

# UC Davis

## UC Davis Previously Published Works

### Title

Alpha-band EEG suppression as a neural marker of sustained attentional engagement to conditioned threat stimuli

### Permalink

<https://escholarship.org/uc/item/0z52h1vs>

### Journal

Social Cognitive and Affective Neuroscience, 17(12)

### ISSN

1749-5016

### Authors

Bacigalupo, Felix  
Luck, Steven J

### Publication Date

2022-12-01

### DOI

10.1093/scan/nsac029

Peer reviewed

# Alpha-band EEG suppression as a neural marker of sustained attentional engagement to conditioned threat stimuli

Felix Bacigalupo<sup>1,2,3,4</sup> and Steven J. Luck<sup>4</sup>

<sup>1</sup>Escuela de Psicología, Facultad de Ciencias Sociales, Pontificia Universidad Católica de Chile, Santiago 8940000, Chile

<sup>2</sup>Departamento de Psiquiatría, Unidad de Trauma y Disociación, Facultad de Medicina, Pontificia Universidad Católica de Chile, Santiago 8940000, Chile

<sup>3</sup>Centro Interdisciplinario de Neurociencia, Pontificia Universidad Católica de Chile (UC Chile), Santiago 8320129, Chile

<sup>4</sup>Center for Mind and Brain, University of California, Davis, CA 95616, USA

Correspondence should be addressed to Felix Bacigalupo, Pontificia Universidad Católica de Chile (UC-Chile). Avenida Vicuña Mackenna 4860, Macul, Santiago, Chile. E-mail: [fobaciga@uc.cl](mailto:fobaciga@uc.cl)

## Abstract

Attention helps us to be aware of the external world, and this may be especially important when a *threat* stimulus predicts an aversive outcome. Electroencephalogram (EEG) alpha-band suppression has long been considered as a neural signature of attentional engagement. The present study was designed to test whether attentional engagement, as indexed by alpha-band suppression, is increased in a sustained manner following a conditioned stimulus (CS) that is paired with an aversive (CS+) vs neutral (CS-) outcome. We tested 70 healthy young adults in aversive conditioning and extinction paradigms. One of three colored circles served as the CS+, which was paired in 50% of the trials with a noise burst (unconditioned stimulus, US). The other colored circles (CS-) were never paired with the US. For conditioning, we found greater alpha-band suppression for the CS+ compared to the CS-; this suppression was sustained through the time of the predicted US. This effect was significantly reduced for extinction. These results indicate that conditioned threat stimuli trigger an increase in attentional engagement as subjects monitor the environment for the predicted aversive stimulus. Moreover, this alpha-band suppression effect may be valuable for future studies examining normal or pathological increases in attentional monitoring following threat stimuli.

**Key words:** attention; conditioning; threat; fear; aversive; alpha; EEG; SCR

## Introduction

To survive, organisms must learn that some stimuli predict an increased probability of an aversive event (e.g. a honking horn predicts an increased probability of a collision). These predictors can be considered *threat* stimuli. The evaluation of threat involves changes in cognitive and affective states together with a set of behavioral and physiological reactions (Grupe and Nitschke, 2013). A better understanding of how humans process threat stimuli will be important for understanding both normal human emotional processing and disorders involving dysregulated threat responses (e.g. anxiety and trauma-related disorders).

Attention appears to play an important role in threat processing. At least two distinct roles of attention can be considered. First, threat stimuli appear to attract attention, presumably so that they can be more readily identified and influence behavior. Second, because threat stimuli predict the possibility of a subsequent aversive event, they may lead to an increase in attentive monitoring of the external environment and a reduction in internally focused processing.

Substantial evidence supports the role of attention in identifying threats. Using behavioral measures, numerous studies have reported increased allocation of attention to threat-related stimuli compared to neutral stimuli. For example, research using the emotional Stroop task has found longer reaction times and higher error rates for aversive vs neutral stimuli, consistent with an automatic attentional allocation to the emotional stimuli that hinders cognitive control (Wingenfeld *et al.*, 2006; Bielecki *et al.*, 2017). Other research using the dot-probe task has found that anxious individuals show facilitated detection of a probe dot when presented at the location of an aversive image compared to when it is presented at the location of a neutral image. However, dot-probe studies with healthy individuals have yielded inconsistent results (MacLeod *et al.*, 1986; MacLeod and Mathews, 1991; Oehlberg and Mineka, 2011; Grafton and MacLeod, 2014).

Event-related potentials (ERPs) studies have also provided evidence that threat stimuli attract attention. For example, threat stimuli elicit an enhanced early posterior negativity (EPN), starting as early as 200 ms after stimulus onset (Schupp *et al.*, 2003).

Received: 25 November 2020; Revised: 6 April 2022; Accepted: 16 April 2022

© The Author(s) 2022. Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs licence (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)

Other research has found threat-related modulation at later stages, for example the late positive potential (LPP), suggesting greater attentional processing for aversive stimuli relative to neutral stimuli (Dieterich et al., 2016). Similarly, research combining ERPs and the dot-probe task in nonclinical samples found that threatening images attract visual-spatial attention, as measured via the N2pc component (Kappenman et al., 2015). Research has also found increased N2pc to angry faces in participants with social anxiety traits (Reutter et al., 2017; Wieser et al., 2018). In addition, research with socially anxious individuals has found increased attentional engagement for threatening faces as measured via steady-state visual evoked potentials (Wieser et al., 2012). There is also evidence that a threat stimulus leads to increased attentiveness to the external environment in preparation for the predicted aversive stimulus. For example, a cue stimulus produces increased attentional engagement during a subsequent delay period if the cue predicts an aversive outcome, as shown by studies using the stimulus preceding negativity (SPN) (Bocker et al., 2001).

Many studies of threat processing use stimuli such as photographs of snakes or angry faces, but better experimental control over the stimuli can be achieved by using aversive conditioning procedures. In these paradigms, a previously neutral stimulus such as an image or sound (the 'conditioned stimulus'; CS) is paired with an intrinsically aversive stimulus, such as a loud noise or mild electrical shock (the 'unconditioned stimulus'; US). Thus, the conditioning procedure turns an ordinarily neutral stimulus into a threat stimulus. This makes it possible to experimentally manipulate whether a given physical stimulus is neutral or associated with an aversive outcome. It also avoids the fact that some natural images (e.g. snakes) will be highly aversive to some individuals but not aversive to others (e.g. people who have snakes as pets).

Behavioral conditioning studies have found that an aversive CS will automatically capture and hold attention (Koster et al., 2004). Using magnetoencephalography, Moratti et al. (2006) found increased steady-state evoked fields potentials to CS+ vs CS- stimuli, and Kappenman et al. (2021) found that CS+ stimuli elicit an N2pc component, thus showing that attentional processing is increased for conditioned threat stimuli (Moratti et al., 2006; Kappenman et al., 2021). It has even been proposed that enhanced attentional processing of the CS+ can occur before 100 ms post-stimulus onset in primary visual cortex (Stolarova et al., 2006). In a previous study, we found increased attentional engagement for threat-related stimuli via measuring the LPP component of the ERP, showing greater LPP amplitude for the CS+ vs the CS- stimuli in an aversive conditioning paradigm (Bacigalupo and Luck, 2018). Similarly, Ferreira de Sa et al. (2019) found greater EPN, LPP and SPN amplitudes for CS+ vs CS- stimuli. All these results are consistent with a transient allocation of attention to conditioned threat stimuli, which presumably aids in the appraisal of these stimuli (Ferreira de Sa et al., 2019). However, it is not clear from these relatively brief electrophysiological effects whether the threat stimulus (the CS+) leads to sustained attentional engagement on the external environment as the subject awaits the predicted aversive stimulus (the US). EEG oscillations in the alpha band (8–12 Hz) are particularly well-suited for examining this kind of sustained anticipatory attention. As demonstrated in the foundational studies of Berger (1929) and Adrian and Matthews (1934), alpha-band amplitude increases when attention is unfocused or internally focused (e.g. when the eyes are closed) and decreases when attention is engaged on stimuli in the external environment (e.g. when the eyes are open, especially if attention is focused on

a specific object) (Berger, 1929; Adrian and Matthews, 1934). More recent studies have shown that alpha-band activity is modulated in a sustained manner following a cue that predicts a subsequent target (Worden et al., 2000). In addition, alpha-band oscillations have been linked to a wide range of attention-related processes, including visual target selection, distractor inhibition, mind wandering and awareness (Klimesch et al., 2007; Harris et al., 2018; Bacigalupo and Luck, 2019; Compton et al., 2019). Alpha-band suppression has been shown to be related to heightened attentional engagement (Klimesch et al., 2001; Heyselaar et al., 2018; Minarik et al., 2018; Gallot et al., 2020), and it is also accompanied by increased cortical excitability (Klimesch et al., 2007; Bollimunta et al., 2008, 2011). Like the N2pc component, alpha-band suppression may be lateralized with respect to the attended location. However, alpha-band suppression can be experimentally dissociated from the N2pc and lasts much longer, suggesting that alpha-band suppression represents an independent and sustained attentional process (Bacigalupo and Luck, 2019). Indeed, alpha-band EEG activity may be sustained throughout the delay period of a working memory task (Foster et al., 2016; Bae and Luck, 2019; de Vries et al., 2019). In addition, it has been well established that the alpha rhythm is generated via recurrent feedback between the cerebral cortex and the thalamus (Lopes da Silva et al., 1980; Chatila et al., 1993; Liu et al., 2012). Thus, alpha-band suppression is a well-validated and well-understood index of sustained attentional engagement.

It therefore seems natural that alpha-band suppression could be used to study the allocation of attention to threat stimuli and the subsequent sustained engagement of attention on the external environment. However, there has been limited empirical research on alpha-band suppression during aversive conditioning (Chien et al., 2017; Panitz et al., 2019; Friedl and Keil, 2020, 2021; Yin et al., 2020). An initial exploratory study using a trace conditioning procedure—which included only seven participants and examined a wide range of oscillation frequencies and electrode sites—found evidence of greater alpha-band suppression following a CS+ than a CS- (Chien et al., 2017). This basic effect was replicated in four subsequent studies that used more complex designs and tested more detailed hypotheses (Panitz et al., 2019; Friedl and Keil, 2020, 2021; Yin et al., 2020). These studies showed that the conditioning persisted for at least 24 h (Panitz et al., 2019), that it was accompanied by changes in the sparseness of functional magnetic resonance imaging signals in the primary visual cortex (Yin et al., 2020) and that it showed a gradual generalization gradient around the location and spatial frequency of the CS+ (Friedl and Keil, 2020, 2021).

However, these studies did not provide a detailed examination of the time course of the alpha-band suppression following the onset of the CS. For example, does the CS+ elicit a brief suppression of alpha-band activity as the participant orients to and appraises the stimulus or is the alpha-band suppression sustained as long as the CS+ is visible? This is a fundamental question about the allocation of attention to conditioned threat stimuli. Although the previous studies provided some evidence of a more sustained response, they either used a brief interval between CS+ and US or did not provide a detailed analysis of the entire CS+ period. The primary goal of the present study was therefore to provide a more focused test of competing hypotheses about the duration of the suppression effect (i.e. a brief orienting of attention vs a sustained allocation of attention). In addition, because the US was presented at a predictable time relative to CS+ onset but appeared on only 50% of the CS+ trials, we were able to ask whether the alpha-band suppression terminated as

soon as it became clear that no US was going to occur or whether the suppression lasted until the offset of the CS+ (indicating sustained vigilance to the CS+ itself).

A secondary goal was to provide a solid foundation for future research on alpha-band suppression and aversive conditioning by providing a detailed description of the conditioning effects with a very simple conditioning paradigm and a large sample size ( $N = 70$ ). This included a comparison of the alpha-band effect with a peripheral nervous system measure that is widely used to study aversive conditioning, the skin conductance response (Ohman et al., 1976; Kirsch and Boucsein, 1994; Marin et al., 2017).

## Methods

The present study consisted of a reanalysis of data from a previous publication (Bacigalupo and Luck, 2018). The participants, stimuli, task and EEG preprocessing methods are described in detail in that paper. Here, we provide an overview of those methods and a detailed description of the time–frequency (TF) methods we used to quantify the alpha-band EEG activity.

