

1 **Visual Perceptual Echo Reflects Learning of Regularities in**

2 **Rapid Luminance Sequences**

3 **Abbreviated title:** Perceptual Echo Reflects Regularity Learning

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26

1 **1. Abstract**

2 A novel neural signature of active visual processing has recently been described in the form  
3 of the ‘perceptual echo’, in which the cross-correlation between a sequence of randomly  
4 fluctuating luminance values and occipital electrophysiological (EEG) signals exhibits a long-  
5 lasting periodic (~100ms cycle) reverberation of the input stimulus (VanRullen & Macdonald,  
6 2012). As yet, however, the mechanisms underlying the perceptual echo and its function remain  
7 unknown. Reasoning that natural visual signals often contain temporally predictable, though non-  
8 periodic features, we hypothesized that the perceptual echo may reflect a periodic process  
9 associated with regularity learning. To test this hypothesis, we presented subjects with successive  
10 repetitions of a rapid non-periodic luminance sequence, and examined the effects on the  
11 perceptual echo, finding that echo amplitude linearly increased with the number of presentations  
12 of a given luminance sequence. These data suggest that the perceptual echo reflects a neural  
13 signature of regularity learning.

14 Furthermore, when a set of repeated sequences was followed by a sequence with inverted  
15 luminance polarities, the echo amplitude decreased to the same level evoked by a novel stimulus  
16 sequence. Crucially, when the original stimulus sequence was re-presented, the echo amplitude  
17 returned to a level consistent with the number of presentations of this sequence, indicating that  
18 the visual system retained sequence-specific information, for many seconds, even in the presence  
19 of intervening visual input.

20 Altogether, our results reveal a previously undiscovered regularity learning mechanism  
21 within the human visual system, reflected by the perceptual echo.

22

23

## 2. Significance Statement

How the brain encodes and learns fast-changing but non-periodic visual input remains unknown, even though such visual input characterises natural scenes. We investigated whether the phenomenon of ‘perceptual echo’ might index such learning. The perceptual echo is a long-lasting reverberation between a rapidly changing visual input and evoked neural activity, apparent in cross-correlations between occipital EEG and stimulus sequences, peaking in the alpha (~10 Hz) range. We indeed found that perceptual echo is enhanced by repeatedly presenting the same visual sequence, indicating that the human visual system can rapidly and automatically learn regularities embedded within fast-changing dynamic sequences. These results point to a previously undiscovered regularity learning mechanism, operating at a rate defined by the alpha frequency.

**Keywords:** *Perceptual Echo, Cross-correlation, Sequence Learning, EEG, Alpha, Reverberation, Regularity Learning.*

### 3. Introduction

There is accumulating evidence that complex spatial-temporal dynamics of visual stimuli are encoded early in the visual processing stream (Chubykin et al., 2013; Cooke & Bear, 2015; Gavornik & Bear, 2014; Zold & Shuler, 2015). However, relatively little is known about how the human visual system tracks, or learns about, such rapidly changing stimulus sequences. One recent finding relevant to this question is the ‘perceptual echo’ (VanRullen and MacDonald, 2012). This is long-lasting reverberation between a rapidly changing visual input and evoked neural activity, apparent in cross-correlations between occipital EEG and the stimulus itself. Specifically, when visually presenting a non-periodic dynamic sequence, whose luminance randomly fluctuated at a rate of 160 Hz, VanRullen and MacDonald found that the occipital EEG response displayed a periodic reverberation or ‘echo’ of the input sequence, which persisted for at least one second, and was found specifically in the alpha (~10 Hz) frequency range of the cross-correlation function, primarily over occipital electrodes and was observable at the group level. Importantly, the absence of such a reverberation when the luminance sequence of each trial was cross-correlated with EEG recorded on a different trial underlines that the perceptual echo is a true oscillatory response to the (non-periodic) visual stimulation sequence, and not a general property of ongoing EEG signals in response to this kind of stimulation. Furthermore, the seconds-long duration of the perceptual ‘echo’ suggests a long-lasting representation of fast-changing sensory information over time. As yet, however, the functional relevance and the underlying mechanism of the perceptual echo have remained unclear.

Here, we examine the idea that perceptual echo in visual cortex is a neural signature of learning of rapid temporal regularities in ongoing sensory stimulation (following previous studies (Gavornik & Bear, 2014, Yao et al., 2007), we use the term learning to refer specifically to evidence of brain signals distinguishing previously presented stimuli from novel stimuli). This

1 idea is motivated by the suggestion that perceptual echo in visual cortex repeatedly “replays”  
2 neural activation associated with afferent visual information. Supporting this view, studies in  
3 awake monkeys (Eagleman & Dragoi, 2012), mice and rats (Gavornik & Bear, 2014; Xu et al.,  
4 2012) found that after learning an association between a cue and a sequence stimulus, presenting  
5 the cue alone can elicit the same (temporally extended) neural activation pattern as evoked by the  
6 actual stimulus. This replay activation pattern has been interpreted as a mechanism that may  
7 facilitate learning and memory consolidation (Euston et al., 2007; Skaggs and McNaughton,  
8 1996).

9       We reasoned that, if the perceptual echo is indeed associated with visual regularity learning,  
10 the perceptual echo response should change across repeated presentations of the same luminance  
11 sequence, as the visual cortex encodes regularities across sequence repetitions. In two  
12 experiments we tested this prediction by using random dynamic luminance sequences that were  
13 predictable across repeated presentations. In Experiment 1, we presented random dynamic  
14 luminance sequences that were each repeated four times and we calculated the perceptual echo  
15 for each presentation. In Experiment 2, we added an ‘inverse’ luminance sequence (which has the  
16 inverse luminance polarity of the original sequence) following the presentation of the fourth  
17 repetition of a sequence, which was followed by an additional presentation of the original  
18 sequence, to test whether changes in perceptual echo were specific to the (non-periodic) temporal  
19 and luminance information within a given sequence.

20       Anticipating our results, Experiment 1 showed that the amplitude of the perceptual echo  
21 increased with the number of sequence presentations of a luminance sequence, in line with the  
22 idea that the perceptual echo reflects a neural signature of regularity learning. Experiment 2  
23 further supported this interpretation by showing the increased perceptual echo response  
24 accompanying repeated sequence presentations was abolished by the presentation of an inverse

1 luminance sequence. In addition, the echo response recovered when the original sequence was  
2 presented again, indicating that the visual system retained information about the sequence even  
3 when challenged by a novel input sequence.

4 Altogether, our data provide first evidence for a mechanism by which the human visual  
5 system rapidly learns regularities in fast non-periodic stimulus sequences, and in doing so  
6 provides a functional account of the alpha-band ‘perceptual echo’ response.

#### 7 **4. Methods**

8 In both experiments participants were seated in a dimly lit electromagnetically shielded  
9 room and their heads were stabilised in a head-and-chin rest to maintain centrality 50 cm away  
10 from a LaCie Electron blue IV 22" CRT Monitor, which had been manually gamma corrected.  
11 Luminance-sequence stimuli were generated and presented using the Psychophysics toolbox  
12 (Brainard, 1997). These were constructed based on VanRullen and Macdonald (2012) as follows.  
13 Each sequence consisted of a disc stimulus subtending a visual angle of 7 degrees and placed at  
14 7.5 degrees above a fixation point (a dim grey circle with 0.2 degrees of visual angle). The  
15 luminance of the disc altered randomly at a rate of 160 Hz, so that each sequence consisted of 500  
16 luminance frames (see Figure 1). Thus, each sequence comprised a rapid non-periodic sequence  
17 of luminance changes. To ensure equal power of all temporal frequencies within each sequence,  
18 all sequences were processed by a whitening procedure. Fourier components of each sequence  
19 were obtained by a fast Fourier transform. Power at all frequencies of each random sequence  
20 were equalised by normalizing the amplitudes of its Fourier components. An inverse Fourier  
21 transform was then applied to reconstruct the sequence. Thus, sequences were not distinguishable  
22 by power characteristics of their temporal frequencies.

23 EEG data in both experiments were recorded using a 64 channel ANT Neuro amplifier at a

1 sampling rate of 2048 Hz. A 64 channel Waveguard EEG cap (ANT Neuro, Enschede) employing  
2 standard Ag/AgCl electrodes placed according to the 10-20 system, using an average reference.  
3 Horizontal and vertical eye movements were recorded using two independent electrode pairs.  
4 Impedances of recording electrodes were maintained below 10k $\Omega$ . No analogue filter was applied  
5 during on-line recording. For both experiments pre-processing and data analyses were performed  
6 using the EEGLAB toolbox (Delorme and Makeig, 2004) under Matlab (Mathworks, Inc. Natick,  
7 MA, USA), and custom Matlab scripts. The acquired EEG data were downsampled to 160Hz and  
8 filtered using a 2-80 Hz bandpass FIR (Finite Impulse Response) filter. Independent component  
9 analysis (ICA) was used to identify and remove ocular artefacts. Data in each trial were then  
10 epoched from 0 to 3.125 seconds time-locked to the stimulus onset (start of the luminance  
11 sequence).

