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**Original Article**

# Prestimulus amygdala spectral activity is associated with visual face awareness

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## Abstract

Alpha cortical oscillations have been proposed to suppress sensory processing in the visual, auditory, and tactile domains, influencing conscious stimulus perception. However, it is unknown whether oscillatory neural activity in the amygdala, a subcortical structure involved in salience detection, has a similar impact on stimulus awareness. Recording intracranial electroencephalography (EEG) from 9 human amygdalae during face detection in a continuous flash suppression task, we found increased spectral prestimulus power and phase coherence, with most consistent effects in the alpha band, when faces were undetected relative to detected, similarly as previously observed in cortex with this task using scalp-EEG. Moreover, selective decreases in the alpha and gamma bands preceded face detection, with individual prestimulus alpha power correlating negatively with detection rate in patients. These findings reveal for the first time that prestimulus subcortical oscillations localized in human amygdala may contribute to perceptual gating mechanisms governing subsequent face detection and offer promising insights on the role of this structure in visual awareness.

*Key words*: alpha; amygdala; iEEG; prestimulus; awareness.

## Introduction

How and where stimulus perception is controlled in the human brain is a fundamental debate in the quest of the neural correlates of consciousness (Dehaene et al. 2006; Koch et al. 2016; Boly et al. 2017; Odegaard et al. 2017). Prestimulus neuronal oscillations reflect the internal brain states before sensory inputs occur and have been shown to reliably predict behavioral performance in different cognitive functions. For instance, higher theta activity (4–8 Hz) in the hippocampus is associated with stronger memory encoding (Herweg et al. 2020). Similarly, higher prestimulus alpha power (8–12 Hz) or phase coherence recorded in sensory or parietal cortices predicts lower detection performance for visual (Ergenoglu et al. 2004; Hanslmayr et al. 2007; Van Dijk et al. 2008; Sadaghiani and Kleinschmidt 2016), auditory (Kayser et al. 2016) and tactile stimuli (Baumgarten et al. 2016). Moreover, several studies using neuromodulation techniques, including transcranial magnetic stimulation (Romei et al. 2010) and neurofeedback (Bagherzadeh et al. 2020), suggest that cortical alpha oscillations may have a direct causal role on the detection of visual stimuli. Through an effect of "pulsed inhibition," target detection is decreased after cortical stimulation at alpha frequency (Romei et al. 2010) or after inducing higher cortical alpha power with neurofeedback training (Bagherzadeh et al. 2020). Thus, converging evidence supports that oscillatory activity in cortical brain regions prior to sensory inputs, particularly in the alpha band, has a critical role in modulating conscious perception and attentional gating, acting as a "windshield wiper" that regulates sensory inputs along the perceptual pathways (Klimesch 2012; Sadaghiani and Kleinschmidt 2016).

To date, it is unknown whether oscillatory activity in subcortical brain regions has a similar link with stimulus perceptual awareness. Of particular interest is the amygdala, a subcortical structure in the medial temporal lobe that is critically implicated in the processing of socially and affectively significant stimuli, such as faces (Vuilleumier 2005; Vuilleumier and Pourtois 2007). This subcortical structure has been suggested to facilitate detection of salient information (Amting et al. 2010;

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Fu and Rutishauser 2018), through its strong bidirectional connections with sensory systems (Vuilleumier 2005; Freese and Amaral 2006) and with attention systems in frontoparietal cortices (see Holland and Gallagher 1999).

Modulations of amygdala activity in relation to stimulus awareness have been consistently reported by studies using emotional stimuli during functional magnetic resonance imaging (fMRI), where attention or awareness of such stimuli is experimentally manipulated. For instance, higher amygdala hemodynamic response after visual stimuli has been shown to co-occur with increased detection of emotional targets in attentional blink tasks, where processing resources are limited due to rapid stimulus presentations (Schwabe et al. 2011; Fu and Rutishauser 2018), or in binocular rivalry tasks, where stimuli presented to one or the other eye are alternately suppressed from awareness through bistable perception (Amting et al. 2010). In contrast, amygdala lesion has been shown to impair such increased detection in these tasks (Anderson and Phelps 2001; Domínguez-Borràs et al. 2020), suggesting that this structure could play a role in facilitating the access of stimuli into awareness. On the other hand, however, the amygdala may also respond to faces or emotional stimuli even when they remain outside conscious detection (Morris et al. 1999; Pasley et al. 2004; Liddell et al. 2005; Jiang and He 2006; see Axelrod et al. 2015 for a review). Hence, the exact role of amygdala activity in relation to stimulus awareness is still poorly understood.