### Participants

Seventy young adults (49 females, 18–29 years with a mean age of 21), with no history of neurological or psychiatric conditions participated in this study. All volunteers signed an informed consent form before their participation, and the study was approved by the UC Davis Institutional Review Board.

### Stimuli and task

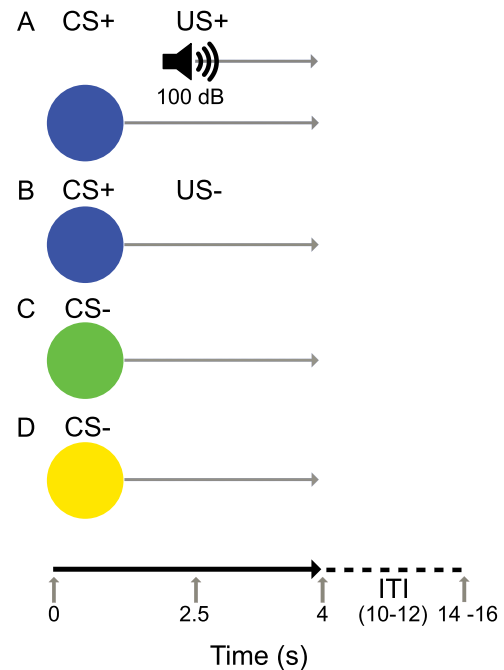
The experimental procedure consisted of a discriminative aversive conditioning paradigm with three phases: (i) habituation, (ii) aversive conditioning and (iii) extinction. In all three phases, participants were seated 100 cm from a liquid crystal display monitor with a black background and a continuously visible fixation point at the center. In each phase, the participants passively viewed a sequence of trials in which a circle ( $1.3^\circ$ ) was presented in the center of the screen. Each stimulus was presented for a duration of 4 s, and an inter-trial interval with random duration between 10 and 12 s occurred between successive stimuli. A photodiode was used measure the monitor delay (8 ms), and the stimulus event code times were shifted accordingly prior to data analysis.

#### Habituation phase

During the habituation phase, the stimulus was a gray ( $15 \text{ cd/cm}^2$ ) circle which was presented for a total of eight trials. Participants were told to relax and pay attention to the stimuli. The habituation phase is a common procedure that helps to ensure that participants understand the experimental procedures together with preventing novelty related EEG and skin conductance responses (SCRs) which could contaminate the data during the conditioning phase (Lonsdorf et al., 2017). The data from this phase were not analyzed.

#### Aversive conditioning phase

The aversive conditioning phase was divided into three separate blocks of trials. For each participant, one of three colors (blue, green or yellow) was randomly chosen as the CS (CS+), being paired with the US (a 100 dB white noise burst) with a partial reinforcement rate of 50%. The other two colors were never paired with the US (CS–). The CS+ and CS– colors were randomly assigned for each participant at the beginning of the experimental session and were maintained throughout the entire experimental session. Thus, the CS+ and CS– colors were constant for a given



**Fig. 1.** Aversive conditioning procedure. For each participant, one color was randomly chosen as the conditioned stimulus (CS+; A and B), whereas the other two colors (CS–) were never paired with the US (C and D). The US consisted of a 1500 ms 100 dB white noise burst. The US was presented on 50% of CS+ trials (denoted CS+US+ trials), beginning 2500 ms after CS+ onset and co-terminating with the CS+ (A). No US was presented on the other 50% of CS+ trials (denoted CS+US– trials) (B). Adapted from Bacigalupo and Luck (2018).

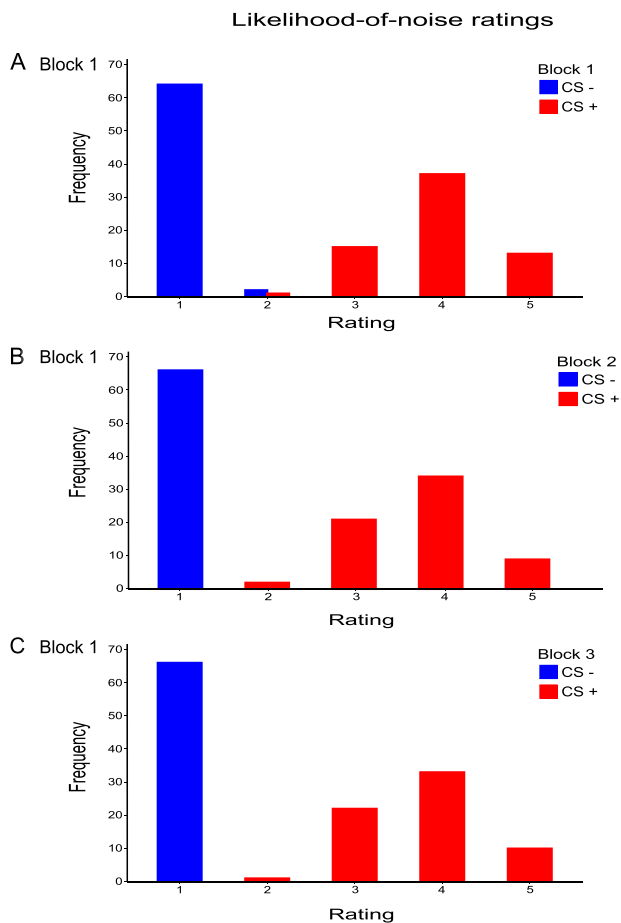
participant but varied across participants. The CS+ color was blue in 24 participants, green in 24 participants and yellow in 22 participants. The stimulus luminance was  $15 \text{ cd/cm}^2$ . The US was presented through two speakers starting 2.5 s after CS+ onset, and it lasted for 1.5 s, co-terminating with the CS+ (Figure 1).

Each block consisted of 32 trials: 8 CS+ paired with US (CS+US+), 8 CS+ without US (CS+US–) and 16 CS–. The stimuli were presented in pseudorandom order with the constraints that on each block the first three stimuli were CS+US+ and that there could not be more than two trials of the same color in a row. Participants were told that only one color would be associated with the noise and that they had to passively attend and determine if there was a relationship between a specific color and the US.

After each aversive conditioning block, the participants used a 5-point scale to report the US likelihood for each color (1 = ‘sure no noise’, 3 = ‘unsure’ and 5 = ‘sure noise’). Each block of the conditioning phase was followed by a period of approximately 40 min. During this period, participants performed an unrelated visual search task without any aversive stimuli (for details, see Bacigalupo and Luck, 2018). This makes the conditioning procedure a little more like the real world, in which episodes of conditioning may be separated by periods in which an individual is engaged in other activities.

#### Extinction

The extinction phase consisted in the presentation of the same-colored circles shown in the conditioning phase, but without the US. In this phase, 6 trials per color were presented in random order, with the constraint that a given color could appear no more than twice in succession (18 trials total). Participants were told



**Fig. 2.** Frequency distribution of the subjective rating of the likelihood of noise for the CS+ and CS- colors, assessed at the end of block 1 (A), block 2 (B) and block 3 (C). Each bar shows the number of participants who gave a given rating during that block. For example, almost all 66 participants gave a rating of '1' for the CS- in each block, so the bar for CS- has a value of nearly 66 for every block. For the CS+, most participants gave a rating of '4', but a substantial number gave ratings of '3' or '5'. Adapted from Bacigalupo and Luck (2018).

that no noises would be presented and were instructed to relax and attend to the colored circles.

### Psychophysiological recording and analysis

The EEG was recorded using a Brain Products ActiCHamp system with electrodes located over the left and right mastoid processes and at 27 standard scalp locations (Fp1, Fp2, F3, F4, F7, F8, C3, C4, P3, P4, P5, P6, P7, P8, P9, P10, PO3, PO4, PO7, PO8, O1, O2, Fz, Cz, Pz, POz and Oz). The horizontal EOG was computed as the difference between the electrodes located approximately 1 cm lateral to each eye, and the vertical EOG was computed as the difference between the electrode below the right eye and the Fp2 electrode. The SCR was recorded simultaneously by this same system, using Brain Products bipolar SCR electrodes placed on the distal phalanges of the second and third digits (Scerbo *et al.*, 1992).

All signals were recorded in single-ended mode with a sampling rate of 1000 Hz and a cascaded integrator-comb antialiasing filter with a half-power cutoff at 260 Hz. The electrode impedances were kept below 80 K $\Omega$ . After acquisition, all data analyses were performed in Matlab using EEGLAB Toolbox (Delorme and Makeig, 2004), ERPLAB Toolbox (Lopez-Calderon

and Luck, 2014) and FieldTrip (Oostenveld *et al.*, 2011). The signals were re-sampled offline to 250 Hz, referenced to the average of the two mastoid electrodes and high-pass filtered using a noncausal Butterworth filter (half-amplitude cutoff = 0.01 Hz and slope = 12 dB/octave). Independent component analysis (ICA) was then applied to the continuous EEG to correct for eye blinks and horizontal eye movements (for details, see Bacigalupo and Luck, 2018). After the ICA procedure, we rejected single trials if the peak-to-peak voltage within the EEG epoch was greater than 300  $\mu$ V in any 200 ms window in any channel. No EEG channels were rejected, so interpolation was not needed.

To avoid contamination from the US, aversive conditioning was assessed by comparing alpha-band power on CS- trials with CS+ trials that did not contain a US (CS+US- trials). We excluded four participants from the data analyses, one because of technical problems with the EEG recording hardware and the other three because of having more than 25% of trials rejected, which is our a priori criterion for good quality EEG data (Bacigalupo and Luck, 2015, 2018, 2019). Thus, sixty-six participants were included in the final analyses. In these remaining participants, an average of 4.2% of trials were rejected because of artifacts (range = 0–22%). The average number of trials remaining for analysis was  $70.3 \pm 3$  (range = 56–72) (excluding the CS+US+ trials). The average number of trials for the CS- condition was  $46.6 \pm 2.3$  (range = 37–48), whereas for the CS+ condition was  $23.7 \pm 0.89$  (range = 19–24).

### Skin conductance response

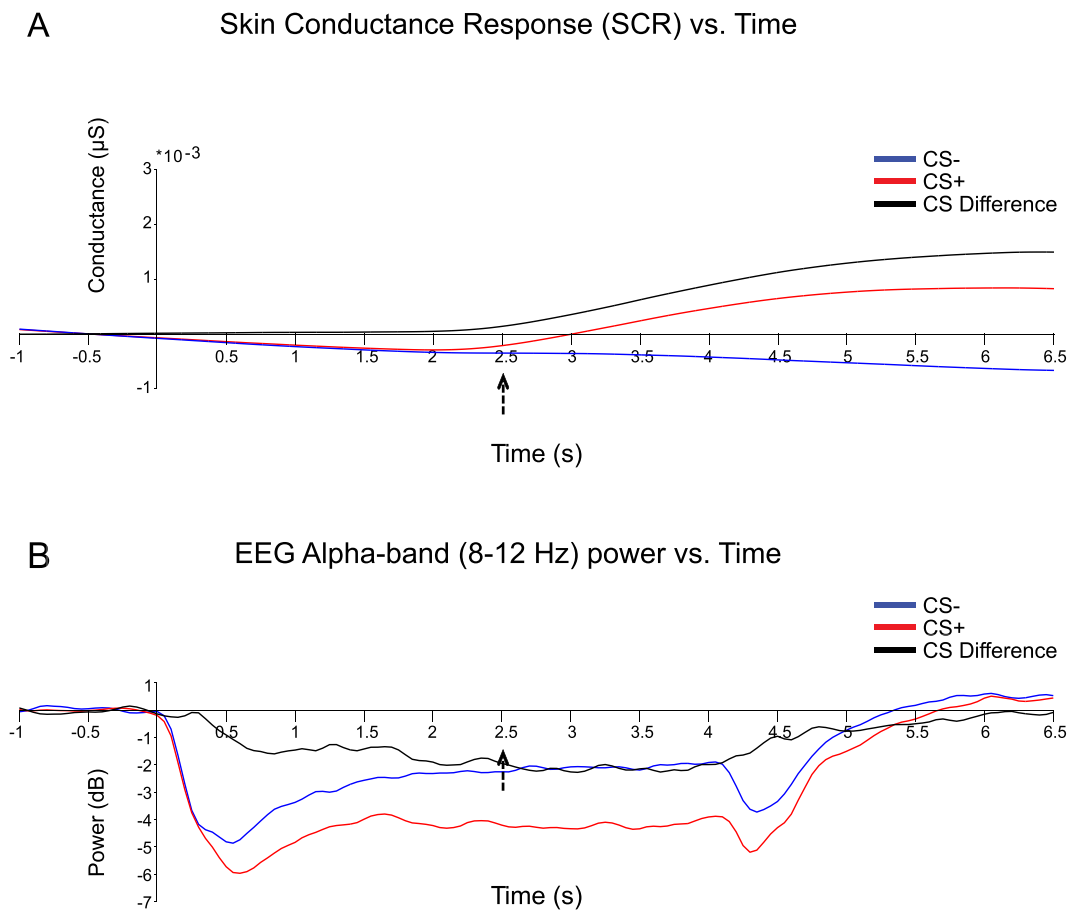
Averaged SCR waveforms were computed using a 14 s epoch, starting 1 s before CS+ or CS- onset. The SCR was measured as the mean amplitude from 4.5 to 6.5 s after stimulus onset using a 1 s prestimulus baseline. These parameters were determined a priori, following from the study of Bacigalupo and Luck (2018). Similar to the EEG analysis, aversive conditioning was assessed by comparing SCR amplitude on CS- trials with CS+US- trials. In the SCR analysis we included 100% of the trials (72 trials per participant, including 24 CS+US- trials and 24 trials for each CS- color).