12

### 13 *Experiment 1*

14 *Participants.* 21 healthy University of Sussex students (11 male) with normal or corrected-  
15 to-normal vision completed the experiment (11 male, 18–36 years; mean age 24.9 years).  
16 Participants provided informed consent before the taking part and received £10 or course credits  
17 as compensation for their time. The experiment was approved by the University of Sussex ethics  
18 committee.

19 *Experimental Design.* Each experimental session comprised of 60 trials utilising 60 unique  
20 random non-periodic luminance sequences. Each trial consisted of four presentations of the same  
21 sequence. Each presentation lasted for 3.125s and successive presentations were separated by an  
22 inter-sequence-interval (ISI) of 3s.

23

24 **Figure 1 to be placed here**

1

2 To ensure participants maintained attention, 60 additional ‘response sequences’ were  
3 distributed within the 60 (experimental) trials. Each ‘response sequence’ comprised a unique non-  
4 periodic luminance sequence, which also contained an embedded square target (3.75 degrees)  
5 distinguished by having a non-changing luminance for 1 sec. The target appeared with onset time  
6 selected from a uniformly distributed random time during the sequence presentation. Participants  
7 were informed that the experiment was a visual detection task in which they were required to  
8 press the spacebar on a standard keyboard at the end of a sequence whenever they detected the  
9 target. Each response sequence was randomly assigned to a position in-between experimental  
10 trials. This was done individually for every response sequence, resulting in the possibility of there  
11 being one, more than one, or zero, response sequence between any two experimental trials. This  
12 design made it unlikely that participants could predict the onset of an experimental trial based on  
13 the occurrence of a response sequence.

14 Participants were not informed that there would be any repetition of the luminance  
15 sequences. The entire experimental session consisted of 300 (240 standard and 60 response)  
16 sequences and took approximately 1 hour to complete. In a post-experiment interview  
17 participants were asked if they noticed any repetition of luminance sequences in the experiment.  
18 The following questions were asked:

19 Did you notice any experimental manipulation during this experiment?

20 Did you notice any relationship between any two sequences?

21 Did you notice any repetition of any of the sequences?

22

23 *Analysis.* To identify the perceptual echo, we calculated cross-correlations between (pre-  
24 processed) EEG time series and luminance time series for all experimental sequences and sensors



1 using the same approach as VanRullen and Macdonald (2012). The cross-correlation procedure  
2 calculated the “impulse response function” (IRF) of the EEG as follows:

$$3 \quad IRF(t) = \sum_T stim(T).eeg(T + t)$$

4

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

7 The amplitude spectra of the cross-correlation functions were calculated on lags between -  
8 1.5s and 1.5s (Figure 2a). For each participant we then averaged the cross-correlations across  
9 each sequence for all sensors, which revealed a long-lasting post-onset oscillation in the alpha  
10 range (Figure 2b). Phase and power were computed by means of a continuous wavelet transform  
11 of single-trial data for the frequency range from 3 to 80 Hz. Grand average inter-trial coherence  
12 (ITC) was calculated across all 14 participants and sequence presentations (4) for data from  
13 Experiment 1 (Figure 2c). Calculations for the spectral estimate of the normalized power  
14 spectrum were run on -1 to 1.5s epoch using 400ms Hanning-windowed sinusoidal wavelet. ITC  
15 values were calculated for 80 EEG frequency bands between 2 to 80 Hz. This revealed that the  
16 long-lasting post-onset oscillation in the alpha range was due to the strong phase coherence  
17 (across trials) of the cross-correlation time series within the alpha frequency range (~10 Hz, see  
18 Figure 2c). These findings replicate the perceptual echo effect observed by VanRullen and  
19 Macdonald (2012). To quantify the amplitude of the echo response, we applied a Fast Fourier  
20 Transform on the average cross-correlation between 0s and 1s for each participant and sensor to  
21 extract the alpha-range (8-12 Hz) power. We emphasize that this is the power of the (average)  
22 cross-correlation function, not of neural oscillations themselves.

23

1 **Figure 2 to be placed here**

2

3 To compare the echo response across successive presentations of a luminance sequence, the  
4 cross-correlations were averaged by the order of presentation for each sensor, across trials (e.g.,  
5 all cross-correlations for the first presentation of a given random luminance sequence were  
6 averaged across trials, and the same for all second, third, and fourth presentations). We then  
7 computed the amplitude of the echo response for each presentation and participant. To verify that  
8 the perceptual echo was driven by the EEG response to a specific luminance sequence and not by  
9 variations in ongoing alpha activity in the raw EEG signal, we created a ‘shuffled’ set of cross-  
10 correlations by randomly rearranging the EEG time series with stimulus sequences from different  
11 trials from Experiment 1. As can be seen from Figure 2b (red line), this procedure leads to a  
12 complete absence of echo response, confirming that the echo response is not driven by the  
13 ongoing alpha-band EEG response.

14 We choose to analyse the cross-correlation between luminance values of stimulus sequences  
15 and event-related EEG signals rather than a more classical visual evoked response in order to  
16 isolate the ‘impulse response function’ of the visual system. An *impulse response* is the reaction  
17 of any dynamic system in *response* to some external change. Classical stimulus evoked responses  
18 (such as Visual Evoked responses, VEP) can be viewed as a special case of impulse response  
19 function where the sensory input event is a single isolated event (Lalor, Pearlmutter, Reilly,  
20 McDarby, & Foxe, 2006). From this perspective, the perceptual echo can be considered as the  
21 superposition of visually evoked responses to each stimulus frame, rather than a (standard) VEP  
22 evoked by the sequence onset. This perspective has some ecological validity since sensory  
23 afferents are rarely single discrete events that would evoke isolated VEPs. Since natural visual  
24 input occurs in a rapid and continuous fashion, impulse response functions are well suited to

1 characterize the response of the visual systems in these circumstances. Overall, since the central  
2 aim of the current study and of previous research investigating the perceptual echo (VanRullen  
3 and Macdonald, 2012) was to examine exactly how the visual system processes these types of  
4 dynamic rapid sequential inputs, we therefore used a type of analysis best suited for this purpose.

5 *Statistical Analysis.* We compared the echo response for each presentation of a luminance  
6 sequence using a polynomial trend analysis which is commonly applied to evaluate the  
7 relationship between levels of variables in fixed-effect models. In the present study, the main  
8 independent variable, the number of sequence presentations, consists of 4 fixed levels (i.e.  
9 presentation 1, 2, 3, 4). The polynomial trend analysis is the most applicable method for assessing  
10 the linear, quadratic, and, cubic trends with the added benefit of avoiding the issue of multiple  
11 comparisons.

12

### 13 *Experiment 2*

14 *Participants.* Eighteen participants took part in Experiment 2 (12 females, 20–36 years;  
15 mean age 25.2 years, none of whom took part in Experiment 1). Participants provided informed  
16 consent before the taking part and received £10 or course credits as compensation for their time.  
17 The experiment was approved by the University of Sussex ethics committee.

18 *Experimental Design.* In Experiment 2, 4 repeated presentations of a specific luminance  
19 sequence were followed, firstly by an inverse version of that luminance sequence, and secondly  
20 by another instance of the original (non-inverse) sequence. Each inverse sequence was created by  
21 inverting the luminance polarity, of the original sequence i.e. reversing black and white relative to  
22 the middle grey level (see Figure 3). This preserved the relative luminance values of the sequence  
23 while also maintaining a flat luminance power spectrum. These manipulations were designed to  
24 test the specificity of changes in echo responses (across presentations) to regularities embedded in

1 the luminance sequences.

2       There were a total of 120 trials in Experiment 2, divided into ‘control’ and ‘experimental’  
3 conditions. In the control condition (60 trials), a specific 3.125s sequence was presented 6 times  
4 with a 3s inter-sequence-interval. In the experimental condition (60 trials), a sequence was  
5 repeated 4 times. Then, on the fifth presentation, the inverse luminance sequence was presented.  
6 Following the inverse luminance sequence, the original sequence was presented again, making a  
7 total of 6 presentations of a sequence for each trial, see Figure 3.