Moreover, modulations of amygdala activity across different conditions of stimulus awareness have been mainly investigated in relation to sensory-driven responses and usually measured with fMRI, e.g. by comparing stimuli processed supraliminally or subliminally during visual masking tasks (Morris et al. 1999; Liddell et al. 2005) or binocular rivalry (Pasley et al. 2004; Jiang and He 2006; see Axelrod et al. for review). However, it remains unknown whether differences in amygdala activity may already arise prior to stimulus onset and thus also contribute to subsequent stimulus detection, as it has been previously reported for cortical activity (Benwell et al. 2017). Notably, the low temporal resolution of MRI does not allow assessing prestimulus fluctuations in amygdala with millisecond precision around stimulus onset time. In the current study, therefore, we recorded intracranial electroencephalography (iEEG) of 7 epileptic patients undergoing neurosurgery to test whether local neural oscillations in this subcortical region ($n = 9$) might indeed be associated to visual detection of faces. Faces are socially relevant stimuli to which the amygdala is especially sensitive, both with neutral or emotional expressions (Vuilleumier and Pourtois 2007). Further, we used faces with different emotional expressions to test whether any emotional advantage in detection would also be associated with distinct patterns of prestimulus activity in amygdala.

To address this question, we leveraged the high temporal and spatial resolution of iEEG and the continuous flash suppression (CFS) method, a powerful technique for controlling awareness of visual stimuli based on binocular rivalry (Tsuchiya and Koch 2005). This technique provides a sustained visual stimulation where 2 different visual streams are presented, one to each eye, before and during the presentation of a target stimulus in either stream. This results in the percept of a single object, corresponding to one of the visual streams at a time (Fig. 1b). CFS-related fluctuations on the side of the dominant eye may thus yield either conscious detection (often in binocular trials) or misses (often in monocular trials) of the target stimulus presented to the non-dominant eye. CFS is one of the most powerful tools to suppress conscious visual perception, usually producing stronger and longer suppressions than other tasks with the same purpose (Tsuchiya and Koch 2005; Yang et al. 2007). Such a task was necessary given that face stimuli are often difficult to suppress from consciousness (Pessoa et al. 2005; Sperdin et al. 2015). Moreover, this task allows for an optimal assessment of prestimulus neural activity, with comparable characteristics across suppressed and unsuppressed conditions. This contrasts with, for instance, attentional blink tasks, where the target is usually presented with varying onset latencies relative to another preceding target (Raymond et al. 1992).

Patients sat comfortably in their bed, with a spatially adjustable stereoscope in front of their eyes to obtain binocular rivalry, and were asked to report faces detected during the CFS stimulation. We then compared spectral power and phase coherence in the amygdala, prior to stimulus onset, in trials where faces were subsequently detected versus undetected. Despite the fact that the neurological bases of CFS stimulation are not yet fully understood, a recent EEG study suggests that the CFS stimulation elicits broadband activity over the visual, parietal, and frontal cortices, with alpha, theta, and gamma activity orchestrating the break of stimuli into consciousness (del Río et al. 2018). Moreover, previous EEG research supports that prestimulus activity influencing awareness is centered around alpha but may not be restricted to this band (Benwell et al. 2017). Accordingly, we examined prestimulus amygdala activity across different frequency bands. Amygdala oscillations are still poorly understood, with rhythms predominantly in the theta and gamma bands, associated to emotional memory, arousal, and saliency detection (Oya et al. 2002; Paré et al. 2002; Sato et al. 2011; Davis et al. 2017; Domínguez-Borràs et al. 2019; Radchuk et al. 2019; Schönfeld and Wojtecki 2019). Alpha oscillations have also been observed in the amygdala, coordinating infralimbic or corticolimbic communication during social decisions (Schaich Borg et al. 2017) or face processing (Zheng et al. 2017).