### Extinction analyses

For extinction analyses we included EEG and SCR data of 58 participants. Because to evaluate the activity during extinction it is necessary to compare it with the activity of the previous conditioning phase, we had to necessarily exclude the subjects that were excluded in the conditioning analysis. Thus, from the initial 66 participants we excluded eight more because of poor data quality, according to our previously set criteria of having more than 25% of trials rejected. Therefore, 58 participants were included in the extinction analyses. An average of 3% of trials was rejected in the participants (range = 0–22%). Considering all participants except the first three ( $N = 55$ ), the average number of trials per participant in this phase was  $17.47 \pm 1$  (range = 14–18). The average number of trials for the CS- condition was  $11.6 \pm 0.8$  (range = 8–12), whereas for the CS+ condition was  $5.85 \pm 0.4$  (range = 4–6). For the first three participants a piloting phase was implemented, using 10 extinction trials per stimulus, summing up to 30 extinction trials total (20 CS- and 10 CS+ trials). Because of experimental time constraints and because extinction effects were evident in the subjective reports, we decided to reduce the number of trials per stimulus from 10 to 6.

To test for extinction effects, comparing the acquisition us extinction phases, we performed paired t-tests.





**Fig. 3.** SCR (A) and EEG alpha-band (8–12 Hz) power (B) over time for CS+, CS– and the conditioning effect (CS+ minus CS–). The SCR started to increase for CS+ trials but not for CS– trials approximately 2.5 s after stimulus onset, and this effect lasted for several seconds after stimulus offset. This result demonstrates that the conditioning procedure was successful. Suppression of the EEG alpha-band signal occurred for both CS+ and CS– stimuli within 200 ms of stimulus onset, but the suppression was larger for CS+ trials than for CS– trials. The CS+ label represents results from CS+US– trials only. The arrows indicate the time of expected US onset (2.5 s after CS+ onset).

### Time–frequency analyses

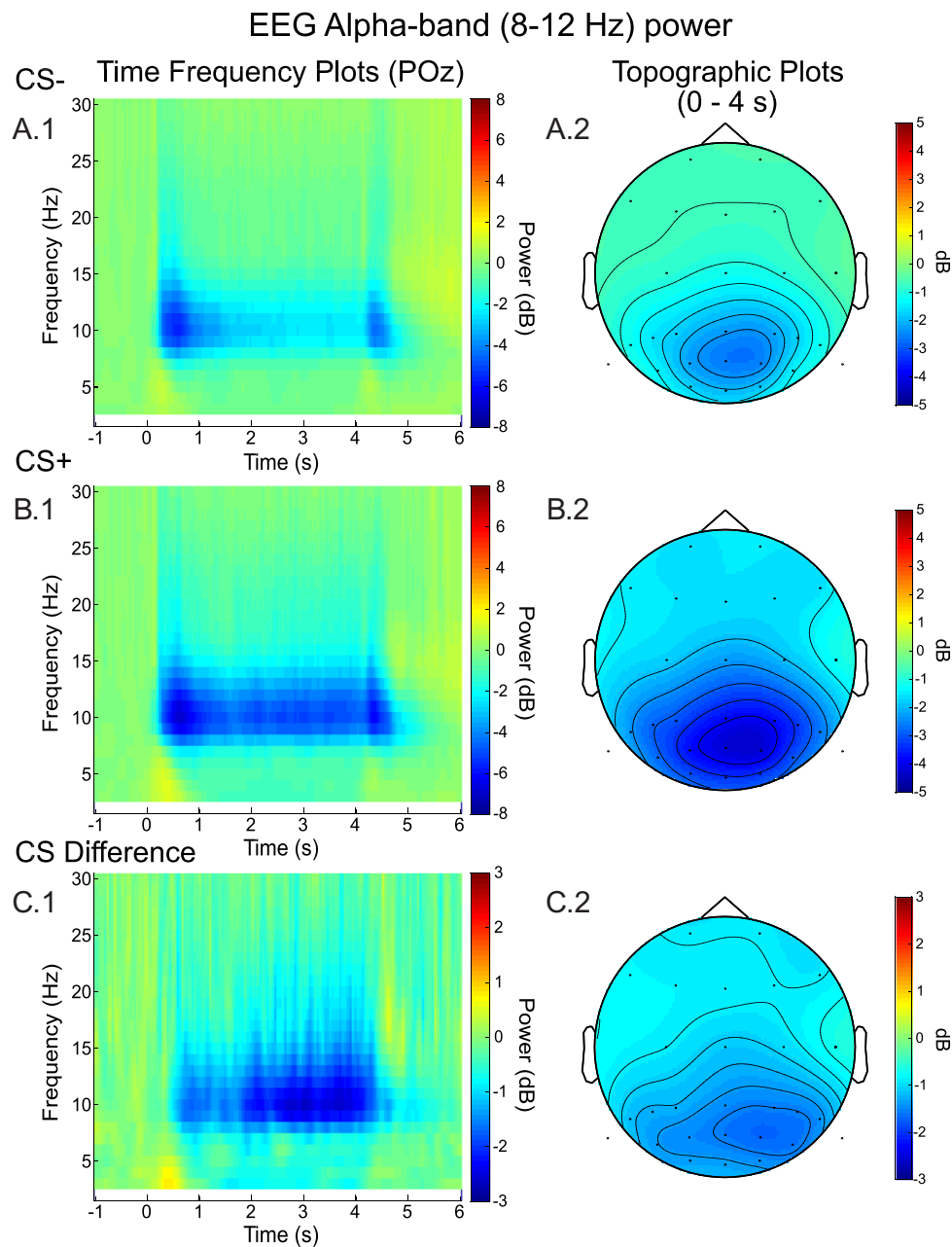
TF analysis was performed on 10 s EEG epochs that began 2.5 s prior to CS onset. The frequency representation of the EEG data was obtained through convolution in the time domain using Morlet wavelets from 2 to 30 Hz (in steps of 1 Hz) and a Gaussian taper, with analysis windows centered every 50 ms, using 5-cycle wavelets (Spaak et al., 2014). At 10 Hz, the temporal precision was 80 ms and the frequency precision was 2 Hz (quantified as the s.d. in time or frequency). Induced power (IP) was computed by subtracting the averaged ERP waveform from the single-trial EEG signals, for each experimental condition. The TF transform was then computed from the resulting single-trial signals, and the transformed data were averaged across trials for each specific time point and frequency.

After computing IP and averaging across trials, the data at each time point ( $t$ ) for a given frequency ( $f$ ) were normalized to the prestimulus power for that frequency on a dB scale. In other words, the normalized value at a given time point represented the change in power relative to the mean baseline power on a log scale. The normalization was implemented using the following equation:  $IP_{\log}(f, t) = 10 \log_{10}(IP_{\%}(f, t))$ , where  $IP_{\%}(f, t) = \frac{IP(f, t)}{\mu B(f)}$  and  $\mu B(f)$  is the mean spectral estimate for all baseline points

at frequency  $f$  (Grandchamp and Delorme, 2011). The normalization was performed separately for each combination of channel, frequency, trial type (CS+ or CS–), and participant.

The normalization used the activity from  $-700$  to  $-200$  ms as the baseline period. First, we selected a 500 ms period so that it would cover five cycles of the mean frequency of interest (10 Hz, one cycle every 100 ms), matching our 5-cycle wavelets. Second, the wavelet transformation results in a smearing of temporal information, and it is important to ensure that the baseline procedure does not end up subtracting signals from after stimulus onset. The temporal s.d. of our TF transform was 80 ms at 10 Hz, so our baseline period of  $-700$  to  $-200$  ms ended more than 2 s.d. before the time of stimulus presentation. Thus, the post-stimulus signals did not contaminate the measurement of baseline activity.

The primary dependent variable in our TF analysis was the mean power from 8 to 12 Hz at the POz electrode site. The frequency band and electrode site were chosen a priori based on previous research from our lab and elsewhere (Brandt, 1997; Chang et al., 2002; Bacigalupo and Luck, 2019). POz was also the electrode with greatest alpha suppression effects. To test whether the alpha-band effects during conditioning were present



**Fig. 4.** EEG alpha-band (8–12 Hz) power TF plots and topographic scalp maps for CS– (A.1; A.2), CS+ (B.1; B.2) and the CS+ minus CS– difference (C.1; C.2). The alpha-band suppression was greater and more sustained on CS+ trials (B.1) than on CS– trials (A.1), with a more pronounced difference between CS+ and CS– during the second half of the stimulus presentation window (C.1). The alpha-band suppression had an occipito-parietal distribution (A.2; B.2; C.2). Note that the CS+ data came from CS+US– trials only.

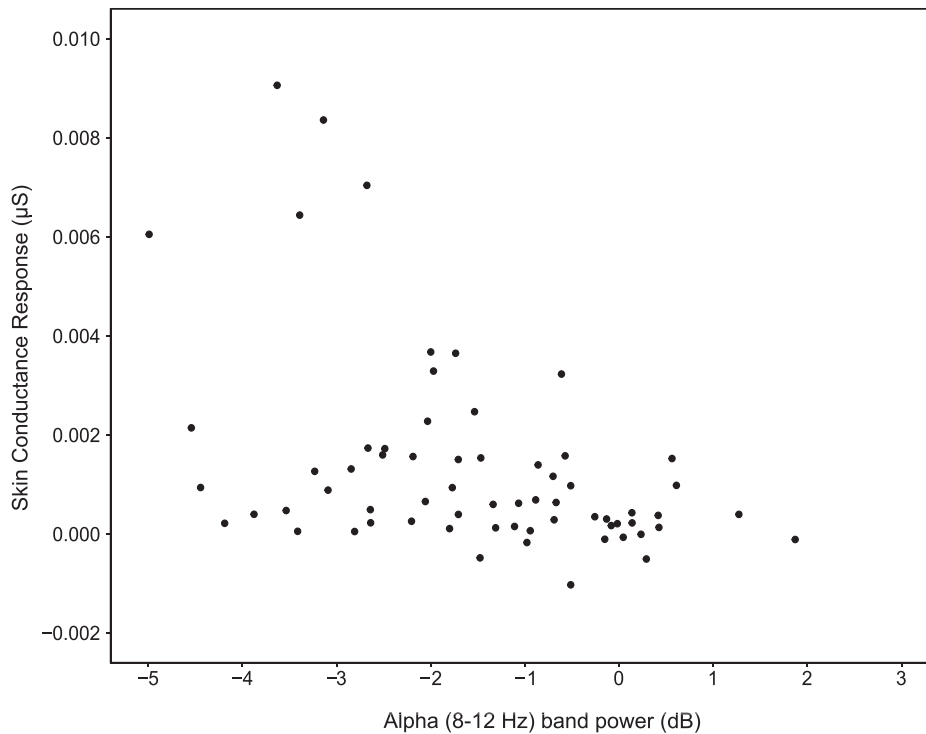
more broadly over parieto-occipital electrode sites, we also used a region-of-interest approach, in which the data were averaged across POz, PO3 and PO4 prior to the statistical analysis. The pattern of statistical significance was identical to what was obtained at POz, so we report only the POz results below.