8

9 **Figure 3 to be placed here**

10

11 Experiment 2 did not use the response sequences of Experiment 1. This was in order avoid a  
12 highly unlikely confound arising from the distribution of response sequences falling by chance  
13 into a regular pattern between trials in Experiment 1. Potentially, this may have led participants to  
14 develop strategies to deploy more attention towards the end of a trial in anticipation of a possible  
15 response sequence. Instead, in Experiment 2, participants were asked to indicate whether the  
16 average luminance level of each sequence was brighter or darker than the luminance of the  
17 fixation circle, by pressing the left arrow for darker and right arrow for lighter, after each  
18 sequence presentation. This modification meant that all sequences were ‘response’ sequences,  
19 ensuring that participants had to maintain equal attention to all sequences. The average luminance  
20 of a sequence was closely comparable across all sequence presentations (the standard deviations  
21 of the average luminance of all sequences relative to the entire luminance dynamic range of all  
22 sequences were .018% in Experiment 1 and .019% in Experiment 2). Therefore, participants  
23 could not use the average luminance of a sequence as a potential cue to encode a sequence. The  
24 luminance of the fixation circle was constant, meaning that the participant’s judgements about the

1 average luminance after each sequence were always based on similar information. Across all  
2 response sequences, participants rated 63.5% of sequences as being brighter than the fixation.  
3 One participant indicated for all sequences that the average luminance was brighter than the  
4 fixation, this may have been due to a perceptual bias when rating similar information across  
5 sequences, the data from this participant still showed a robust echo response and survived the  
6 exclusion criteria.

7 *Statistical Analysis.* The same procedure used in Experiment 1 was used to identify the  
8 perceptual echo for all 6 presentations of a sequence (including the inverse sequence) for each  
9 trial in Experiment 2.

10 Traditional frequentist hypothesis testing (e.g., t-test) does not provide a quantitative  
11 measure about how strongly the data supports the null hypothesis. In Experiment 2, for cases in  
12 which permutation t-tests did not display significant differences in echo amplitude between  
13 presentation number, we therefore used Bayesian analysis to further evaluate to what extent the  
14 echo amplitude supported the null hypothesis (i.e., a conclusion of no difference in echo  
15 amplitude between presentations) or the alternative hypothesis, (i.e. echo amplitude was different  
16 between presentations). We quantified how close to the null or alternative hypothesis each result  
17 was by Bayes Factor (BF) analyses of paired sample t-tests using JASP (JASP Team, 2016) with a  
18 default Cauchy prior of .707 half-width at half-maximum (Rouder, Speckman, Sun, Morey, &  
19 Iverson, 2009).

20 *Exclusion criteria.* In both experiments, we found that the magnitude of the echo response  
21 varied widely across individuals. Participants with no significant perceptual echo were excluded  
22 from the data analysis, as follows. First, cross-correlation time series were averaged across all  
23 trials, then the distribution of absolute values across lags were derived from the averaged cross-  
24 correlation for real and shuffled data separately. The non-parametric Kolmogorov–Smirnov test

1 was then performed to examine the similarity of the two distributions. We excluded those  
2 participants with  $p > .001$  (i.e., those participants for whom echo responses were not significantly  
3 different between the shuffled and non-shuffled data). Seven out of twenty-one participants were  
4 excluded using this procedure in Experiment 1. Four participants were excluded using this  
5 procedure in Experiment 2, meaning that 14 participants' data were retained for further analyses.

## 6 **5. Results**

7 **Experiment 1.** Figure 4 shows the average alpha (8-12 Hz) power of the cross-correlation  
8 from Experiment 1, i.e., the amplitude of the perceptual echo, across all participants and sequence  
9 presentations. We refer to this amplitude simply as 'echo response' from here on. We found a  
10 maximal echo response over occipital sensors, centred over POz, consistent with previous  
11 findings (VanRullen & Macdonald, 2012). To maximize the sensitivity to any potential effect of  
12 stimulus sequence repetition on echo response, the following analyses were therefore conducted  
13 with data from POz only.

14

15 **Figure 4 to be placed here**

16

17 To test whether repetitions of a luminance sequence modulated echo response, we compared  
18 the echo responses for each sequence presentation in Experiment 1 using polynomial trend  
19 contrasts (Figure 5A). Supporting our hypothesis that successive presentations would increase  
20 echo response, we found a strong linear trend from presentation 1 to presentation 4 ( $F(1, 13) =$   
21  $7.32, p = .018$ ). Post-hoc paired t-tests revealed a larger echo response for presentation 4  
22 compared to presentation 1 (bootstrapping test with 10,000 resamples,  $p < .01$ ), see Figure 5a  
23 (Howell, 2012).

1

2 **Figure 5 to be placed here**

3

4 One might wonder whether the increase described above could be attributed to a general  
5 effect of the repetition of luminance sequences on the spectral power of the occipital EEG. To test  
6 this possibility, we computed the EEG amplitude spectra of the 3.125 epochs for every luminance  
7 sequence presentation and then averaged the amplitude spectra across each sequence presentation.  
8 We then compared the average EEG amplitude spectra for each sequence presentation using  
9 polynomial contrasts, which did not reveal a significant linear relationship between presentation 1  
10 to presentation 4 ( $F(1, 13) = .65, p = .44$ ). Further post-hoc paired *t*-tests between the 4  
11 presentations confirmed this result ( $p > .28$  for all presentations). We next compared the linear  
12 trend for the perceptual echo and raw EEG alpha amplitudes. Paired *t*-tests revealed a  
13 significantly stronger linear trend for echo amplitude compared to raw EEG alpha amplitude  $t(13)$   
14  $= 2.56, p = .019$  as a result of sequence repetition. To further examine the relationship between  
15 the perceptual echo and EEG alpha amplitudes, we performed correlation analyses and computed  
16 correlation coefficients using the data from each individual participant. We then tested whether  
17 the correlation coefficients were significantly above the chance level (zero) at the group level. We  
18 found no significant correlation between raw EEG alpha and the perceptual echo amplitude  
19 across presentations using both Pearson correlation (average correlation coefficient across  
20 subjects  $= -.22, t(13) = -1.28, p = .22$ ) and Spearman correlation tests (average correlation  
21 coefficient  $= -.12, t(13) = -0.93, p = .37$ ), indicating that there is no significant linear relationship  
22 between the amplitude of the perceptual echo and ongoing EEG alpha activity. Taken together,  
23 the increase in echo response with successive sequence presentations observed in Experiment 1  
24 cannot be attributed to a general effect of EEG alpha response to these stimuli (see Figure 5c).

1 To examine the topography of the change in echo response from the first to the last  
2 presentation, we performed t-tests on echo amplitude between presentation 1 and presentation 4  
3 across subjects and electrodes and plotted the t-values. The largest difference in echo response  
4 was observed over occipital electrodes (see Figure 5b).

5 To examine the time course of the repetition enhancement of the echo response, we next  
6 computed the difference in echo response between presentations 1 and 4 in time-frequency space  
7 using FFTs (Hanning window tapering from -100 to 1000ms post stimulus onset and a frequency  
8 range of 2-80Hz). This confirmed the repetition enhancement of the echo response, by showing  
9 that the echo response for presentation 4 was significantly larger than for presentation 1, with this  
10 effect concentrated within the period of the cross-correlation between 375 - 505 ms after  
11 sequence onset ( $p < .05$  FDR corrected, Figure 5d).

12 In the post-test questionnaire, all participants responded 'no' to all of the questions, ruling  
13 out explicit learning of a sequence as driving the increase in echo response with repeated  
14 sequence presentations.

15 Summarising, the results from Experiment 1 demonstrate that the amplitude of the  
16 perceptual echo response increases in a linear fashion with successive repetitions of a specific  
17 dynamic luminance sequence, even though participants were not aware of these repetitions. This  
18 finding shows that the visual system can encode regularities defining repetitions of a specific  
19 luminance sequence. We next set out to determine the robustness and stability of this finding.

20 **Experiment 2.** Experiment 2 was designed to investigate the robustness of the increase in  
21 echo response with repeated sequence presentations, across time and intervening sensory input.  
22 We reasoned that, if the echo response reflects regularity learning, the dissimilar luminance  
23 polarities of an inverse sequence should abolish any signature of such learning in the echo  
24 response, since the luminance contingencies of the sequence as a whole would be completely



1 different while all other temporal and visual characteristics are preserved. We further reasoned  
2 that, if the learning process is robust across time and to intervening sensory input, the echo  
3 response amplitude should recover or further increase when the original sequence re-appeared  
4 following the inverse luminance sequence.

5 To assess whether the main effect of sequence repetition on echo response was also present  
6 in Experiment 2, we compared the echo response from presentation 1 to presentation 4 (data was  
7 pooled from experimental and control conditions) using a polynomial contrast analysis to test the  
8 linear dependence between presentations 1 to 4. Although showing an unexpectedly high average  
9 echo response for the 3rd presentation, the results remain supportive of a linear trend from  
10 presentation 1 to presentation 4,  $F(1, 13) = 6.35, p = .026$ , see Figure 6a. Similar to Experiment 1  
11 post-hoc paired  $t$ -tests revealed a larger echo response for presentation 4 compared to presentation  
12 1 (bootstrapping test with 10,000 resamples,  $p < .01$ ).