Based on previous reports on the role of prestimulus cortical oscillations in awareness (Sadaghiani and Kleinschmidt 2016), a link between prestimulus

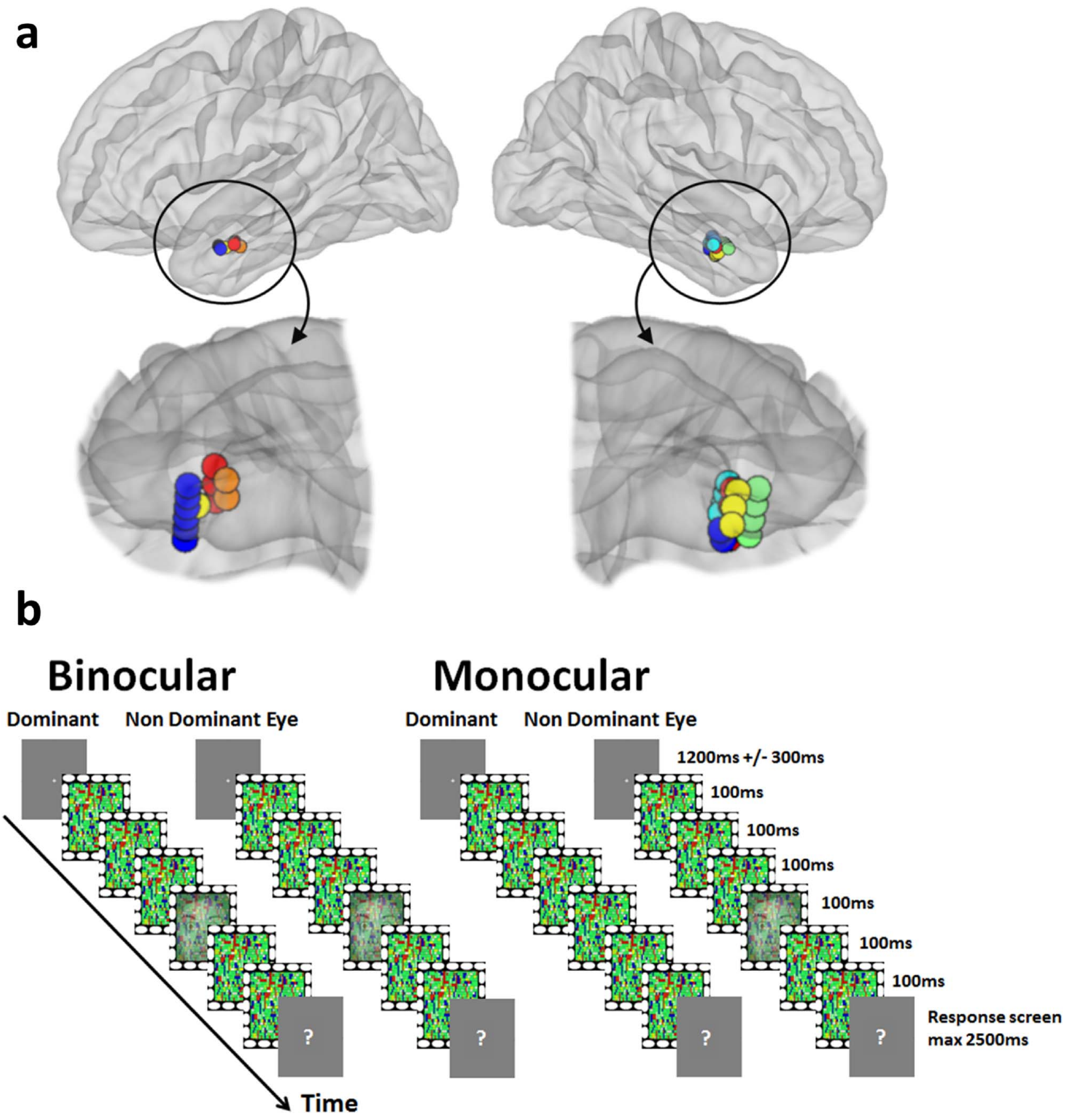

**Fig. 1.** Electrode localization in the amygdala and trial structure of the task. a) All electrodes are plotted on an average brain template, color-coded by patient: top row, lateral views of the left and right hemispheres; bottom row, inferior views of the left and right anterior temporal lobes. b) Trial structure in the CFS task. After an initial fixation cross (1,200 ± 300 ms), 3 Mondrian patterns were presented (100 ms each), followed by either a face or a scrambled face (100 ms) and followed in turn by 2 other Mondrian patterns (again each for 100 ms). Target stimulus presentation was binocular in 50% of trials and monocular in the other 50%. Patients were asked to respond as soon as possible whether they saw a face or not.