Alpha-band suppression effects were measured using multiple time windows, described in detail in the Results section. Note that all the analyses were performed by comparing CS– trials to CS+US– trials, thus avoiding contamination by the US on CS+US+ trials. Thus, the CS+ label in the data figures represents results from CS+US– trials only.

## Statistical analysis

The threshold for statistical significance was 0.05. Statistical analyses were performed using R statistical software version 3.3.2 (R Core Team, 2013). For the analysis of behavioral subjective reports, Kruskal–Wallis and Wilcoxon nonparametric tests were performed. Paired samples t-tests were used for comparing SCR amplitude or alpha-band power differences between CS+ and CS– conditions. One-sample t-tests were used when the differences between CS+ and CS– trials were compared to zero. Repeated-measures analyses of variance (ANOVAs) were performed for the analysis of condition  $\times$  time-window analysis (CS–, CS+ and time windows: 0–1 s, 1–2 s, 2–3 s and 3–4 s) and for the condition  $\times$  block

## EEG Alpha-band (8-12 Hz) power vs. Skin Conductance Response



**Fig. 5.** Relationship between the alpha-band conditioning effect and the SCR conditioning effect (CS+ minus CS- difference scores for both measures). Participants who showed a greater alpha-band conditioning effect also showed an increased conditioning effect for the SCR, as depicted by the regression line. The correlation is negative because more negative values mean more suppression for the alpha-band EEG measure. Note that the CS+ data came from CS+US- trials only.

analysis (CS-, CS+ and blocks 1, 2 and 3). Multiple comparisons between conditions were performed using Tukey tests with Bonferroni correction. For alpha-band/SCR correlation analyses, Spearman ranked correlations were computed.

## Results

### Aversive conditioning: behavioral subjective reports

Figure 2 shows the ratings obtained at the end of each block in which participants reported the subjective likelihood that the CS+ and CS- stimuli would be followed by a noise burst. As previously reported (Bacigalupo and Luck, 2018), the subjective likelihood was greater for the CS+ color than for the CS- color at the end of each conditioning block. The difference between CS+ and CS- trials was statistically significant in each block (Wilcoxon Vs: 2211, all  $P$  values  $< 0.001$ ). To test whether ratings within CS+ and CS- categories changed across blocks, we performed Kruskal-Wallis tests, which yielded no significant differences across blocks (CS+:  $H_{(2)} = 2.53$ ,  $P = 0.28$ ; CS-:  $H_{(2)} = 4.02$ ,  $P = 0.13$ ). Thus, participants successfully learned the stimuli contingencies.

### Aversive conditioning: skin conductance response

As reported previously (Bacigalupo and Luck, 2018) and as shown in Figure 3A, the SCR started increasing in amplitude on CS+ trials relative to CS- trials beginning approximately 2.5 s after CS onset. Greater SCR activity was then present on CS+ trials than on CS- trials for the next several seconds, even after the

CS offset at 4 s. The SCR difference between CS+ and CS- stimuli (mean amplitude from 4.5 to 6.5 s after stimulus onset) was statistically significant ( $t_{(65)} = 5.46$ ,  $P < 0.001$ ). This replicates classical findings and demonstrates that the conditioning procedure was successful.

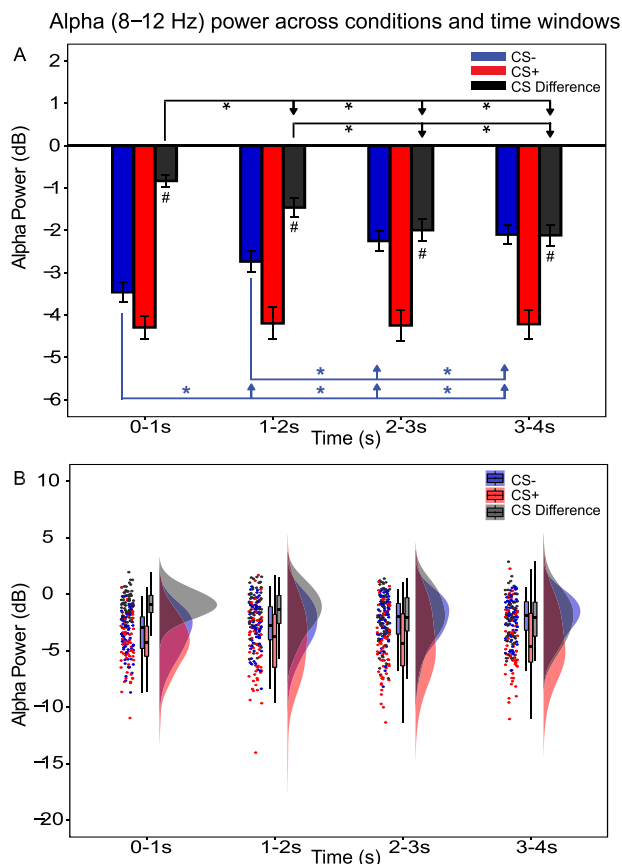
### Aversive conditioning: alpha-band (8–12 Hz) EEG power

As shown in Figures 3B and 4, alpha-band EEG activity decreased after the appearance of both the CS+ and CS-. This 'alpha-band suppression effect' exhibited the typical parieto-occipital scalp distribution (Figures 4.A.2 and B.2). However, the suppression was larger and more sustained following the CS+ than following the CS-. The difference between the alpha-band suppression for CS+ vs CS- trials also had a parieto-occipital scalp distribution (Figure 4.C.2).

There was a greater reduction of alpha-band activity for CS+ trials relative to CS- trials during the CS presentation window, as demonstrated by the statistically significant differences for the CS+ vs CS- mean alpha-band power between 0 and 4 s ( $t_{(65)} = -8.25$ ,  $P < 0.001$ ). Thus, like the SCR, alpha suppression was influenced by aversive conditioning, but with a much more rapid onset. As can be observed in Figure 3, suppression of the EEG alpha-band signal 'occurred' for both CS+ and CS- stimuli within 200 ms of stimulus onset, being larger for CS+ trials than for CS- trials. As mentioned, the SCR started to increase for CS+ trials but not for CS- trials approximately 2.5 s after stimulus onset.

Given the link between alpha suppression and attention, the increased alpha suppression for the CS+ presumably reflects





**Fig. 6.** Summary statistics for EEG alpha-band (8–12 Hz) power over 1-s time windows for CS-, CS+ and the CS+ minus CS- difference. The data are summarized both with bar plots showing mean  $\pm$  SEM (A) and with scatterplots, boxplots and density plots showing the estimated distribution (B). The alpha-band power difference between CS+ and CS- trials was statistically significant across all time windows and was greater during the second half of the stimulus presentation window. On CS- trials, alpha-band power decreased over time, suggesting diminished attentional engagement. However, alpha-band suppression was sustained on CS+ trials, suggesting continued attentional monitoring in anticipation of the US. \*# =  $P < 0.05$ . Note that the CS+ data came from CS+US- trials only.

increased attentional engagement when an aversive stimulus, i.e. threat, is expected.

Figure 5 shows the relationship between the alpha-band suppression effect and the SCR conditioning effect, quantifying each effect as the difference between CS+US- and CS- trials. Greater alpha-band suppression (i.e. a larger negative value for the alpha measure) was associated with a larger SCR effect. This was statistically analyzed using the Spearman rank-order correlation test, which yielded a significant negative correlation ( $r_{(64)} = -0.46$ ,  $P < 0.001$ ). Thus, participants who showed the greatest attention to threat, measured via alpha-band suppression, also showed the greatest activation of the sympathetic nervous system, measured via SCR.

### Aversive conditioning: time course of alpha-band suppression

As can be observed in Figures 3B and 4.c.1, the alpha-band suppression effect (difference between CS+ and CS-) ramped up rapidly after CS onset and was then maintained through CS offset. Note that the figures show the CS+US- trials to avoid contamination by the US response. When the US was presented (i.e. on

CS+US+ trials), the US always occurred at the same time (2.5 s after CS+ onset, as indicated by the arrow in Figure 3B). Thus, the waveforms in Figure 3B show that the alpha-band suppression effect lasted well after the time at which the US was expected. Indeed, the difference between CS+ and CS- trials was numerically greater after the expected time of the US than before this time (i.e. after vs before the arrow in Figure 3B).

To statistically analyze the time course of the conditioning effects, we divided the stimulus presentation time window into four 1-s windows (0–1 s, 1–2 s, 2–3 s and 3–4 s). Figure 6 shows the alpha-band suppression values measured from these time windows, and Figure 7 shows the corresponding scalp maps. As can be observed from these figures, alpha-band suppression on the CS- trials decreased over the period of the CS, whereas the suppression on CS+ trials was stable over the entire CS presentation period. As a result, the difference between CS+US- and CS- trials increased over time. These results were statistically analyzed using an ANOVA with factors of condition (CS+US-, CS-) and time window. Consistent with the preceding description, the ANOVA yielded a significant main effect for condition ( $F_{(1,455)} = 238.98$ ,  $P < 0.001$ ), for time window ( $F_{(3,455)} = 9.59$ ,  $P < 0.001$ ) and for the interaction between condition and time window ( $F_{(3,455)} = 8.02$ ,  $P < 0.001$ ). Separate t-tests for the alpha suppression difference between CS+US- trials and CS- trials yielded statistically significant differences for all four time windows (0–1 s,  $t_{(65)} = -6.03$ ; 1–2 s,  $t_{(65)} = -6.38$ ; 2–3 s,  $t_{(65)} = -7.51$ ; 3–4 s,  $t_{(65)} = -8.46$ ; all  $P$  values  $< 0.001$ ).

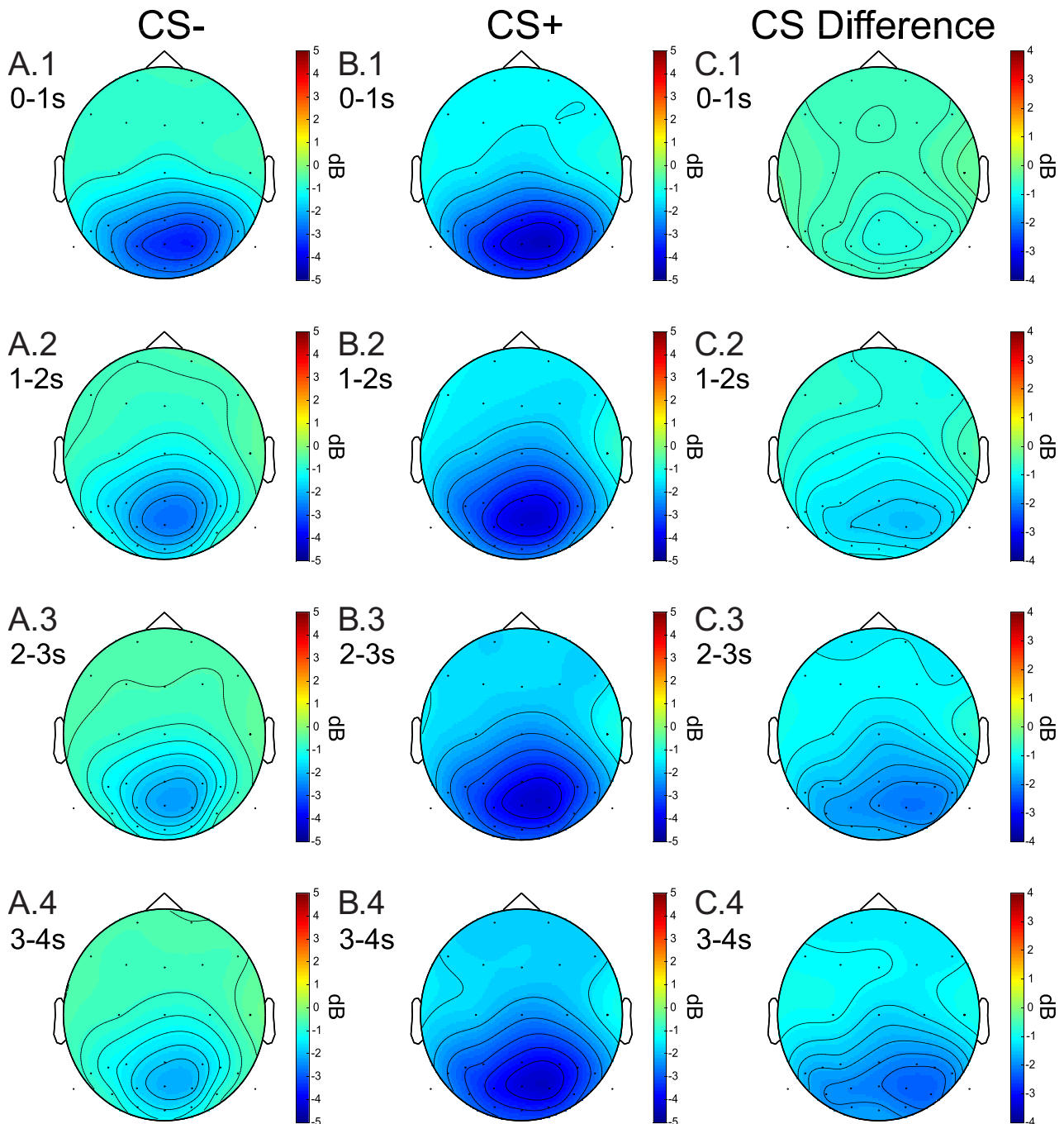
To test whether these effects were due to a reduction in alpha-band suppression over time on CS- trials or due to increased alpha-band suppression on CS+US- trials, we performed separate one-way ANOVAs for the CS- trials, for the CS+US- trials, and for the difference between CS+US- and CS- trials, with time window as the factor. For CS- trials, the ANOVA yielded a significant main effect of time window ( $F_{(3, 195)} = 43.51$ ,  $P < 0.001$ ), consistent with the reduced suppression after the first 1-s period on CS- trials that can be observed in Figures 6 and 7. As shown in Figure 6, pairwise comparisons between time windows yielded significant differences for the CS- between the early periods (0–1 s vs 1–2 s) and between each of these periods and each of the two later windows. Thus, EEG alpha-band suppression for the CS- was greater in the early time windows than in the late time windows.