13

14 **Figure 6 to be placed here**

15

16 We next examined whether presentation of an inverse luminance sequence would abolish the  
17 increase in echo response seen after four successive presentations. When considering which  
18 sequence presentation in the control condition to compare with the inverse sequence, we took into  
19 account that other factors such as (for example) neural adaptation and changes of vigilance may  
20 occur across a series of successive stimulus presentations as used in the current study. We  
21 reasoned that these factors would only depend on the presentation number, but not on stimulus  
22 type (e.g., inverted vs. non-inverted). To match the overall presentation number we therefore  
23 compared the echo response elicited by the 5<sup>th</sup> presentation (control condition) with the inverse  
24 sequence (i.e. the 5<sup>th</sup> presentation in the experimental condition), because in this comparison the

1 number of stimulus presentations is equated, and only the stimulus type (or the immediately  
2 preceding stimulus history) differs. We found that the echo response elicited by the inverse  
3 sequence was significantly lower than elicited by a 5<sup>th</sup> (non-inverse) presentation (two-tailed  
4 paired t-test,  $t(13) = 4.36, p < .002$ , bootstrap, 10,000 resamples)(see Figure 6b).

5 We also compared the echo response elicited by the inverse sequence and presentation 1 in  
6 experimental trials and found no significant differences between the two presentations (two-tailed  
7 paired t-test,  $t(13) = .02, p = .71$ , bootstrap, 10,000 resamples). We found  $BF = .29$  (less than .33),  
8 which strongly supports the null (i.e., no difference) over the alternative hypothesis (Dienes,  
9 2011).

10 Together these results indicate that an inverse luminance sequence, carefully controlled for a  
11 range of perceptual properties, was processed in a similar manner as a new luminance sequence,  
12 in terms of echo response. This confirms that the visual system is encoding precise sequence  
13 information, rather than only general properties of luminance sequences (e.g. time-frequency  
14 dynamic, auto-correlation) or its visual characteristics (e.g. luminance range and variance), since  
15 these more general features are shared with the inverse luminance sequence.

16 We next compared the topography of the echo response for the 5<sup>th</sup> sequence presentations  
17 between experimental and control trials. We performed t-tests on echo response between these  
18 presentations across subjects and electrodes and plotted the resulting t-values, see Figure 7a.  
19 Similar to Experiment 1, the largest difference in the echo response was found over occipital  
20 electrodes, with a maximum over POz.

21

22 **Figure 7 to be placed here**

23

24 We then examined whether sequence information encoded across presentations 1 to 4 could

1 persist even after the presentation of an inverse luminance sequence. We reasoned that if such  
2 information does persist, re-presenting the original sequence after the inverse luminance sequence  
3 should restore the echo response to a level comparable to six sequential presentations of a  
4 particular sequence. Using the same logic as above, we compared the echo response elicited by  
5 presentation 6 (control condition) with replay (i.e., the 6<sup>th</sup> presentation in the experimental  
6 condition), as the number of stimulus presentations is directly comparable, and only the stimulus  
7 type (or the immediately preceding stimulus history) differs. No significant difference was  
8 observed (Figure 6c); indeed, echo amplitudes for these two presentations were almost identical ( $t$   
9 = .01,  $p = .99$ ). We computed BF to evaluate whether the echo response elicited by the replay  
10 sequence was supportive of the null hypothesis (i.e. no difference in echo amplitude between the  
11 replay and presentation 6) or the alternative hypothesis, (i.e. echo amplitude is different between  
12 replay and presentation 6). A BF = .27 provides strong evidence (less than .33) for accepting the  
13 null over the alternative hypothesis, indicating that sequence-specific information about a  
14 particular luminance sequence persists, for over 9 seconds, even in the presence of intervening  
15 visual input.

16 We also examined the topography of the difference in echo response between presentation 6  
17 (control) and replay (experimental) sequences. We performed t-tests on echo response between  
18 these presentations across participants and electrodes and plotted the resulting t-values, see Figure  
19 7b. There were no significant differences at any sensor, indicating that the echo response to the  
20 replay luminance sequence displayed a similar topography and magnitude as presentation 6.

21 Finally, to further validate the linear trend of echo response for each presentation of a  
22 luminance sequence found in both Experiments, we generated 2000 surrogate shuffled data sets in  
23 which each EEG time series recorded for a specific trial number (matching the trial number in the  
24 main analysis) was cross-correlated with a luminance sequence presented in a different (shuffled)

1 trial, but with the same presentation number. We reasoned that if the observed linear trend of the  
2 echo response was caused by an EEG induced effect, and was not specific to the input stimulus  
3 sequence, we should observe a similar linear trend in the shuffled data sets to that observed in the  
4 real data (Figure 5 and 6).

5 We performed permutation tests in which the linear trend for the real data was compared  
6 with the linear trends of the 2000 shuffled datasets separately for each experiment. For  
7 each surrogate cross-correlation dataset, we performed a linear trend test, producing an F-value  
8 for each of the 2000 shuffled datasets for each experiment. We then computed  $p$ -values by  
9 examining the rank of F-values from the linear trend reported in the manuscript for both  
10 experiments to the F-value distribution for the 2000 shuffled datasets. The results of this  
11 permutation test, showed  $p = .012$  for Experiment 1 and  $p = .014$  for Experiment 2, with both  
12 distributions of  $t$ -values being centred around 0, strongly supporting our conclusion that the linear  
13 trend in perceptual echo for successive presentations of the same luminance sequence is stimulus-  
14 dependent, and cannot be attributed due to broader EEG induced effects.

15

16

## 6. Discussion

17 In two experiments, we investigated the functional relevance of the previously observed  
18 alpha-band ‘perceptual echo’, testing the hypothesis that it reflects a regularity learning  
19 mechanism that can encode dynamic visual sequences within the visual cortex. Supporting this  
20 hypothesis, experiment 1 showed that the amplitude of the perceptual echo (the echo response) is  
21 enhanced by repetitions of an identical rapid non-periodic luminance sequence. Control analyses  
22 using shuffled data excluded the possibility that increases in echo response could be attributed to  
23 general changes in induced alpha-band EEG responses resulting from sequence repetitions,

1 suggesting instead that these increases reflected a neural signature of regularity learning.  
2 Experiment 2 established that the repetition enhancement of perceptual response reflects specific  
3 sequence information. Following 4 presentations of a specific sequence we presented an inverse  
4 luminance sequence, which preserved all non-sequential spectral and temporal properties of the  
5 original sequence. Strikingly, the echo response for the inverse sequence returned to a level  
6 comparable to presentation of a novel sequence (see Figure 6b). When the original stimulus  
7 sequence was presented again (following the inverse sequence), the echo response recovered to a  
8 level consistent with the number of presentations of this sequence, demonstrating that information  
9 about an encoded sequence persisted for over 9 seconds and was robust to intervening visual  
10 input.

11 Previous behavioural studies have demonstrated that humans are able to learn temporal  
12 sequences presented at different rates (1.7-8.3 Hz) consisting of spatiotemporal information  
13 (Song, Jr, & Howard, 2008), combinations of visual features (colour and spatial) (Gheysen et al.,  
14 2011) and object orientations (Luft et al., 2015). Our results extend these findings by showing  
15 that the visual system is capable of sequence learning even with stimuli presented orders of  
16 magnitude faster (160 Hz) than previously used. This sensitivity to rapidly changing input is in  
17 line with known properties of the human auditory system, where auditory sequence learning has  
18 been described behaviourally for random and meaningless input signals (Gaussian random noise;  
19 Agus et al., (2010)). Notably, as in the present study, behavioural signatures of sequence-specific  
20 learning were found to persist for seconds and be robust to intervening auditory inputs.

21 Considering the neural substrates of sequence learning, both human and animal studies have  
22 implicated brain regions outside primary sensory areas. For example, in monkeys, information  
23 about spatiotemporal sequences is encoded in inferior temporal cortex and also in V4 (Li &  
24 DiCarlo, 2008; Meyer & Olson, 2011). However, Gavornik and Bear (2014) found that, in mice,

1 it was possible to detect the encoding of spatiotemporal sequence information early in the visual  
2 stream, within primary visual cortex. These findings are compatible with the surface localisation  
3 of the perceptual echo – and its increase across repeated sequence presentations – to (human)  
4 visual regions.