amygdala activity and subsequent stimulus detection would support a direct functional implication of the amygdala in brain circuits mediating visual stimulus awareness, as suggested in previous literature (Amting et al. 2010; Schwabe et al. 2011). We therefore hypothesized that undetected stimuli, relative to detected, should be preceded by selective increases in local amygdala activity across different frequency bands and predominantly in the alpha range. Finally, by comparing different emotional face conditions, we also aimed at assessing whether prestimulus difference in amygdala activity would influence any emotional advantage in subsequent face detection.

## Methods

### Participants

Seven epileptic patients (2 females) took part in the study prior to brain surgery for pharmacologically intractable epilepsy. The patients had normal or corrected-to-normal vision. Three patients had initially bilateral implants in the amygdala, 1 was implanted on the left amygdala, and 3 patients were implanted on the right amygdala. However, one amygdala (the right amygdala of Patient 6) was finally excluded from analysis due to poor signal quality, leaving 2 bilateral amygdalae, 2 left amygdalae, and 3 right amygdalae in the dataset (see Table 1 for demographics, clinical details, and implant information, which only indicates the amygdalae retained for analysis). Implant locations were chosen solely based on clinical criteria. Written informed consent was obtained from each patient, in agreement with the ethical committee of the University Hospital of Geneva (Switzerland). Patients presented overall normal performance in attention functions, as assessed by neuropsychological tests in the hospital, except 2 patients (P01, P04) who presented mild attention deficits. On the other hand, 5 patients presented mild (P01, P02, P03) or severe (P04 and P05) episodic memory deficits and, in turn, P01 and P07 showed mild working memory deficits. Finally, 4 patients showed executive function deficits (P01, P02, P03, and P04). None of these cognitive limitations prevented our patients from correctly understanding and performing the task (see Sections 2.5 and 3).

## Electrode localization and visualization

Electrode localization and visualization were performed using the open-source iELVis toolbox (https://www.github.com/iELVis/iELVis; see Groppe et al. 2017). Briefly, for each patient, a preimplant 3D T1 anatomical MRI scan was segmented using FreeSurfer (http://surfer.nmr.mgh.harvard.edu/; see Fischl 2012). A postimplant high-resolution computed tomography scan was coregistered with the preimplant MRI. Radiodense electrode artifacts were identified manually using BioImage Suite 3 (https://medicine.yale.edu/bioimaging/suite/; see Joshi et al. 2011) and reported to the segmented brain volume. Electrodes were considered to lie in the amygdala if the tissue in a 3 × 3 × 3 voxel cube surrounding the electrode was predominantly segmented as amygdala by FreeSurfer (see Mercier et al. 2017 for a similar approach). Electrode coordinates from individual patients were projected on to an average brain template using an affine transformation.

## Stimuli

Stimuli were created with face images taken from the Karolinska (Lundqvist et al. 1998) and the Nimstim (Tottenham et al. 2009) databases. These consisted of 14 neutral, 14 angry, and 14 fearful faces (displayed by the same actors, 50% females, across emotion expressions), plus 14 control stimuli with the same background but an oval mask, filled with a scrambled neutral face. Please note that emotion-related amygdala activity is not reported here, as we focused only on prestimulus activity related to perceptual awareness. The use of fearful, angry, and neutral faces was motivated to assess any potential

