain significant up to a delay of more than 1 s (white arrow).

(E) Scalp topography (color scale represents area under the 10 Hz envelope of the echo function) reveals that the 10 Hz echoes take place mainly in occipital electrodes.

See also [Figure S1](#).

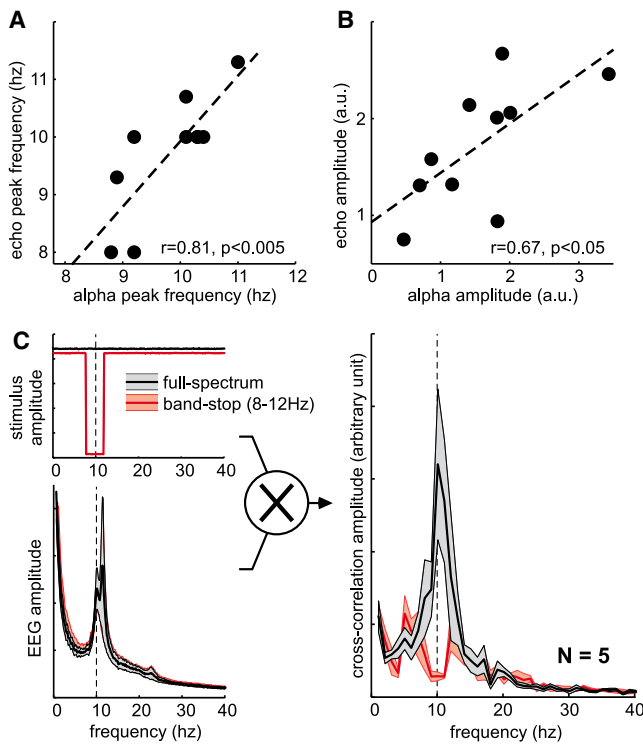


Figure 3. Echo Functions Relate to Alpha Rhythms

(A and B) Correlations (across participants, $n = 10$) between individual echo functions and alpha rhythms (measured during periods of rest with eyes closed) in terms of peak frequency (A) and peak amplitude (B). (C) On separate (randomly interleaved) trials, random luminance sequences were displayed with either a full temporal spectrum (black lines) or a spectrum with zero power in the 8–12 Hz range (red lines). The EEG recorded (average of five observers) during these two trial types had virtually identical amplitude spectra, both with a peak at alpha frequencies (~ 10 Hz). However, the cross-correlation between stimulus and EEG sequences only revealed a 10 Hz echo for the full-spectrum stimuli (right). Thus, the visual system must selectively reverberate the ~ 10 Hz components of the stimulus.

with a peak around 10 Hz. However, only the full-spectrum sequences gave rise to a 10 Hz echo function (Figure 3C). This implies that the visual system selectively reverberates the ~ 10 Hz components of the input stimulation—when these components are absent, no reverberation occurs.

Perceptual Correlates

Do observers perceptually experience the reverberation, or is it an internal process essentially irrelevant to subjective perception? We instructed two observers to watch random full-spectrum dynamic sequences (62.5 s duration) and report any subjective impression of regular flicker by moving a joystick in proportion with the experienced flicker intensity. By cross-correlating their responses with changes in the oscillatory amplitude of the stimulus over time at each frequency, we found that the intensity of reported flicker at any given time depended most strongly on the 8–15 Hz amplitude of the stimulus displayed approximately 0.5 to 1 s before (Figure 4A). Because this frequency range contains the stimulus component frequencies that are most effective at inducing echo functions (see Figure 3C), we conclude that echo functions are accompanied by a subjective impression of flicker (this conclusion is also consistent with most observers' verbal reports following the experiments).