5       What mechanisms could be responsible for the increase in echo response observed with  
6 successive presentations of luminance sequences? One possibility is that this increase may be a  
7 consequence of the increasing similarity, across sequence repetitions, between luminance changes  
8 in the stimulus sequence and changes in the evoked EEG response. This would result in stronger  
9 cross-correlations between the EEG and the luminance sequence, with successive presentations,  
10 and hence an increase in echo amplitude. This could be thought of as ‘sharpening’ of the neuronal  
11 assemblies representing visual sequences, reflecting increasingly precise representations of  
12 repeated sequences. Supporting this interpretation, previous studies on perceptual learning have  
13 shown that repeated exposure to the same visual input sharpens the responsiveness of neuronal  
14 assemblies representing these inputs (Seitz & Dinse, 2007). For example, monkeys trained on an  
15 orientation discrimination task show a post-training decrease in response variability and an  
16 increase in the slope of orientation-tuning curves in V4 for the trained orientations (Yang &  
17 Maunsell, 2004). Similarly, the phenomenon of repetition suppression may be caused by a  
18 sharpening or tuning mechanism, which occurs when repeated exposure to a stimulus leads to a  
19 more precise and more efficient neural representation of that stimulus (Desimone, 1996; Kok,  
20 Jehee, & de Lange, 2012). At a mechanistic level, neuronal sharpening is thought to depend on  
21 Hebbian processes, among which spike-timing dependent plasticity (STDP) is particularly  
22 significant when dealing with temporal relationships (Bi & Poo, 1998). Relevant to the present  
23 study, STDP has been shown to make neurons extremely sensitive to repeating spatio-temporal  
24 patterns (Guyonneau et al., 2005; Masquelier, Guyonneau, & Thorpe, 2008a, 2008b) and displays

1 the highest speed and efficacy when spike timing is reliable (Markram et al., 1997). Therefore,  
2 the repeated presentation of a luminance sequence may have increased both the sensitivity and  
3 reliability of neural responses facilitating the rapid encoding of sequence information reflected in  
4 the changes in perceptual echo we describe.

5       Could the results of the present study be accounted for by stimulus related changes to  
6 ongoing alpha activity or phase modulation of alpha oscillations? It is possible that the *amplitude*  
7 of specific evoked EEG responses to the luminance sequence could increase across successive  
8 repetitions. This would lead to an increased signal to noise ratio and thus also to stronger cross-  
9 correlations between the EEG time series and luminance sequences. While the opposite  
10 phenomenon is commonly observed (repetition suppression), a wide range of studies  
11 investigating perceptual learning have indeed found that the neural response to a stimulus can be  
12 enhanced by repeated exposure to identical sensory input (Karni & Sagi, 1991; Vogels, 2010).  
13 Indeed, the original investigation of the perceptual echo by VanRullen and Macdonald (2012)  
14 found that the frequency peak and power of the spontaneous alpha rhythm correlated with the  
15 frequency peak and amplitude of the perceptual echo across subjects. This finding suggests that  
16 the perceptual echo is intimately linked to occipital alpha rhythms. Additionally, the perceptual  
17 echo can only be observed after averaging the cross-correlation time series across trials, which  
18 suggests that phase modulation time-locked to each stimulus frame is a key feature of the  
19 perceptual echo. Indeed, we show that there is a strong phase coherence between cross-  
20 correlation time series centred within the alpha frequency range (Figure 2c). Therefore, both the  
21 ongoing alpha rhythm and phase modulation of this rhythm are critical in the production of the  
22 perceptual echo.

23       However, our data does not support the conclusion that these factors can account for the  
24 modulation of the perceptual echo in response to repeated presentations of rapid luminance

1 sequences. First, the power of the raw EEG alpha did not display the same linear trend as found  
2 for the perceptual echo across stimulus presentation, which would be expected if the neural  
3 response to sequence repetition were driven by modulations in the amplitude of the alpha-band  
4 evoked EEG signal (see Figure 5C). Second, both the current study and previous research by  
5 VanRullen and Macdonald (2012) show that when the cross-correlation is performed on EEG  
6 time series and stimulus sequences from different trials, the ~10Hz power in cross-correlation is  
7 abolished (Figure 2B). Together these findings strongly suggest that the perceptual echo is not  
8 driven by EEG responses to rapid luminance sequences and that it is indeed stimulus-dependent.

9 In summary, the enhancement of the echo response with successive presentations of a  
10 sequence is most plausibly due to an increase in similarity between luminance changes in the  
11 stimulus sequence and changes in the evoked EEG response. A candidate mechanism for this  
12 process is STDP, through sharpening the population response for each specific sequence, leading  
13 to an enhanced echo response with successive presentations of a sequence. The echo response is  
14 linked to occipital alpha rhythms a phase-modulation within this frequency range, however it is  
15 stimulus dependent and independent of general features of EEG.

16 A striking – indeed defining - feature of the perceptual echo is its periodicity. One  
17 interpretation of this feature is that the visual system is *actively engaging* in repeated patterns of  
18 activity in response to ongoing sensory stimulation. In this view, the periodicity of the perceptual  
19 echo may reflect a process that updates and replays temporal representations at a rate defined by  
20 occipital alpha. This interpretation is in line with ‘predictive processing’ accounts of perception  
21 and brain function, in which the brain continuously generates and updates predictions about  
22 incoming sensory signals (Clark, 2012; Friston, 2005; Hohwy, 2013; Seth, 2014). Extended  
23 formulations of this account suggest that hierarchical predictive generative models update prior  
24 knowledge by extracting and encoding hidden spatial and temporal regularities in the



1 environment (Tenenbaum, et al., 2011). In our study, increases in echo response with successive  
2 repetitions of a sequence demonstrate that participants were (implicitly) learning information  
3 about each sequence, which may reflect perceptual predictions (Bayesian priors) being updated  
4 with each sequence. In this view the perceptual echo may reflect an iterative process that updates  
5 priors about the luminance dynamics of a sequence, communicating perceptual predictions at rate  
6 defined by the alpha frequency. Further research will be needed to examine connections between  
7 perceptual echo and predictive processing, for example by manipulating expectations about  
8 temporal regularities, within or across sequence presentations.

## 9 **7. Conclusion**

10 The perceptual echo is a long-lasting periodic reverberation in the EEG response to dynamic  
11 visual stimulation, reflected by an alpha-band peak in the cross-correlation function between a  
12 rapidly changing random dynamic luminance sequence and the raw occipital EEG response. We  
13 investigated the functional properties of the perceptual echo, finding that it can be enhanced by  
14 repeatedly presenting the same visual sequence, indicating that the human visual system can  
15 rapidly and automatically learn regularities embedded within such fast-changing dynamic  
16 stimulus sequences. By comparing echo responses for inverse and non-inverse luminance  
17 sequences, we further showed that the increase in echo response was sensitive to specific  
18 sequence information. Finally, we show that the encoded sequence information can persist over  
19 many seconds even in the presence of additional intervening sensory input. Together, our results  
20 provide evidence that the perceptual echo reflects the existence of a previously undiscovered  
21 regularity learning mechanism, which operates at a rate defined by the alpha frequency band.

22

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## 9. Legends

1  
2 *9.1. Figure 1: Example of trial structure in Experiment 1. For each trial a specific*  
3 *random luminance sequence (e.g. sequence A) was presented four times. Each luminance*  
4 *sequence lasted 3.125s and consisted of a disc with randomly changing luminance at 160*  
5 *Hz. Sequences were separated by an inter-sequence-interval (ISI) of 3s. 'Response'*  
6 *sequences, which contained an embedded square image (1s duration, random onset time*  
7 *within sequence), were distributed at random points in-between trials throughout the*  
8 *experiment. Participants were requested to press a key after each sequence if they noticed*  
9 *a square.*

10  
11 *9.2. Figure 2: Recording and computation of perceptual echo for a representative*  
12 *subject. A. For each luminance sequence presentation and EEG sensor, we computed the*  
13 *cross-correlation (-1.5s:1.5s) between the luminance value series and the EEG time*  
14 *series. This provides an ensemble of cross-correlation time series for each luminance*  
15 *sequence, indexed by sensor and presentation number. B. As in VanRullen and*  
16 *Macdonald (2012), averaging the cross-correlations for each luminance sequence*  
17 *revealed a long lasting oscillation (~1.5 sec) in the alpha range: the 'perceptual echo'*  
18 *(blue line). The red line shows the same analysis with shuffled data (see methods), in*  
19 *which no perceptual echo is observed. C. Grand average inter-trial phase coherence*  
20 *(ITC) of the cross-correlation time series, averaged across all participants and sequence*  
21 *presentations (4) from Experiment 1. The group level analysis reveals that the perceptual*  
22 *echo is due to the strong ITC within the alpha frequency range (~10 Hz). Phase and*  
23 *power were computed by means of a continuous wavelet transform of single-trial data for*  
24 *the frequency range from 2 to 80 Hz. Calculations for the spectral estimate of the*  
25 *normalized power spectrum were run on -1 to 1.5s epoch using 400ms Hanning-*  
26 *windowed sinusoidal wavelet. ITC values were calculated for 80 EEG frequency bands*  
27 *between 2 to 80 Hz.*

28  
29 *9.3. Figure 3: Experiment 2 trial structure. In a control trial, 6 presentations of the same*  
30 *sequence were shown. In an experimental trial, after 4 presentations of a given sequence,*  
31 *the inverse-polarity luminance sequence was presented, followed by a final replay of the*

1 original (non-inverse) sequence. Each sequence lasted 3.125s, separated by an inter-  
2 sequence-interval of 3s.