In contrast, the effect of time window was not significant in the ANOVA for the CS+US- trials ( $F_{(3, 195)} = 0.108$ ,  $P = 0.95$ ). However, the ANOVA for the CS+ vs CS- difference yielded a significant main effect of time window ( $F_{(3, 195)} = 19.22$ ,  $P < 0.001$ ). Pairwise comparisons yielded statistically significant differences between all time periods except for 2–3 s vs 3–4 s (see Figure 6). Notably, the conditioning effect was significantly larger from 3 to 4 s than from 1 to 2 s, despite the fact that the US onset was never after 2.5 s. However, the conditioning effect clearly fell off rapidly once the CS+ terminated (see Figure 3B). Thus, the alpha-band suppression tracked the time course of the CS+ quite closely and did not end at 2.5 s, the time at which participants could have inferred that no US would be presented.

### Aversive conditioning: block-by-block analyses

The results shown so far were collapsed across the three conditioning blocks to maximize the signal-to-noise ratio. We also assessed whether the conditioning effects changed across blocks. The results are shown in Figures 8–10. The basic conditioning effect on alpha-band activity (CS+US- vs CS-) was visible during the first block of trials, indicating rapid learning, and was stable over blocks. This was verified statistically with an ANOVA on the

## EEG Alpha-band (8-12 Hz) power across time topographic plots



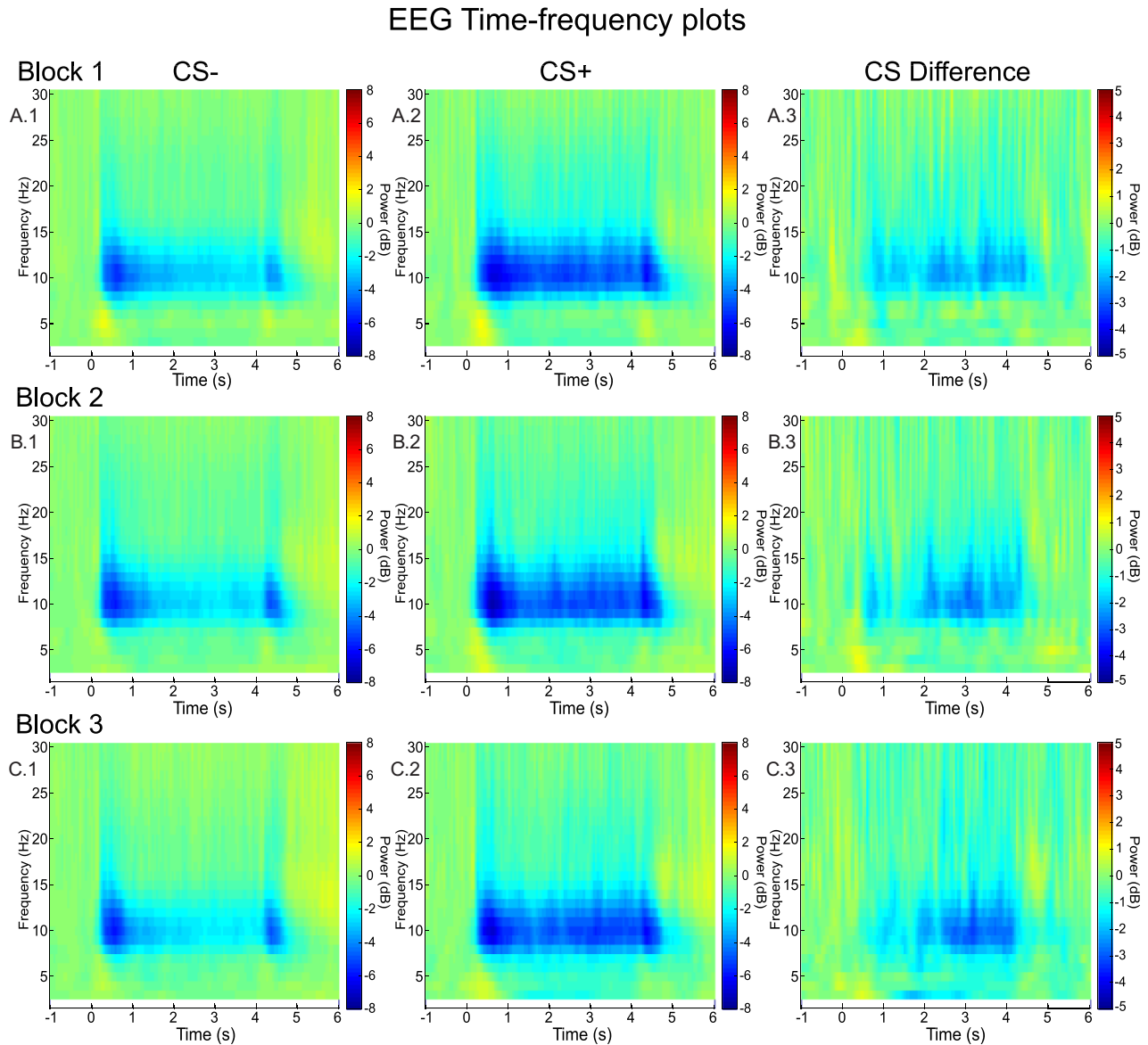
**Fig. 7.** Topographic maps of alpha-band (8–12 Hz) EEG power topographic during 1-s time windows for CS– (A.1–A.4), CS+ (B.1–B.4) and the CS+ minus CS– difference (C.1–C.4). The alpha-band suppression effect had an occipito-parietal distribution. On CS– trials, alpha-band power decreased over time, suggesting diminished attentional engagement. However, the alpha-band suppression was sustained on CS+ trials, suggesting continued attentional monitoring in anticipation of the US. Note that the CS+ data came from CS+US– trials only.

CS+ vs CS– difference in alpha-band activity, including conditioning block as factor, which yielded no significant differences across blocks ( $F_{(2, 130)} = 0.275, P = 0.76$ ).

In contrast, the SCR showed a dramatic amplitude reduction over blocks on CS+ trials, as can be observed in Figure 10B. The SCR conditioning effect (CS+ minus CS–) also decreased by more than 50% between the first block and the third block (Figure 10D). This was verified by analyzing these difference

scores in an ANOVA including block as factor, which yielded a significant effect of block ( $F_{(2, 130)} = 10.9, P < 0.001$ ). Further pairwise comparisons showed a statistically significant reduction in the SCR difference scores between block 1 and block 2 ( $z = -3.5, P = 0.0013$ ) and between block 1 and block 3 ( $z = -4.4, P < 0.001$ ). These results show that alpha-band suppression is stable over conditioning blocks, whereas SCR shows significant habituation effects.

## EEG Alpha-band (8-12 Hz) power across blocks



**Fig. 8.** TF plots for CS-, CS+ and the CS+ minus CS- difference, shown separately for each of the three blocks. The greater suppression of alpha-band activity for CS+ than for CS- was observed in all three blocks. Note that the CS+ data came from CS+US- trials only.

We also repeated the alpha-SCR correlation analyses described previously but performed separately for each of the three conditioning blocks. This yielded statistically significant negative correlations between the alpha-band suppression effect and the SCR conditioning effect for the first ( $r_{(64)} = -0.267$ ,  $P = 0.03$ ) and second blocks ( $r_{(64)} = -0.274$ ,  $P = 0.025$ ), but not for the third block ( $r_{(64)} = -0.011$ ,  $P = 0.92$ ). The absence of correlation for the third conditioning block is probably a side effect of the SCR habituation, because it is unlikely to find a correlation when one of the variables approaches zero.

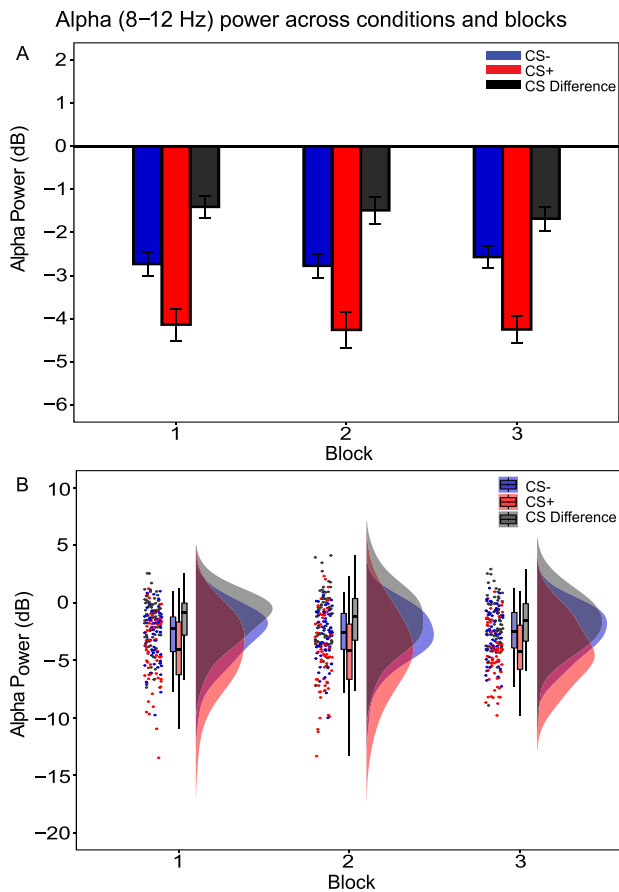
### Extinction

As can be observed in Figures 11 and 12, the conditioning effects for both alpha and SCR were greatly reduced compared to the last conditioning block. To test this statistically, we performed separate paired t-tests for SCR and alpha-band suppression effects

(CS+ minus CS- trials), comparing the last conditioning block and the extinction phase. Significant decreases between the last conditioning block and the extinction block were obtained for both SCR ( $t_{(100)} = 2.94$ ,  $P = 0.0039$ ) and alpha-band suppression ( $t_{(113.86)} = -2.48$ ,  $P = 0.014$ ).