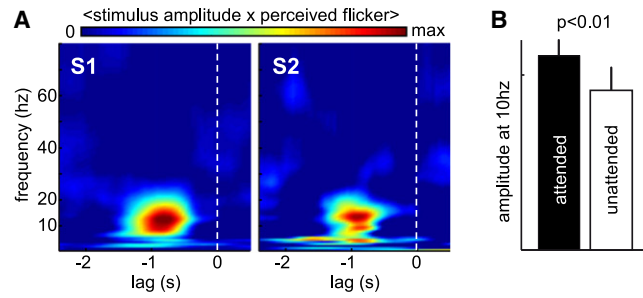


Figure 4. Perceptual and Attentional Effects

(A) Two observers were asked to watch random luminance sequences (full-spectrum, 62.5 s duration) and report any experience of regular flicker by moving a joystick along one axis according to the perceived flicker intensity. By cross-correlating the band-pass filtered stimulus sequence with the sequence of reported flicker, we isolated the components of the stimulus that tended to cause a subsequent perception of regular flicker. For both observers, flicker perception tended to be preceded by an increase of 8–15 Hz stimulus amplitude, compatible with the notion that the perceptual effects of the ~ 10 Hz echo functions include a subjective impression of flicker.

(B) Observers ($n = 10$) watched two independent random luminance sequences simultaneously on the left and right of fixation, paying covert attention to one of the sequences that had been previously indicated by a cue. The direction of the cue was randomly varied on different trials. Echo functions were computed separately for both sequences. Although the response to both attended and unattended stimulus sequences included a ~ 10 Hz oscillation, the echo was 22% stronger for the attended stimulus (paired t test, $p < 0.01$; error bars denote SEM). See also Figure S2.

Effects of Attention

Finally, we explored the effects of attention on echo functions. Observers ($n = 10$) fixated the center of the screen while two independent random sequences (full-spectrum) were displayed simultaneously in separate discs on the left and right of fixation. A cue (100% validity) at the beginning of each block of trials indicated to the observer which side was relevant for a target-detection task. We computed the cross-correlation of the EEG separately with the attended and unattended luminance sequences on each trial. Both stimuli gave rise to an echo function around 10 Hz (Figure 4B), but the amplitude of the oscillation was 22% greater for the attended stimulus (paired t test, $t[9] = 2.93$, $p = 0.008$). The enhancement of the echo function with attention is intriguing, because alpha rhythms generally tend to decrease under the effect of attention [12–15], as verified also in our EEG data (see Figure S2). Hence, although echo functions are related to alpha rhythms, as noted previously, they also appear to possess distinct functional properties (Figure S2).

Discussion

A recent upsurge of studies have revealed that the amplitude [14–19] and phase [20] of ongoing, spontaneous alpha oscillations in the last few hundred milliseconds before a stimulus is presented can have drastic consequences for the subsequent perception of this stimulus. In contrast to these studies concerned with prestimulus baseline oscillations, we focused here on the impact of visual stimulus processing on the ensuing alpha rhythm. Numerous experiments have shown that the amplitude of the alpha rhythm is strongly but negatively affected by visual stimulation [1, 8] and by increasing attention [14, 21] or task demands [22, 23]. These negative changes of alpha amplitude are induced by the sensory

stimulation but generally not phase-locked to it, which is why they are not readily visible in standard VEP analyses [8]. Under certain conditions, however, alpha can also be positively related to perception: when using recurrent or periodic visual stimulations, the so-called “steady-state” brain response is strongest for stimuli that recur about ten times per s [9, 10]. This is also the stimulation frequency that generates the most vivid subjective sensation [24], sometimes even accompanied by epileptic seizures [25] or visual hallucinations [26–28]. To summarize, the existing literature suggests that alpha rhythms should provide their main contribution to EEG responses when the visual input sequence is periodic. On the other hand, EEG responses to nonperiodic visual sequences should be well described by a noisy superposition of short-lived VEPs, one for each stimulus transient [11, 29]. Contrary to this standard view, we have demonstrated an extended and alpha-frequency-specific EEG response to a nonperiodic stimulation sequence. This 1 s long echo function suggests that luminance changes in our random visual stimulus affect occipital brain activity for 1 s or more—much longer than previously thought [6, 7]. Equivalently, because correlation is a symmetrical operation, our results also imply that at any given moment, the electrical activity in visual cortex is affected by the history of external events that occurred up to 1 s earlier. Furthermore, echoes are not comparable for all stimulus frequency components, but selectively reverberate the 10 Hz fluctuations. From a signal-processing point of view, they are thus akin to a ~10 Hz band-pass filter, with a 1 s long support window. Hence, alpha oscillations are the visual system’s naturally preferred method of processing dynamic, broadband visual input, via the implementation of a series of “echoes” of the input sequence. It is important to keep in mind that under ecological viewing conditions, such as during the performance of exploratory eye movements, the visual environment varies with a broad temporal frequency spectrum that also contains a 10 Hz component. Therefore, this 10 Hz reverberation, demonstrated here with artificial and random stimulus sequences, should also be pertinent to natural vision.