3

4 9.4. Figure 4: The topography of the echo response averaged across all sequence  
5 presentations and participants. The topographic plot displays the 8-12 Hz envelope of the  
6 echo response and reveals a maximum at POz with a gradual decrease from posterior to  
7 anterior electrodes (Arbitrary Units (a.u.)).

8

9 9.5. Figure 5: A. Experiment 1. Perceptual echo amplitude (echo response) for each  
10 sequence presentation, averaged across all participants, for electrode POz. The echo  
11 response displayed a linear increase across successive presentations.. B. t-value map of  
12 echo response comparing presentation 4 to presentation 1 across all participants. The  
13 maximum difference in echo response was located over occipital electrodes. (× indicates  
14 areas of significant difference between presentations, multiple t-test between all  
15 electrodes, Bonferroni corrected) C. Average of all participants' power from 8-12 Hz  
16 ( $\mu V^2$ ) for each sequence presentation for all trials for electrode POz. Average alpha  
17 power of the EEG time series was not affected by the repetition of a luminance sequence.  
18 Average power is measured in microvolts squared. D. Time-frequency analysis of the  
19 effect of sequence repetition on perceptual echo power. The plot shows the difference in  
20 time-frequency analysis of the perceptual echo (cross-correlation function) between  
21 presentation 4 and presentation 1, averaged across luminance sequences and subjects,  
22 for POz. The echo differs significantly between presentations 4 and 1 within the alpha  
23 frequency range from ~375 to 505ms (8-12Hz). The outlined area highlighted with a red  
24 arrow indicates significant differences using multiple t-tests,  $p < .05$ , False Discovery Rate  
25 (FDR) corrected. Average echo amplitude is measured in Arbitrary Units (a.u.); To  
26 effectively represent the variance within subjects, error bars show standard error of the  
27 difference between the first presentation and all subsequent presentations. \*\* $P < .01$

28

29 9.6. Figure 6: A. Echo response as a function of repetition of luminance sequences. For  
30 the first 4 presentations of a given sequence, we observed a linear increase in echo

1 response with successive presentations, similar to Experiment 1 (data pooled across  
2 experimental and control trials). **B.** Critically, a subsequent ‘inverse’ sequence  
3 (experimental trials) showed a reduction in echo response to a level similar to initial  
4 presentation of a luminance sequence, as compared to a fifth presentation of a non-  
5 inverse sequence. **C.** Re-presenting the original sequence following the inverse sequence  
6 (Replay, experimental trials), showed a recovery of echo response indistinguishable from  
7 a 6<sup>th</sup> successive presentation. Echo response is measured in Arbitrary Units, a.u. To  
8 effectively represent the variance within subjects, error bars show standard error of the  
9 difference between the first presentation and all subsequent presentations. \*\* $P < .01$ . For  
10 clarity the colours of each bar plot are consistent with Figure 3.

11

12 9.7. Figure 7: **A.** t-value map of echo response difference between presentation 5  
13 (control condition) and the inverse luminance sequence (experimental condition) for all  
14 subjects, in Experiment 2. A significant difference was centred over occipital electrode  
15 POz (outlined, FDR corrected). **B.** t-value map of echo response difference between  
16 presentation 6 (control condition) and the replay sequence (experimental condition) for  
17 all subjects, in Experiment 2. There were no significant differences in echo response  
18 between the two presentations. No other regional differences, positive or negative,  
19 reached statistical significance.

20

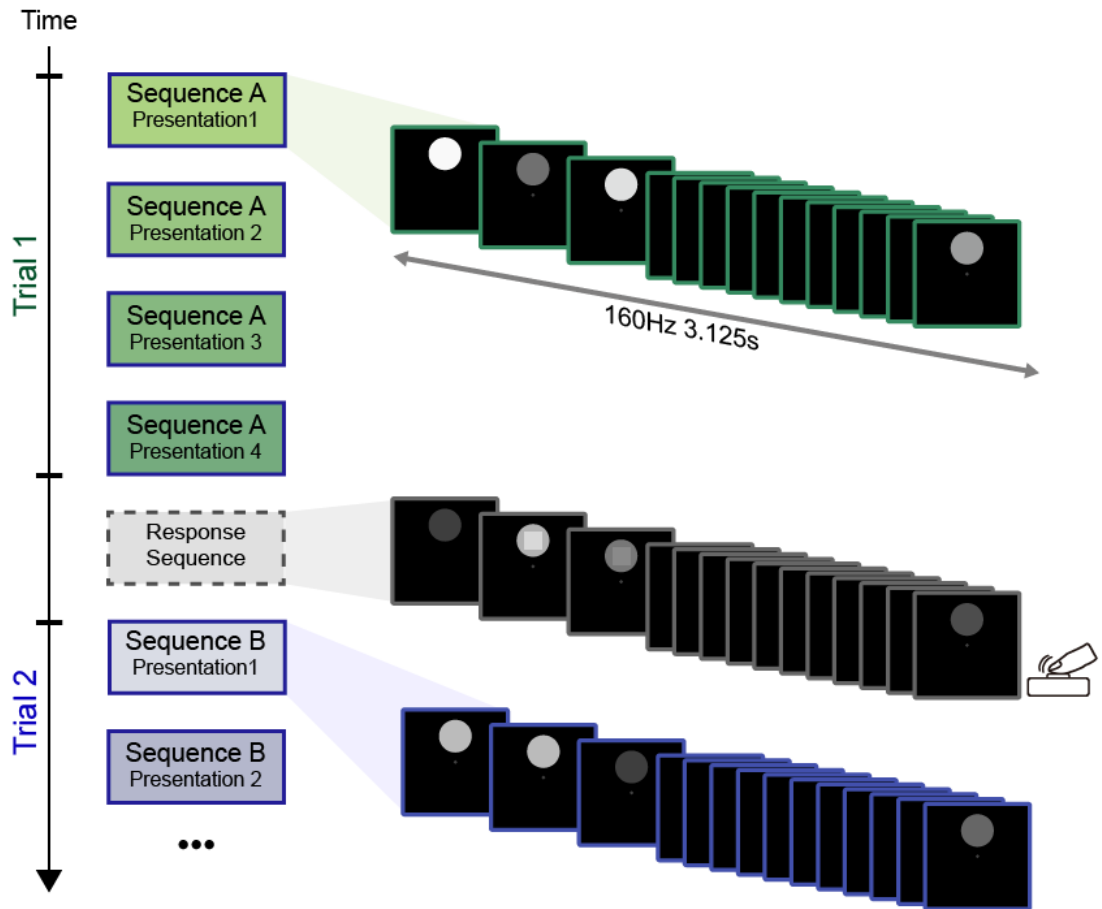
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## 10. Illustrations