**Table 1.** Patient demographic and clinical data.

| Patient | Sex | Handedness | Age (years) | Age at onset of epilepsy (years) | Etiology | Seizure focus | Resection | Seizure frequency | Seizure type | Education completed | Side of implantation | Number of electrodes × number of contacts | Dominant eye |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | M | R | 34 | 23 | Idiopathic | Temporal R | Right superolateral temporal/ temporal lobectomy | Monthly | CPS | Secondary | L + R | 2 × 8 | R |
| 2 | F | R | 21 | 19 | Idiopathic | Orbitofrontal R | Right orbitofrontal/ventropolar lobectomy | Weekly | SG TCS | Secondary | R | 1 × 8 | L |
| 3 | F | L | 26 | 21 | Idiopathic | Insular R | Right anterior temporal/ temporal lobectomy | Monthly | SG TCS | Primary | R | 1 × 8 | L |
| 4 | M | R | 34 | 27 | Bitemporal hypometabolism | Frontotemporal | Right posterior cingulate gyrus and precuneus cortectomy | Weekly | SG TCS | Secondary | R | 1 × 12 | R |
| 5 | M | R | 40 | 10 | Bitemporal hypometabolism<br>Left hippocampal sclerosis<br>Orbitofrontal lesions | Frontotemporal | Left anterior temporal lobe resection and left anterior insula cortectomy | Monthly | SG TCS | Primary | L | 1 × 8 | R |
| 6 | M | R | 31 | 21 | Left anterior temporal hypometabolism | Frontocentral | No resection | Monthly | SG TCS | Secondary | L | 1 × 10 | R |
| 7 | M | R | 50 | 38 | Right hippocampal sclerosis | Insular R and orbitofrontal R | No resection | Weekly | SG TCS | Tertiary | L + R | 1 × 10/1 × 12 | L |

M, male; F, female; R, right; L, left; CPS, complex partial seizure; SG TCS, secondary generalized tonic clonic seizure; SPS, simple partial seizure.

advantage of emotional faces in reaching awareness, as often reported in similar paradigms, particularly with angry and fearful expressions (Alpers and Gerdes 2007; Yang et al. 2007; Maratos et al. 2008; De Martino et al. 2009; Amting et al. 2010), and to determine whether such advantage was associated with different patterns of prestimulus activity. However, our behavioral results (see below) revealed that face detection rates did not differ across the different expression conditions, and all subsequent analyses were therefore performed after pooling all emotional stimuli together. All stimuli were superimposed with a Mondrian pattern to reduce their detectability and surrounded by fusion contours to promote stable binocular alignment of the images. The 14 Mondrian patterns were generated on the website http://www.isloyhere.com/mondriaan.php. All stimuli were normalized for luminance.

## Experimental procedure

We used an adapted version of the CFS task (Tsuchiya and Koch 2005), suitable for iEEG recordings with short trials, to evaluate the influence of intrinsic prestimulus amygdala activity on visual face awareness. The task design and parameters were derived from previous work on subliminal perception, where the nondominant eye is presented with the visual target in the monocular condition, leading to subliminal perception, and both eyes are presented with the visual target in the binocular condition (Tsuchiya and Koch 2005; Jiang and He 2006). Patients sat comfortably in their bed, in front of a laptop where the CFS task was displayed. Participants were tested for defining their dominant eye to optimize CFS conditions. Prior to testing, a stereoscope was placed in front of their eyes to ensure the expected effects of binocular rivalry. A proper alignment of the binocularly presented stimuli was verified for each individual, by carefully adjusting the mirrors of the stereoscope prior to the test, until the participant saw one unique image on screen (with fusion contours aligned).

Each trial started with a white fixation cross (duration 1,200 ± 300 ms), followed by the succession of 3 Mondrian patterns (each for 100 ms) to both eyes; then, either a face or a control scrambled face image was briefly presented (for 100 ms) in one or both eyes, followed by the succession of 2 other Mondrian patterns (each for 100 ms again), creating a binocular CFS visual stream (10 Hz; see Fig. 1). Subsequently, a white question mark was displayed for maximum 2500 ms or until participant's response, during which participants had to answer as fast as possible with a response button whether they saw a face (or a part of a face, e.g. 1 or 2 eyes) or not. Note that fingers associated with the response were counterbalanced across participants (index or middle finger). There were 280 trials with faces in monocular stimulation and 280 trials with faces in binocular stimulation, each of them including 70 trials per emotional expression and 70 control trials with scramble faces (see next section). The experiment was divided into 8 blocks presented the same day, with breaks offered to the participants between each block. All the patients performed the study during daytime.

Stimulus presentation was controlled with the software E-prime (Neurobehavioral Systems, Albany, CA, USA). The latency of stimulus onset on screen, relative to the iEEG triggers, was monitored offline with a photodiode. Stimulus onset delay was of around 10 ± 1 ms post-trigger onset and stable throughout the experiment. The data were corrected for this delay in the analysis by adding 10 ms to all trigger onset values.