One could ask why 10 Hz echoes are not usually observed in classic VEP studies. First, it is conceivable that they might be present to some extent but remain unnoticed because grand-average event-related potentials (ERPs) cancel out oscillations that are not phase-locked across subjects—and because ERP guidelines encourage authors to reject trials with significant alpha activity [30]. When advanced analysis techniques are employed to select and isolate alpha sources, 10 Hz oscillations can in fact be observed in the VEP—a phenomenon called “alpha ringing” [5, 31]. Second, it is also likely that the random dynamic stimulus used in our paradigm is optimal for revealing these echoes: by constantly flickering at multiple frequencies, it constrains the response of the visual system over time—much more than a single flash followed by a static screen, during which brain activity would be left free to vary considerably.

What is the neural mechanism at the origin of the 10 Hz perceptual echoes? Although our EEG data cannot directly answer this question, our findings are reminiscent of a body of physiological studies dating back to the middle of the 20th century. Early recordings in sensory pathways revealed that the normal response to a unitary event often included repetitive “afterdischarges” at a rate of approximately 10 Hz [32–34]. Furthermore, short trains of stimulation induced enhanced activity when the stimulus reoccurred around ten times per s,

a phenomenon coined “augmenting responses” [35, 36]. These frequency-specific responses were initially linked to thalamocortical reverberation [37], although it later became apparent that they also depend on intrinsic properties of both thalamic and cortical circuits [38–42]. In this context, an augmentation of thalamic and/or cortical responses specific to the 10 Hz components of the stimulus sequence would logically result in perceptual echoes similar to the ones we observed.

Finally, what could be the functional relevance of these 10 Hz perceptual echoes? Because they allow the visual system to retain sensory information for extended periods of time (up to 1 s), one obvious possibility could be that they assist the brain in forming an immediate sensory or “iconic” memory. Seventeen years ago, Francis Crick postulated [43] that thalamocortical reverberation could implement a form of iconic memory. Here we showed that this reverberation may have a signature in the 10 Hz frequency range. Overall, our results point to a potential functional role for the enigmatic alpha rhythms: that of maintaining sensory representations over time.

Experimental Procedures

Except where stated otherwise, all experiments involved random visual sequences (6.25 s duration) displayed within a peripheral disc stimulus (3.5 degrees radius at 7.5 degrees eccentricity) on a black background. The screen refresh rate of 160 Hz allowed us to present temporal frequencies ranging between 0 and 80 Hz. Each randomly generated sequence was tailored to have equal power at all frequencies, by normalizing the amplitudes of its Fourier components before applying an inverse Fourier transform. Sequences ranged from black (0.1 cd/m²) to white (59 cd/m²). Observers covertly monitored the stimulus to detect a 1 s long target square (3.75 degrees) appearing inside the disc on a random 25% of trials. The target onset occurred at a random time (uniform distribution, excluding the first and last 0.25 s) within the sequence. The area within the square followed the same sequence of luminance changes as the disc stimulus, but scaled in amplitude (using a staircase procedure) so that detection performance was fixed at approximately 82%. Observers were instructed to press a button at the end of the sequence if they had detected the target. Both target-present and target-absent trials were included in the cross-correlation analysis (but we also verified that our main results were consistent in both conditions). In one variant of the experiment (Figure 4B), two independent random sequences were presented on the left and right of fixation; observers were cued to monitor targets appearing in one of the sequences (varied across trials) and ignore the other. In another variant of the experiment (Figure S1C), the luminance sequence was presented at fixation on some trials and in the periphery on others, so as to determine the influence of retinal eccentricity.