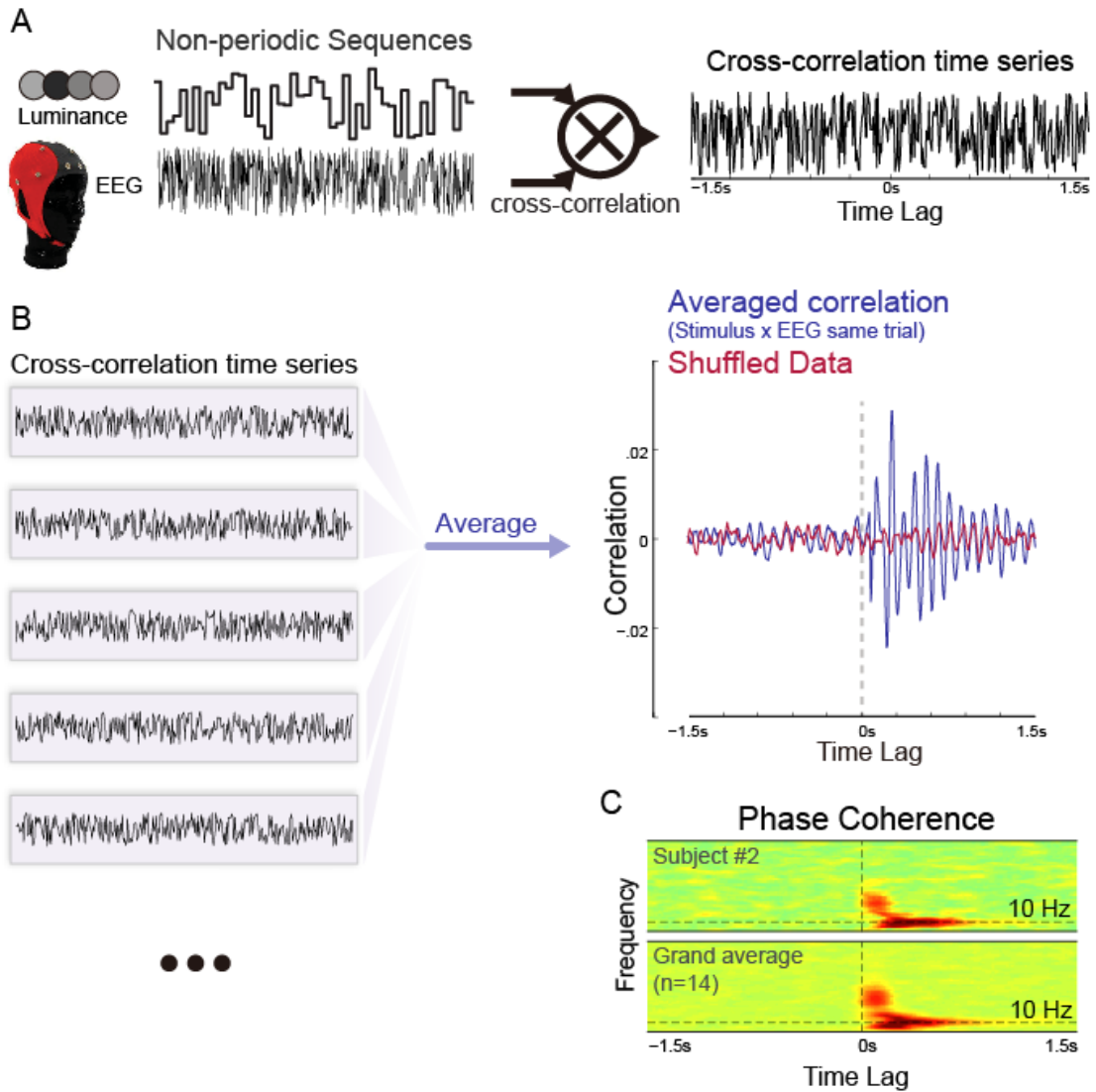
2 10.1. Figure 1.



3



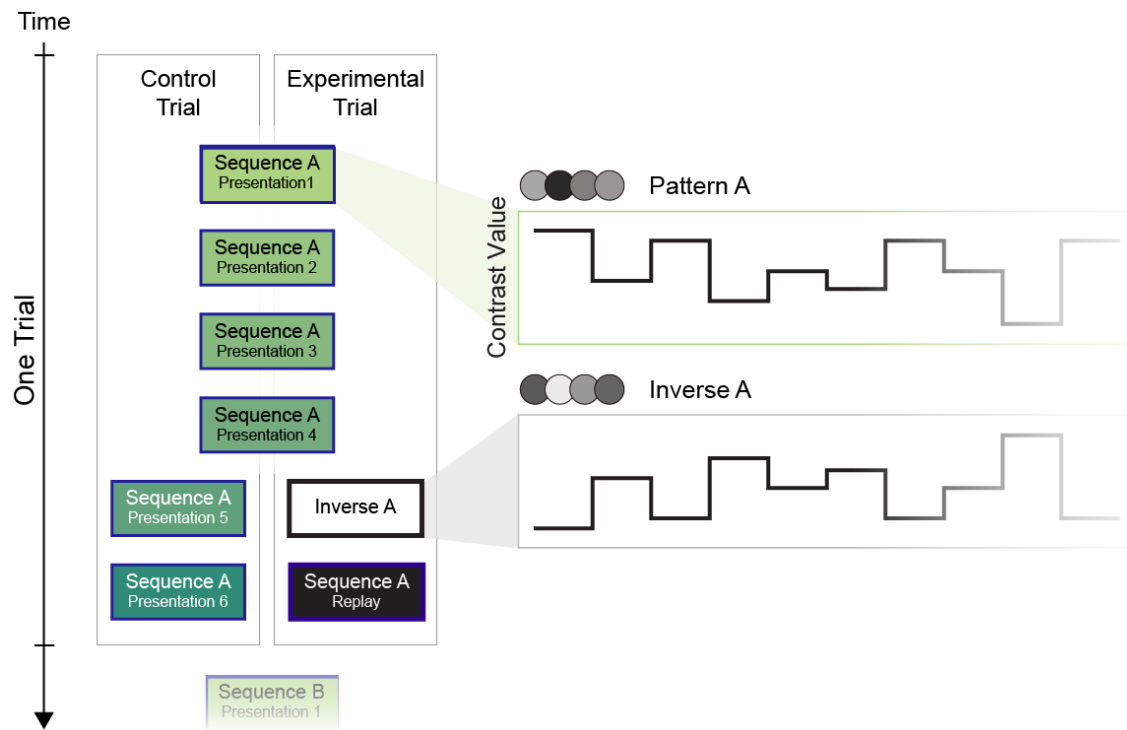
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2

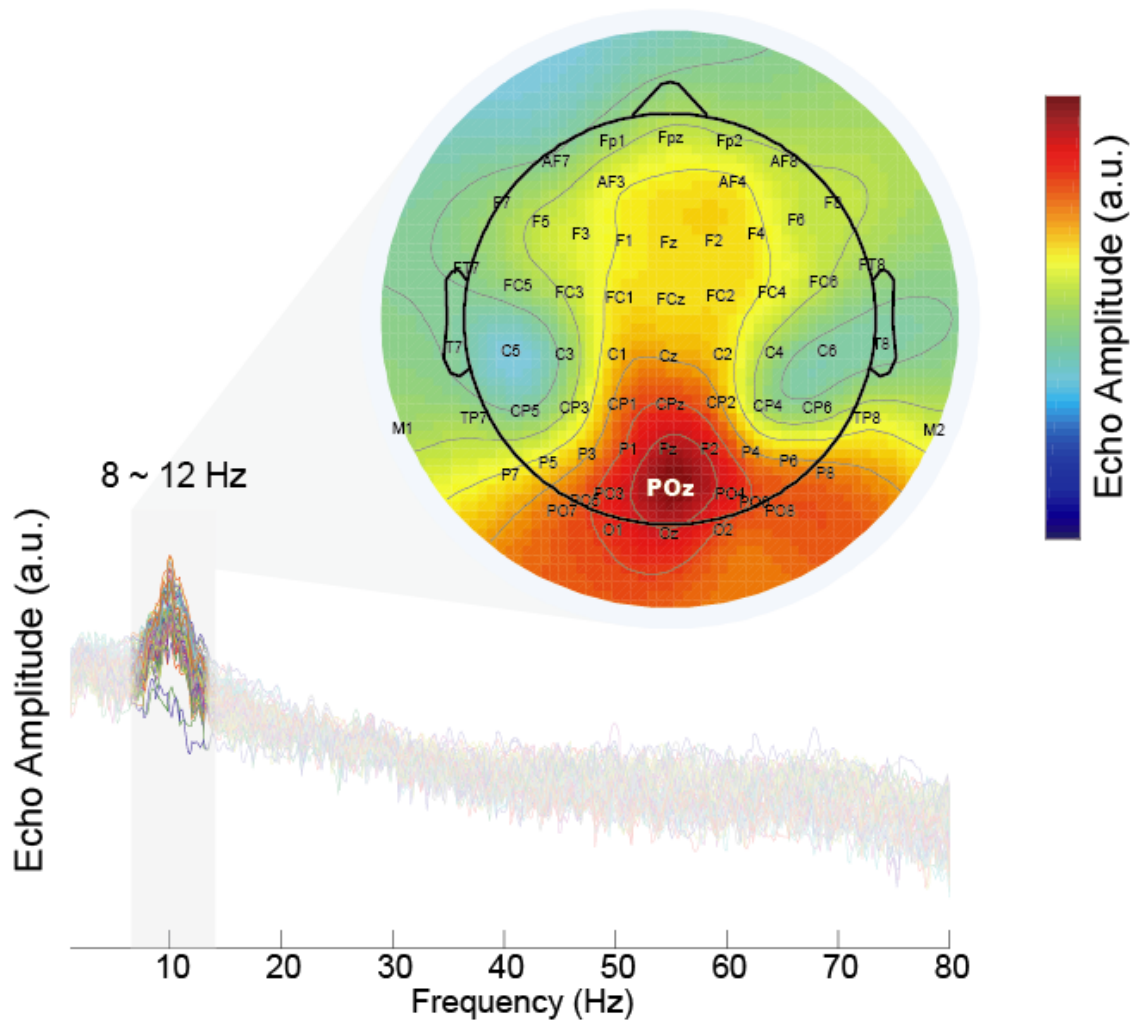
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1 10.3. Figure 3.