### Discussion

The main goal of this study was to determine whether stimuli that predict the likelihood of a subsequent aversive event (threat stimuli) elicit transient attentional engagement, presumably reflecting the appraisal of the threat stimulus and/or sustained attentional engagement that reflects a continued enhancement of threat processing. We used an aversive conditioning procedure to create an experimentally controlled threat stimulus (the CS+), and we used suppression of alpha-band EEG



**Fig. 9.** Summary statistics for EEG alpha-band (8–12 Hz) power during each of the three trial blocks for CS-, CS+ and the CS+ minus CS- difference. The data are summarized both with bar plots showing mean  $\pm$  SEM (A) and with scatterplots, boxplots and density plots showing the estimated distribution (B). The alpha-band power difference between CS+ and CS- trials was stable over blocks. Note that the CS+ data came from CS+US- trials only.

activity to assess attentional engagement. Consistent with other measures of attention and prior EEG studies (Moratti et al., 2006; Stolarova et al., 2006), we found evidence that threat stimuli trigger enhanced attentional processing. That is, alpha-band suppression was greater for the CS+ than for the CS- within 500 ms of stimulus onset, as also shown by previous research (Chien et al., 2017; Panitz et al., 2019; Friedl and Keil, 2020, 2021; Yin et al., 2020). The main question was how long this effect would be sustained.

In the present study, the CS duration was 4 s, and when the US was present (on CS+US+ trials), the US began 2.5 s after the CS and co-terminated with the CS (see stimulus timing in Figure 1 and the arrows in Figure 3). We found that the greater alpha-band suppression for CS+ trials than for CS- trials persisted through the termination of the CS+. Given decades of evidence that alpha power reflects the degree of internal vs external attentional engagement (Klimesch et al., 2007; Benedek et al., 2014), with lower alpha associated with greater cortical responsiveness to external stimuli (Bollimunta et al., 2008; Romei et al., 2008), the sustained alpha suppression following the CS+ indicates that the CS+ triggered a period of sustained attentional engagement that persisted throughout the entire duration of the CS+, even after the time at which the US would be expected. Thus, whereas previous research using ERPs indicates that threat stimuli trigger a transient attentional response (e.g. Moratti et al., 2006; Ferreira de

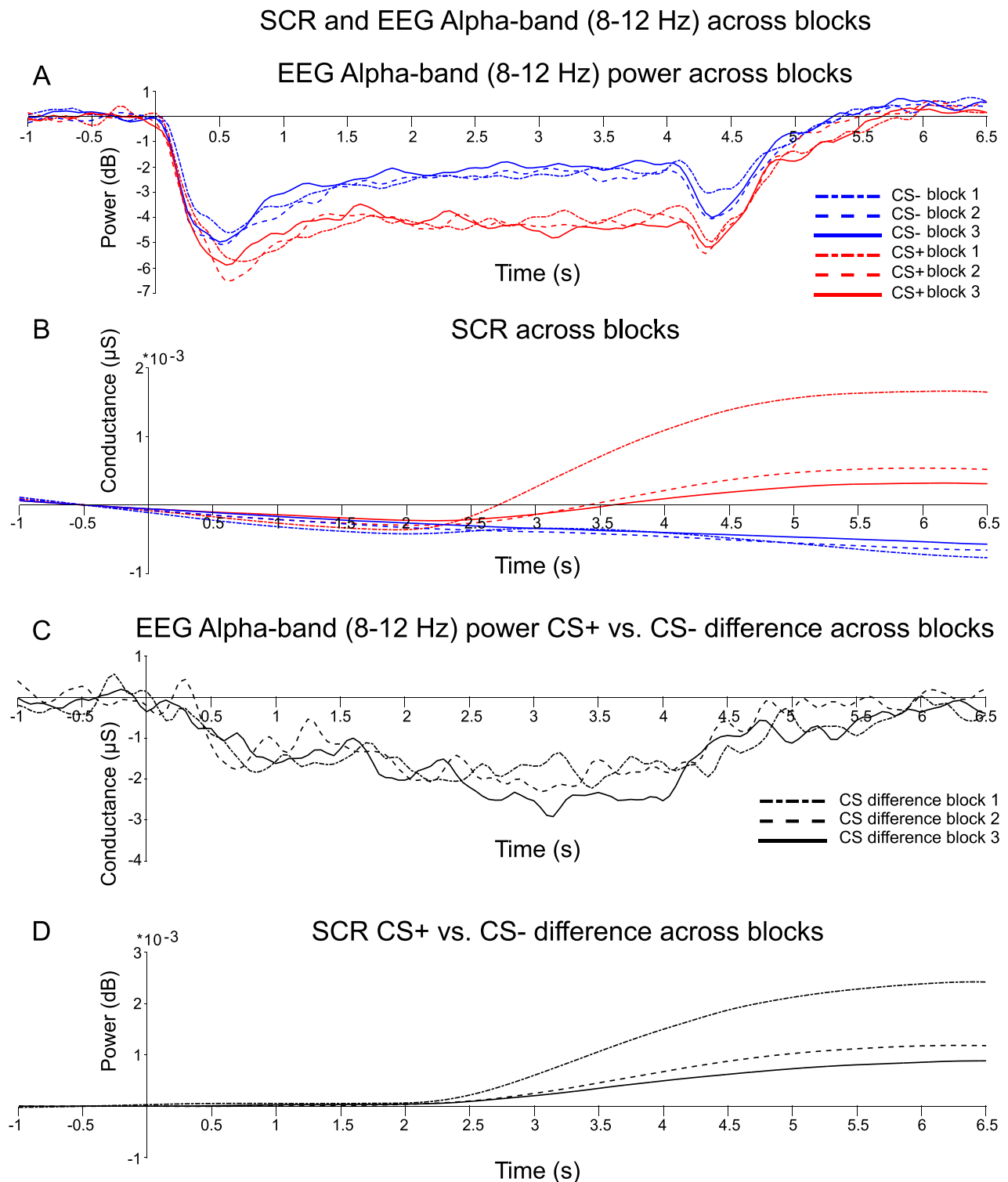
Sa et al., 2019; Kappenman et al., 2015), presumably related to the appraisal of the threat stimulus itself, the present results indicate that threat stimuli may also trigger a state of increased vigilance that lasts as long as the threat stimulus is visible (Schupp et al., 2003). A hint of this can be seen in previous studies of alpha-band suppression (Chien et al., 2017; Panitz et al., 2019; Friedl and Keil, 2020, 2021), but the present results more clearly establish that the suppression effect lasts for the entire duration of the CS, at least in the present conditioning paradigm.

On CS+US- trials, participants should have realized that the US was not going to be presented once 2.5 s had elapsed. However, the alpha-band suppression conditioning effect actually increased over the course of the CS, with a larger effect from 3 to 4 s than from 1 to 2 s. This was true even in the third block of the conditioning procedure (see Figure 10C). Why did the alpha-band suppression persist even after participants should have realized that they were 'safe'? A likely explanation is that the association between the color of the CS+ and the US was strong enough to force the sustained allocation of attention as long as the CS+ color was visible. This would be consistent with other evidence indicating that conditioning leads to a durable attraction of attention (Anderson, 2019). However, we cannot rule out the possibility that the duration of the alpha-band effect would become shorter with more blocks of conditioning, as the timing of the US became better learned.

Another interesting aspect of the present results is that the alpha-band effects were largest over visual cortex even though the US was an auditory stimulus. This suggests that participants were maintaining their attention on the visual CS+ rather than shifting their attention toward the auditory modality, which is also consistent with the finding that the alpha-band suppression lasted until the end of the CS+ on CS+US- trials. This further suggests that the CS+ has become an object of intrinsic interest and not just a predictor of the US. As an analogy, people may focus their visual attention strongly on a gun during an armed robbery, even though the feared outcome (being shot) would initially be signaled in the auditory modality and then be experienced as pain in the somatosensory modality.

The finding of a sustained suppression of alpha-band activity following a CS+ is important theoretically, but it may also have practical importance in studying anxiety and trauma-related disorders, which often involve hypervigilance. That is, research on these disorders could use transient attention-related ERP components (e.g. N2pc and LPP) to assess enhanced appraisal of the threat stimulus itself, combined with alpha suppression to assess sustained vigilance following the threat stimulus. Therefore, alpha suppression may be a candidate biomarker for hypervigilance, which is a key symptom in anxiety and trauma-related disorders (Craske et al., 2009). The heightened state of arousal is related to disabling symptoms such as panic attacks and insomnia, and there is evidence supporting the role of hypervigilance in the development of anxiety disorders in children who have experienced trauma and abuse (Hoehn-Saric and McLeod, 2000; Longley et al., 2006; Werner et al., 2020). The fact that the sustained alpha-band suppression in the present study continued even after the actual threat of the US was over also supports the use of this measure for examining hypervigilance. Thus, alpha suppression may provide a useful method for studying the mechanism by which hypervigilance affects individuals with anxious symptoms.

Some alpha suppression was present for the CS- until the stimulus terminated (see Figure 3B), suggesting that subjects continued to engage in low-level vigilance following the CS-. This may be a simple generalization effect, reflecting the fact that



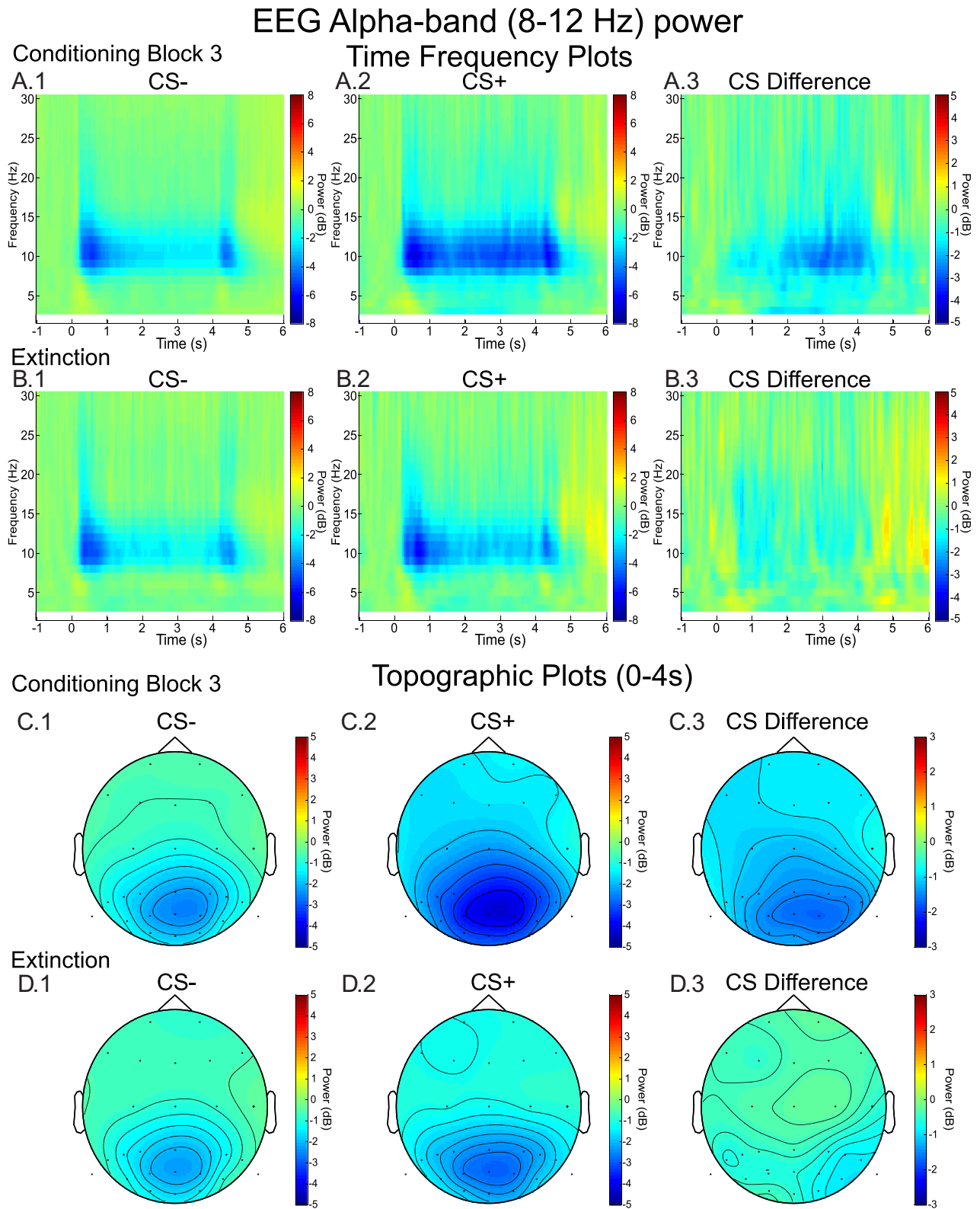
**Fig. 10.** Time course of the EEG and SCR measures separated by trial block. (A) EEG alpha-band (8–12 Hz) power for CS+ and CS- trials. The greater suppression of alpha-band activity for CS+ than for CS- was observed in all three blocks. (B) SCR amplitude for CS+ and CS- trial. The greater SCR activity for CS+ than for CS- declined over blocks. (C) Difference between CS+ and CS- trials for EEG alpha-band activity. This difference was stable across blocks. (D) Difference between CS+ and CS- trials for the SCR. This difference decreased significantly across blocks, thus showing habituation. Note that the CS+ data came from CS+US- trials only.

the CS- was similar to the CS+ in features such as size and shape. Alternatively, given that real-world threat probabilities may change over time, the sustained alpha suppression for the CS- may reflect the need to keep monitoring for aversive stimuli

even after a stimulus that has previously been associated with the absence of a negative outcome.