EEG was recorded continuously using a 64 channel ActiveTwo Biosemi system. Horizontal and vertical electrooculograms were recorded by three additional electrodes around the subjects’ eyes. The EEG was down-sampled to 160 Hz before cross-correlation with the stimulus sequences. All stimulus time points except the first 0.5 s and the last 1.5 s of the sequence were entered in the cross-correlation, which was computed at all lags between –0.2 and 1.5 s. (Similar results were obtained with correlations computed over only the first or the second half of the stimulus). The cross-correlation procedure was aimed at calculating the “impulse response function” (IRF) of the EEG as follows:

$$IRF(t) = \sum_T stim(T) \cdot eeg(T+t)$$

where *stim* and *eeg* denote the standardized stimulus sequence and the corresponding standardized EEG response, respectively.

The amplitude spectra of the cross-correlation functions were computed using a fast Fourier transform on the delays between 0.2 and 1.2 s. The amplitude spectra of the EEG (see Figures 1 and 3C) were obtained by fast Fourier transform of entire EEG epochs. In addition, for some subjects, EEG was also recorded during periods of rest with eyes closed (1–2 min), and the peak frequency and amplitude of the individual alpha rhythm were determined using a fast Fourier transform (see Figures 3A and 3B).

Overall, 13 observers (including the two authors), with normal or corrected-to-normal vision, participated in the various experiments. The

number of participants for each experiment is indicated in the main text. All experiments were performed with approval of the local ethical committee.

Supplemental Information

Supplemental Information includes two figures and can be found with this article online at doi:10.1016/j.cub.2012.03.050.