2

1 10.4. Figure 4.



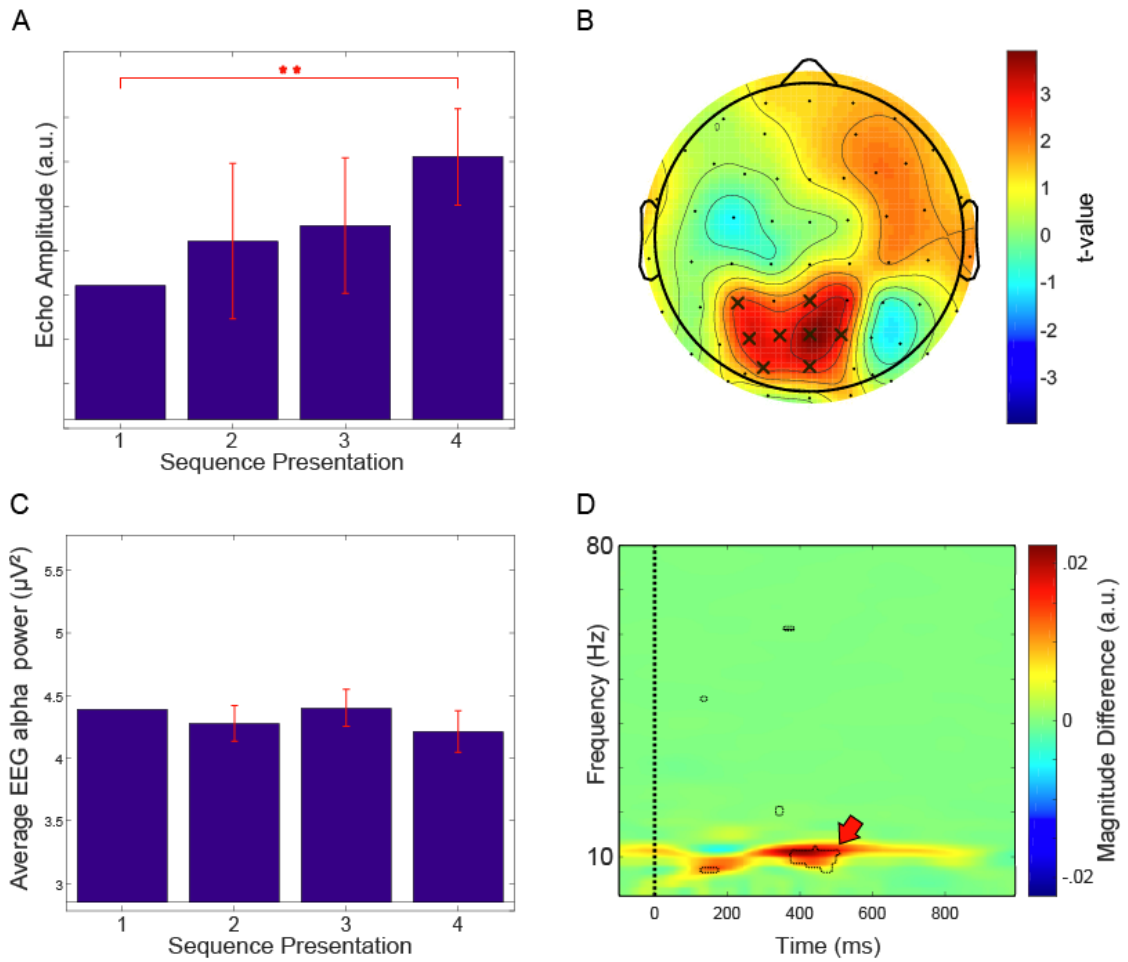
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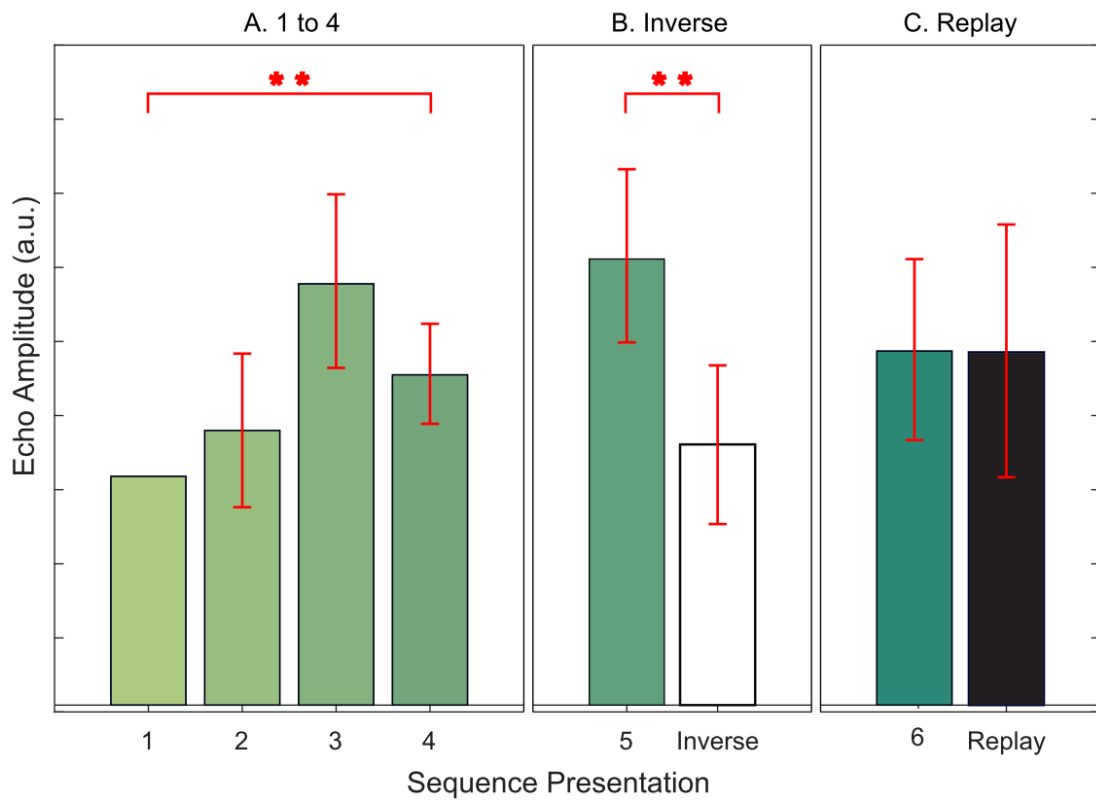
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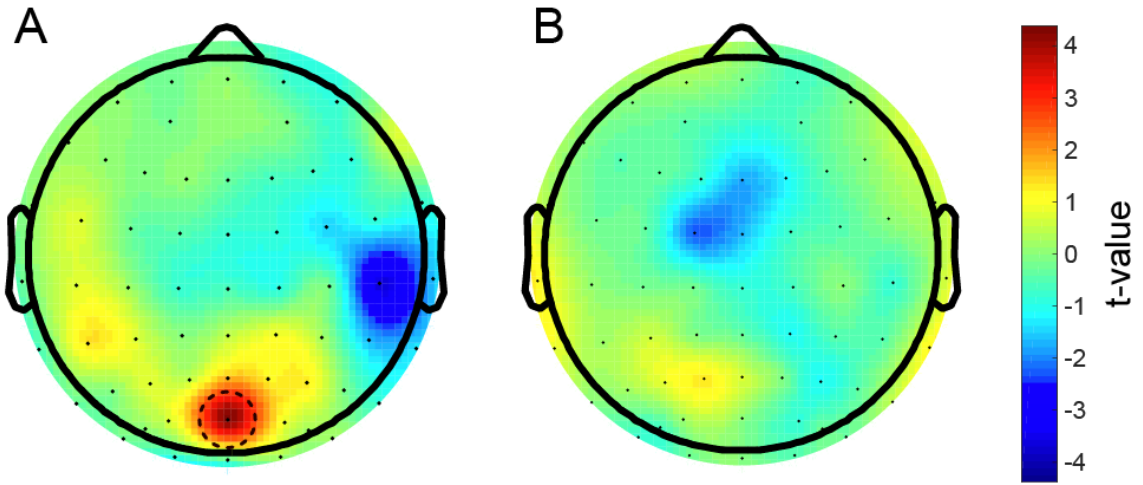
1 10.6. Figure 6.



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1 10.7. Figure 7.



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