It should be noted that the number of CS+ trials was equal to the number of CS- trials, but because there were two CS-





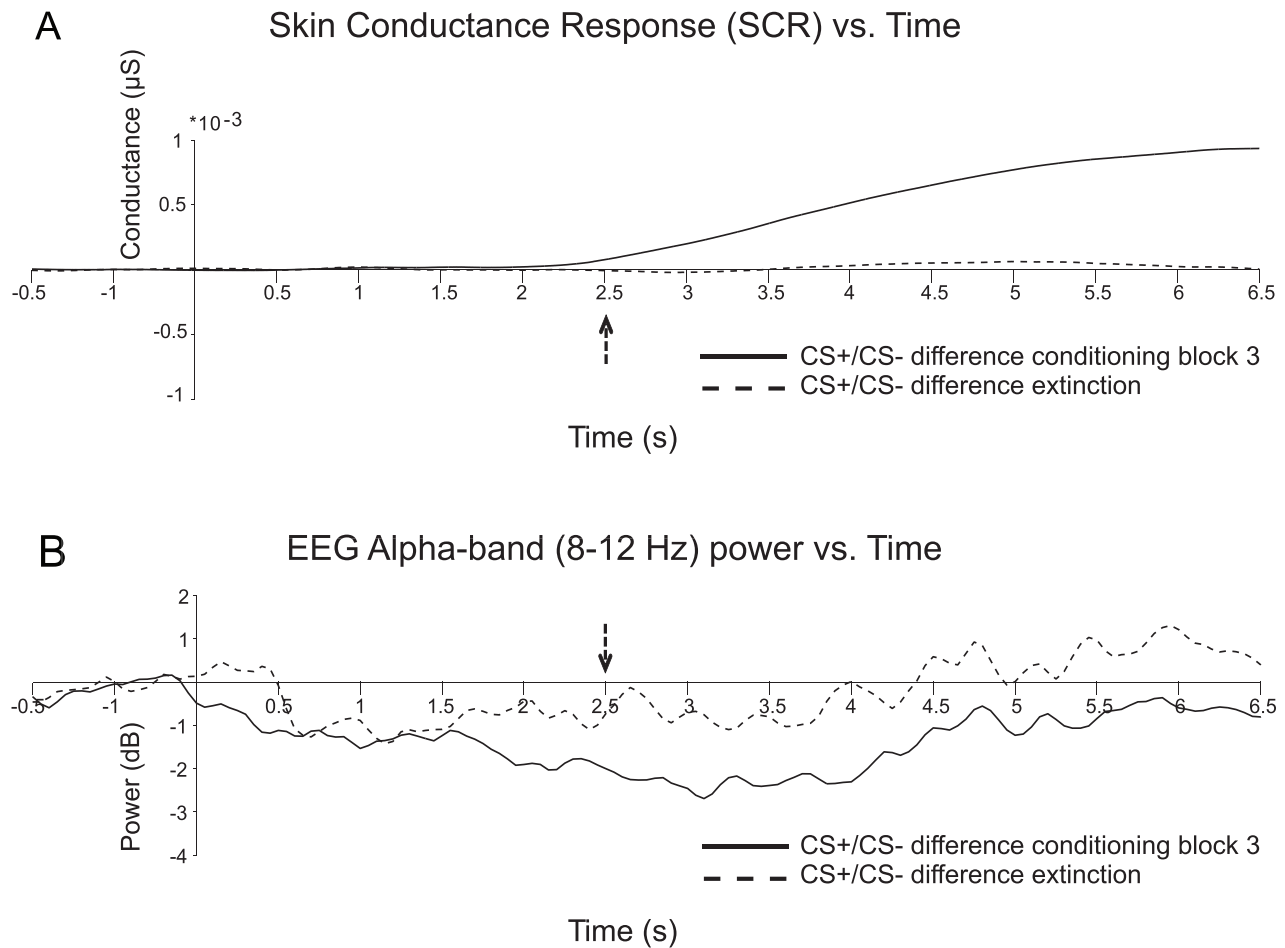
**Fig. 11.** EEG alpha-band (8–12 Hz) TF plots and topographic scalp maps for CS+, CS– and the difference between CS+ and CS– during the last conditioning block (A.1–A.3; c.1–c.3) and the extinction block (B.1–B.3; D.1–D.3). In conditioning block 3, alpha-band suppression was greater on CS+ trials (A.2; C.2) than on CS– trials (A.1; C.1). The difference in alpha-band suppression between CS+ and CS– trials during conditioning block 3 can be observed in A.3 and C.3. This effect was significantly reduced during extinction (B.3 and D.3).

colors but only one CS+ color in each trial block, the CS+ color occurred twice as often as each individual CS– color. This difference in probability could lead to greater adaptation for the CS+

color than for the CS– colors, which in turn would produce less attention-related activity for the CS+ color (Kohn, 2007). However, we found the opposite pattern, with a greater attentional



## Conditioning and extinction SCR and alpha-band suppression



**Fig. 12.** Difference waveforms (CS+ minus CS-) for the third conditioning block and extinction. A. SCR amplitude. B. EEG alpha-band (8–12 Hz) power. Both SCR amplitude and alpha-band power showed significant reductions for extinction compared to the third conditioning block.

response (i.e. alpha-band suppression) for the CS+ color than for the CS- colors. Thus, the difference in probabilities cannot easily explain the observed results.

In addition to alpha-band EEG suppression, we also measured the SCR, a peripheral nervous system measure that is commonly used to assess aversive conditioning (Ohman et al., 1976; Kirsch and Boucsein, 1994; Marin et al., 2017). We had previously shown that the SCR was larger for the CS+ than for the CS- in this dataset (Bacigalupo and Luck, 2018), but that this effect declined over blocks. When we looked at the conditioning effect (CS+ minus CS-) for both the SCR and alpha, we found a statistically significant negative correlation between alpha-band suppression and SCR amplitude. That is, participants who showed the greatest conditioning effect measured via alpha-band suppression also showed the greatest conditioning effect measured via SCR.

One possible explanation for this correlation is that the heightened attention to the CS+ indexed by the alpha-band suppression led to activation of the fight-flight-freeze response system that the SCR is thought to index (Critchley, 2002; Laine et al., 2009). Another possibility is that both mechanisms are triggered by the same neural signal, which theoretically could be generated in

the central nucleus of the amygdala (Phelps and LeDoux, 2005; Ross et al., 2017). However, our block-by-block showed different habituation patterns for these two measures. That is, the SCR conditioning effect decreased dramatically across blocks, whereas the alpha-band conditioning effect was largely stable (Figures 8–10). Additional research is needed to determine the relationship between alpha-band suppression and SCR in the context of threat processing.

Although our interpretation is that the greater alpha-band suppression effect for CS+ vs CS- stimulus is a marker of heightened arousal related to threat/aversive expectancy, an alternative view would be that alpha-band suppression signals increased attention to novelty, regardless of the valence of the expected stimulus. In this study, valence and arousal were not evaluated behaviorally, and it is likely that both dimensions were tightly linked to the nature of the stimuli (CS+: high-arousal and aversive/negative valence; CS-: low-arousal and neutral valence). Thus, the present study does not allow disentangling which specific feature (valence or arousal) is marked by alpha-band suppression. Future research may help to clarify the role of attention-related alpha-band suppression in the evaluation of stimuli with different emotional valence and also with different

predicting values of aversive/appetitive outcomes in the context of associative learning and other types of memory (Kensinger and Corkin, 2004; Costanzi et al., 2019).

The results of the extinction phase showed that alpha-band suppression decreased, as would be expected for a marker of attention-related threat processing. Because during extinction the participants learned that the CS+ was no longer a threat-related cue, it was not necessary to be in a state of increased arousal for attending the environment. It is important to notice that the participants knew that no noise would be presented during this phase. Therefore, the CS+ stimulus was most likely considered non-threatening right from the start of extinction phase. Thus, both the alpha-band power reduction and the SCR amplitude decrease during extinction could be explained by explicit learning i.e. top-down driven mechanisms. This might be an interesting topic for future research, testing whether there are differences in attention-related neural activity between implicit vs explicit extinction learning and the effects on phenomena such as extinction retrieval, spontaneous recovery, fear reinstatement and renewal (Maren and Holmes, 2016; Oyarzun et al., 2019).

Although SCR has been used for several decades to assess aversive conditioning and extinction, it has two main limitations: (i) it is an indirect measure of brain function (measured at the fingertips) and (ii) it has a delayed onset (2–3 s). However, cognitive function is fast, occurring at a millisecond time scale. Thus, alternative methods are needed to study more directly the role of neurocognitive functions such as attention in aversive conditioning. Although it has been argued that EEG-based methods for assessing aversive conditioning are difficult to implement (Lonsdorf et al., 2017), our results show that it is possible to use EEG-based measures such as alpha-band suppression to study the role of attention in aversive conditioning. Previously, we have also shown that another EEG-based method, namely the LPP component, can be used to study attentional processes during aversive associative learning (Bacigalupo and Luck, 2018). Since then, other researchers have used ERP components, including the LPP, for studying the role of attention in aversive conditioning (Ferreira de Sa et al., 2019). Thus, EEG-based measures may become increasingly used to study aversive conditioning and extinction, bringing together behavioral and neural methods that were first developed almost 100 years ago in the works of Pavlov, Berger and Adrian (Pavlov, 1927; Berger, 1929; Adrian and Matthews, 1934).

## Funding

This research was made possible by National Institutes of Health grants R03MH098119 and R01MH076226 awarded to S. J. L. and Fondecyt-ANID grant N°11180723 awarded to F. B.

## Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

## References

- Adrian, E.D., Matthews, B.H. (1934). The interpretation of potential waves in the cortex. *The Journal of Physiology*, **81**, 440–71.
- Anderson, B.A. (2019). Neurobiology of value-driven attention. *Current Opinion in Psychology*, **29**, 27–33.
- Bacigalupo, F., Luck, S.J. (2015). The allocation of attention and working memory in visual crowding. *Journal of Cognitive Neuroscience*, **27**, 1180–93.
- Bacigalupo, F., Luck, S.J. (2018). Event-related potential components as measures of aversive conditioning in humans. *Psychophysiology*, **55**(4).
- Bacigalupo, F., Luck, S.J. (2019). Lateralized suppression of alpha-band EEG activity as a mechanism of target processing. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **39**, 900–17.
- Bae, G.Y., Luck, S.J. (2019). Decoding motion direction using the topography of sustained ERPs and alpha oscillations. *Neuroimage*, **184**, 242–55.
- Benedek, M., Schickel, R.J., Jauk, E., Fink, A., Neubauer, A.C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, **56**, 393–400.
- Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, **87**, 527–70.
- Bielecki, M., Popiel, A., Zawadzki, B., Sedek, G. (2017). Age as moderator of emotional Stroop task performance in posttraumatic stress disorder (PTSD). *Frontiers in Psychology*, **8**, 1614.
- Bocker, K.B., Baas, J.M., Kenemans, J.L., Verbaten, M.N. (2001). Stimulus-preceding negativity induced by fear: a manifestation of affective anticipation. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, **43**, 77–90.
- Bollimunta, A., Chen, Y., Schroeder, C.E., Ding, M. (2008). Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **28**, 9976–88.
- Bollimunta, A., Mo, J., Schroeder, C.E., Ding, M. (2011). Neuronal mechanisms and attentional modulation of corticothalamic alpha oscillations. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **31**, 4935–43.
- Brandt, M.E. (1997). Visual and auditory evoked phase resetting of the alpha EEG. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, **26**, 285–98.
- Chang, P.F., Arendt-Nielsen, L., Chen, A.C. (2002). Dynamic changes and spatial correlation of EEG activities during cold pressor test in man. *Brain Research Bulletin*, **57**, 667–75.
- Chatila, M., Milleret, C., Rougeul, A., Buser, P. (1993). Alpha rhythm in the cat thalamus. *Comptes rendus de l'Academie des sciences. Serie III, Sciences de la vie*, **316**, 51–8.
- Chien, J.H., Colloca, L., Korzeniewska, A., et al. (2017). Oscillatory EEG activity induced by conditioning stimuli during fear conditioning reflects Salience and Valence of these stimuli more than Expectancy. *Neuroscience*, **346**, 81–93.
- Compton, R.J., Gearinger, D., Wild, H. (2019). The wandering mind oscillates: EEG alpha power is enhanced during moments of mind-wandering. *Cognitive, Affective & Behavioral Neuroscience*, **19**, 1184–91.
- Core Team, R. (2013). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Costanzi, M., Cianfanelli, B., Sarauli, D., et al. (2019). The effect of emotional valence and arousal on visuo-spatial working memory: incidental emotional learning and memory for object-location. *Frontiers in Psychology*, **10**, 2587.
- Craske, M.G., Rauch, S.L., Ursano, R., Prenoveau, J., Pine, D.S., Zinbarg, R.E. (2009). What is an anxiety disorder? *Depression and Anxiety*, **26**, 1066–85.
- Critchley, H.D. (2002). Electrodermal responses: what happens in the brain. *Neuroscientist*, **8**, 132–42.
- de Vries, I.E.J., van Driel, J., Olivers, C.N.L. (2019). Decoding the status of working memory representations in preparation of visual selection. *Neuroimage*, **191**, 549–59.

- Delorme, A., Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, **134**, 9–21.
- Dieterich, R., Endrass, T., Kathmann, N. (2016). Uncertainty is associated with increased selective attention and sustained stimulus processing. *Cognitive, Affective & Behavioral Neuroscience*, **16**, 447–56.
- Ferreira de Sa, D.S., Michael, T., Wilhelm, F.H., Peyk, P. (2019). Learning to see the threat: temporal dynamics of ERPs of motivated attention in fear conditioning. *Social Cognitive and Affective Neuroscience*, **14**, 189–203.
- Foster, J.J., Sutterer, D.W., Serences, J.T., Vogel, E.K., Awh, E. (2016). The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology*, **115**, 168–77.
- Friedl, W.M., Keil, A. (2020). Effects of experience on spatial frequency tuning in the visual system: behavioral, visuocortical, and alpha-band responses. *Journal of Cognitive Neuroscience*, **32**, 1153–69.
- Friedl, W.M., Keil, A. (2021). Aversive conditioning of spatial position sharpens neural population-level tuning in visual cortex and selectively alters alpha-band activity. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **41**, 5723–33.
- Gallotto, S., Duecker, F., Oever, S.T., Schuhmann, T., de Graaf, T.A., Sack, A.T. (2020). Relating alpha power modulations to competing visuospatial attention theories. *Neuroimage*, **207**, 116429.
- Grafton, B., MacLeod, C. (2014). Enhanced probing of attentional bias: the independence of anxiety-linked selectivity in attentional engagement with and disengagement from negative information. *Cognition & Emotion*, **28**, 1287–302.
- Grandchamp, R., Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology*, **2**, 236.
- Grupe, D.W., Nitschke, J.B. (2013). Uncertainty and anticipation in anxiety: an integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, **14**, 488–501.
- Harris, A.M., Dux, P.E., Mattingley, J.B. (2018). Awareness is related to reduced post-stimulus alpha power: a no-report inattention blindness study. *The European Journal of Neuroscience*, **52**(11), 4411–22.
- Heyselaar, E., Mazaheri, A., Hagoort, P., Segaert, K. (2018). Changes in alpha activity reveal that social opinion modulates attention allocation during face processing. *Neuroimage*, **174**, 432–40.
- Hoehn-Saric, R., McLeod, D.R. (2000). Anxiety and arousal: physiological changes and their perception. *Journal of Affective Disorders*, **61**, 217–24.
- Kappenman, E.S., MacNamara, A., Proudfit, G.H. (2015). Electrocortical evidence for rapid allocation of attention to threat in the dot-probe task. *Social Cognitive and Affective Neuroscience*, **10**(4), 577–83.
- Kappenman, E.S., Geddert, R., Farrens, J.L., McDonald, J.J., Hajcak, G. (2021). Recoiling from threat: anxiety is related to heightened suppression of threat, not increased attention to threat. *Clinical Psychological Science*, **9**, 434–48.
- Kensinger, E.A., Corkin, S. (2004). Two routes to emotional memory: distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 3310–5.
- Kirsch, P., Boucsein, W. (1994). Electrodermal Pavlovian conditioning with prepared and unprepared stimuli. *Integrative Physiological and Behavioral Science: The Official Journal of the Pavlovian Society*, **29**, 134–40.
- Klimesch, W., Doppelmayr, M., Yonelinas, A., et al. (2001). Theta synchronization during episodic retrieval: neural correlates of conscious awareness. *Brain Research. Cognitive Brain Research*, **12**, 33–8.
- Klimesch, W., Sauseng, P., Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, **53**, 63–88.
- Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. *Journal of Neurophysiology*, **97**, 3155–64.
- Koster, E.H., Crombez, G., Van Damme, S., Verschuere, B., De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion*, **4**, 312–7.
- Laine, C.M., Spitler, K.M., Mosher, C.P., Gothard, K.M. (2009). Behavioral triggers of skin conductance responses and their neural correlates in the primate amygdala. *Journal of Neurophysiology*, **101**, 1749–54.
- Liu, Z., de Zwart, J.A., Yao, B., van Gelderen, P., Kuo, L.W., Duyn, J.H. (2012). Finding thalamic BOLD correlates to posterior alpha EEG. *Neuroimage*, **63**, 1060–9.
- Longley, S.L., Watson, D., Noyes, R., Jr, Yoder, K. (2006). Panic and phobic anxiety: associations among neuroticism, physiological hyperarousal, anxiety sensitivity, and three phobias. *Journal of Anxiety Disorders*, **20**, 718–39.
- Lonsdorf, T.B., et al. (2017). Don't fear 'fear conditioning': methodological considerations for the design and analysis of studies on human fear acquisition, extinction, and return of fear. *Neuroscience and Biobehavioral Reviews*, **77**, 247–85.
- Lopes da Silva, F.H., Vos, J.E., Mooibroek, J., Van Rotterdam, A. (1980). Relative contributions of intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by partial coherence analysis. *Electroencephalography and Clinical Neurophysiology*, **50**, 449–56.
- Lopez-Calderon, J., Luck, S.J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, **8**, 213.
- MacLeod, C., Mathews, A., Tata, P. (1986). Attentional bias in emotional disorders. *Journal of Abnormal Psychology*, **95**, 15–20.
- MacLeod, C., Mathews, A. (1991). Biased cognitive operations in anxiety: accessibility of information or assignment of processing priorities? *Behaviour Research and Therapy*, **29**, 599–610.
- Maren, S., Holmes, A. (2016). Stress and fear extinction. *Neuropsychopharmacology*, **41**, 58–79.
- Marin, M.F., Zsido, R.G., Song, H., et al. (2017). Skin conductance responses and neural activations during fear conditioning and extinction recall across anxiety disorders. *JAMA Psychiatry*, **74**, 622–31.
- Minarik, T., Berger, B., Sauseng, P. (2018). The involvement of alpha oscillations in voluntary attention directed towards encoding episodic memories. *Neuroimage*, **166**, 307–16.
- Moratti, S., Keil, A., Miller, G.A. (2006). Fear but not awareness predicts enhanced sensory processing in fear conditioning. *Psychophysiology*, **43**, 216–26.
- Oehlberg, K., Mineka, S. (2011). Fear conditioning and attention to threat: an integrative approach to understanding the etiology of anxiety disorders. In: Schachtman, T.R. and Reilly, S., editors. *Associative Learning and Conditioning Theory: Human and non-human Applications*. Oxford University Press. Oxford University Press. [10.1093/acprof:oso/9780199735969.001.0001](https://doi.org/10.1093/acprof:oso/9780199735969.001.0001).
- Ohman, A., Fredrikson, M., Hugdahl, K., Rimmö, P.A. (1976). The premise of equipotentiality in human classical conditioning: conditioned electrodermal responses to potentially phobic stimuli. *Journal of Experimental Psychology. General*, **105**, 313–37.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M. (2011). FieldTrip: open source software for advanced analysis of MEG, EEG, and

- invasive electrophysiological data. *Computational Intelligence and Neuroscience*, **2011**, 156869.
- Oyarzun, J.P., Camara, E., Kouider, S., Fuentemilla, L., de Diego-balaguer, R. (2019). Implicit but not explicit extinction to threat-conditioned stimulus prevents spontaneous recovery of threat-potentiated startle responses in humans. *Brain and Behavior*, **9**, e01157.
- Panitz, C., Keil, A., Mueller, E.M. (2019). Extinction-resistant attention to long-term conditioned threat is indexed by selective visuocortical alpha suppression in humans. *Scientific Reports*, **9**(1), 15809.
- Pavlov, I.P. (1927). *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex*. Translated and Edited by Anrep, G.V. London: Oxford University Press, 142.
- Phelps, E.A., LeDoux, J.E. (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron*, **48**, 175–87.
- Reutter, M., Hewig, J., Wieser, M.J., Osinsky, R. (2017). The N2pc component reliably captures attentional bias in social anxiety. *Psychophysiology*, **54**, 519–27.
- Romei, V., Rihs, T., Brodbeck, V., Thut, G. (2008). Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *Neuroreport*, **19**, 203–8.
- Ross, D.A., Arbuckle, M.R., Travis, M.J., Dwyer, J.B., van Schalkwyk, G.I., Ressler, K.J. (2017). An integrated neuroscience perspective on formulation and treatment planning for posttraumatic stress disorder: an educational review. *JAMA Psychiatry*, **74**, 407–15.
- Scerbo, A.S., Freedman, L.W., Raine, A., Dawson, M.E., Venables, P.H. (1992). A major effect of recording site on measurement of electrodermal activity. *Psychophysiology*, **29**, 241–6.
- Schupp, H.T., Junghofer, M., Weike, A.I., Hamm, A.O. (2003). Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. *Neuroreport*, **14**, 1107–10.
- Spaak, E., de Lange, F.P., Jensen, O. (2014). Local entrainment of  $\alpha$  oscillations by visual stimuli causes cyclic modulation of perception. *Journal of Neuroscience*, **34**(10), 3536–44.
- Stolarova, M., Keil, A., Moratti, S. (2006). Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. *Cerebral Cortex (New York, N.Y.: 1991)*, **16**, 876–87.
- Werner, G.G., Riemann, D., Ehring, T. (2020). Fear of sleep and trauma-induced insomnia: a review and conceptual model. *Sleep Medicine Reviews*, **55**, 101383.
- Wieser, M.J., McTeague, L.M., Keil, A. (2012). Competition effects of threatening faces in social anxiety. *Emotion*, **12**, 1050–60.
- Wieser, M.J., Hambach, A., Weymar, M. (2018). Neurophysiological correlates of attentional bias for emotional faces in socially anxious individuals - Evidence from a visual search task and N2pc. *Biological Psychology*, **132**, 192–201.
- Wingenfeld, K., Bullig, R., Mensebach, C., Hartje, W., Driessen, M., Beblo, T. (2006). Attention bias towards personally relevant stimuli: the individual emotional Stroop task. *Psychological Reports*, **99**, 781–93.
- Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **20**, RC63.
- Yin, S., Bo, K., Liu, Y., Thigpen, N., Keil, A., Ding, M. (2020). Fear conditioning prompts sparser representations of conditioned threat in primary visual cortex. *Social Cognitive and Affective Neuroscience*.