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Supplemental Information

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Supplemental Inventory

Supplemental Figures

Figure S1, related to Figure 2

Figure S2, related to Figure 4

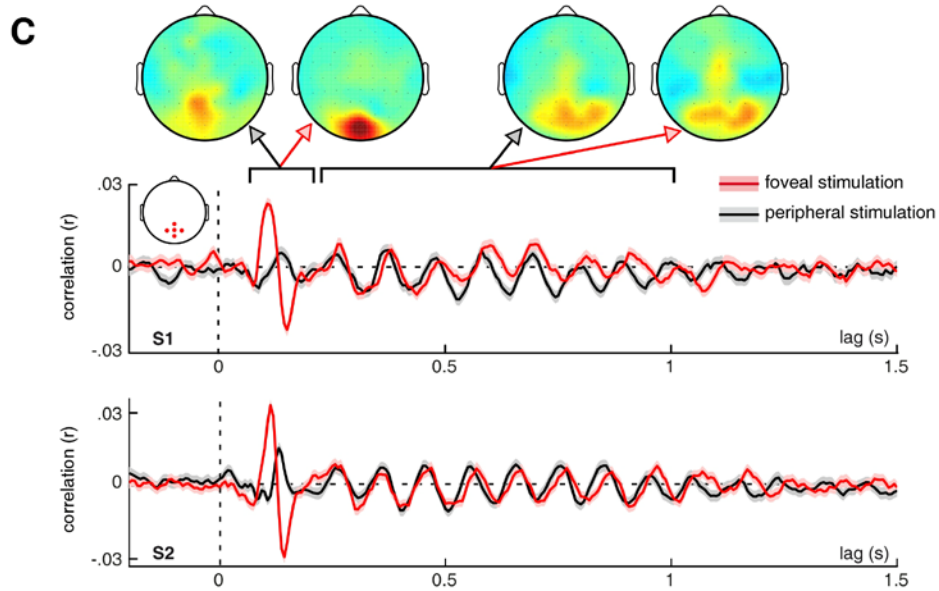
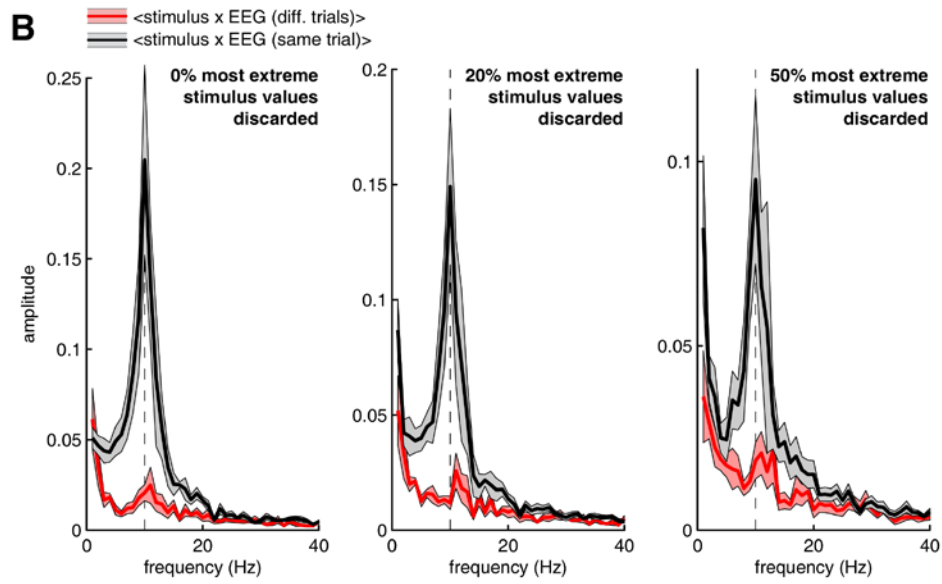
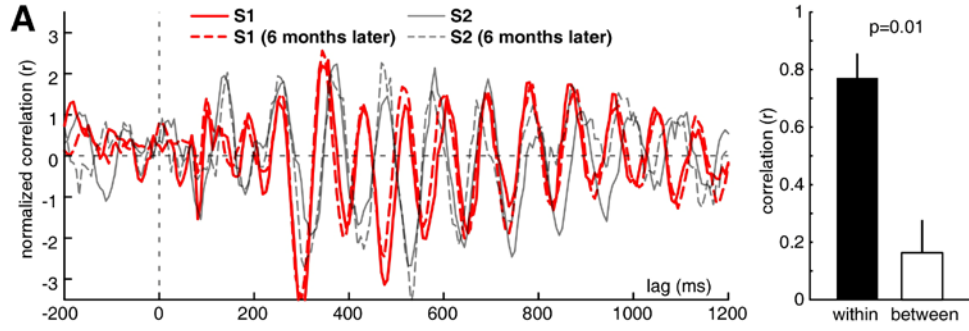


Figure S1. Further Properties of Echo Functions, Related to Figure 2

(A) Test/re-test at 6 months intervals. Left: Two echo functions measured at 6-months intervals (different random luminance sequences were used for the test and re-test). Red lines correspond to individual functions from one observer, blue lines from another one. The overlap between functions obtained from a single observer is stronger than between the two observers. Right: Average (N=3) correlations across delays (200ms to 1200ms) of the echo functions measured at 6-months intervals for the same participants ("within") and for different participants ("between").

(B) Echo functions are not merely a response to extreme stimulus values. To verify that the measured reverberations were not a byproduct of a phase-reset or oscillatory response that would be evoked only by a few, stronger-than-average stimulus events, we recomputed cross-correlations after having removed various proportions of the most extreme stimulus values (0%, 20% or 50%, from left to right). The plots represent the amplitude spectra (measured at delays between 200 and 1200ms) of echo functions (black) or their corresponding surrogate (red). Apart from a change of scale (expected because of the decreasing variability in stimulus values), removing the most extreme values clearly did not result in a disappearance of the echo functions –as would have been expected based on the alternative interpretation. NB: the same conclusion was obtained when various proportions of the largest stimulus transients (i.e. luminance increments or decrements) were discarded from the cross-correlation analysis (not shown).

(C) Separable effects of retinal eccentricity on VEP vs. echo functions. The random luminance sequence was presented either 7.5 degrees above fixation (black lines, same experimental condition as that depicted in Figure 2 of the main text) or centered at fixation (red lines). Though retinal eccentricity greatly affected the shape and topography of the VEP (measured during the early part of the cross-correlation functions, i.e. [0-200ms]; scalp maps shown on top-left), it left the longer-lasting echo functions mostly unaffected, both in terms of temporal profile and scalp topography (top-right scalp maps).

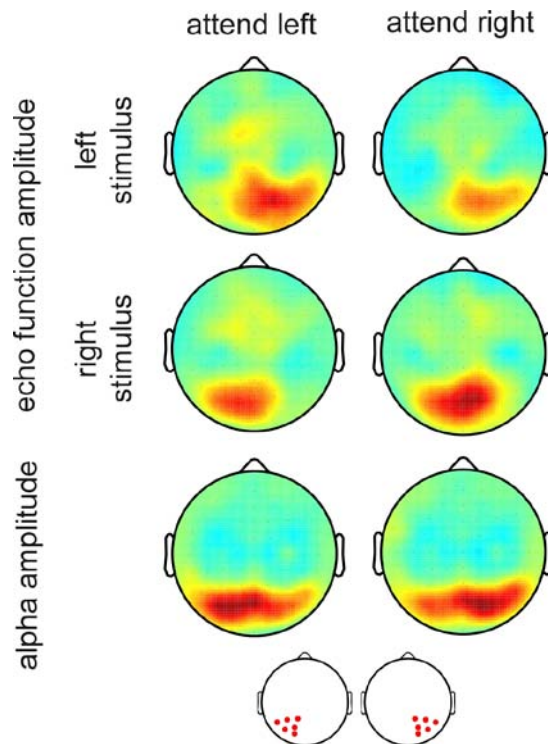


Figure S2. Separable Effects of Attention on Echo Functions vs. Alpha Amplitude, Related to Figure 4

Echo function amplitude was computed (for 10 observers) as the integral of the envelope of the 8-12Hz oscillation in the echo function over delays ranging from 200 to 1200ms. Alpha amplitude was computed as the EEG Fourier amplitude between 8-12Hz over the entire course of each trial. Regions of interest were defined for electrodes in the left and right hemisphere (see insets at bottom). A 2-way ANOVA on echo function amplitude (with factors: attend left/right X left/right hemisphere; the echo is considered here only in response to the contralateral stimulus sequence) revealed no main effect of attention location or hemisphere, but a significant interaction between the two factors ($F(1, 9) = 18.31$, $p = .002$, $p. \eta^2 = .67$). Pairwise comparisons revealed that echo amplitude was significantly greater over the right hemisphere in the attend left condition ($p < .05$), and over the left hemisphere in the attend right condition ($p < .05$), i.e., echo amplitude increased with attention. The same 2-way ANOVA on alpha amplitude (attend left/right X left/right hemisphere) revealed again no main effect of attention location or hemisphere but a significant interaction ($F(1, 9) = 10.62$, $p = .010$, $p. \eta^2 = .54$). However, this time the pairwise comparisons revealed the opposite interaction: alpha amplitude was significantly lower for the right hemisphere (processing the left stimulus) in the attend left condition ($p < .05$), and was marginally significantly lower for the left hemisphere (processing the right stimulus) in the attend right condition ($p < .10$), i.e., alpha amplitude decreased with attention. To summarize, attention had opposite effects on contralateral alpha amplitude and echo function amplitude. (NB: a direct comparison between echo and alpha amplitude would not be appropriate since the two variables are expressed with different units (correlation r vs. μV)).