## Behavioral analysis

For behavioral analysis, we compared face detection (by means of a receiver operating characteristic analysis) and response times across monocular and binocular trials by means of paired 2-tailed *t*-tests using Matlab. Effect size (*d*) was computed with Cohen's *d* (Cohen 1992), as the difference of the means across conditions and patients, divided by the pooled standard deviation across conditions and patients. Detection *d*' was analyzed (Gaillard et al. 2009) and compared among monocular and binocular trials with the same procedure as above. We performed these tests in order to confirm the effectivity of the CFS task, in which perceptual suppression is more likely to occur during monocular than during binocular presentations (e.g. del Río et al. 2018). However, for subsequent iEEG analyses, and in order to include the maximum number of trials in the conditions of interest, so as to maximize statistical power, we separated trials into those where faces were correctly detected (Detected condition) versus undetected (Undetected condition), regardless of whether stimuli were monocularly or binocularly presented. Importantly, given that behavioral analyses for monocular trials showed overall hit rates near chance level (and with overall poorer detection than binocular trials, see Section 3), we carefully ensured that prestimulus amygdala activity across monocular and binocular trials would not differ for any of the conditions of interest analyzed (i.e. Detected or Undetected; see next sections).

## Data acquisition

Intracranial EEG data were acquired with a sampling rate of 2,048 Hz with a Micromed System Plus (Micromed, Mogliano Veneto, Italy) and with electrode arrays consisting of 8–12 stainless contacts (AD-Tech, electrode diameter: 3 mm, intercontact spacing: 2 mm). Reference was initially set to Cz for the recording, and data were then re-referenced to the nearest white matter contact of the same electrode for analysis (which was ~6 mm distant from the active contact), resulting in a nonadjacent bipolar montage. This re-referencing allowed us to isolate local amygdala activity while maximally removing the influence of distant activity on intra-amygdala data (Yao et al. 2019).

## Signal preprocessing

A band-pass filter (0.01–200 Hz) and a notch filter (50, 100, 150 Hz) were applied with the Cartool (Brunet et al. 2011) software. Signal preprocessing was implemented with custom-written scripts for the toolbox Fieldtrip (Oostenveld et al. 2011) in Matlab (Mathworks, R2012). The signal was downsampled to 512 Hz. Epochs from −1 to 2 s were extracted. A baseline correction (relative change) was performed from −500 to −300 ms prior to stimulus presentation, corresponding to the 200 ms prior to CFS stimulation onset. Please note that this window was considered optimal for enabling the observation of CFS influence on iEEG amygdala activity, while avoiding signal contamination by motor response, and following standard methodology in previous studies (e.g. Hanslmayr et al. 2007). Time–frequency evoked responses were obtained with a Morlet wavelet approach for frequencies ranging from 3 to 200 Hz with a 1 Hz step, similarly to a previous report studying CFS effect on scalp-EEG response (del Río et al. 2018), with a number of cycles of 4 for low frequencies (theta and alpha, see below) and a number of cycles of 7 for high frequencies (beta and gamma, see below). The signal was divided into 4 frequency bands, from 4 to 8 Hz (theta), 8 to 12 Hz (alpha), 12 to 30 Hz (beta), and from 30 to 150 Hz (gamma). Importantly, each trial was visually inspected, and trials containing artifacts (i.e. epileptic spikes, excessive noise) were excluded from further analyses. Trials were averaged for each condition and each contact. Finally, data were averaged across selected contacts within each amygdala for each experimental condition (Detected, Undetected). Control trials (with scramble faces), trials with behavioral omissions or false alarms (∼14 trials per subject), were excluded from further analyses. On average, 91 trials were included for iEEG analyses for the Detected condition (33 monocular, 58 binocular) and 130 trials for the Undetected condition (82 monocular, 50 binocular).

## Separating oscillatory from scale-free iEEG activity

Amygdala activity (i.e. in response to visual stimulation) has been well documented. However, whether its activity corresponds to genuine oscillatory neuronal mechanisms has not been formally tested to date. Here, we uncovered this neurophysiological aspect in the context of CFS stimulation. Using a similar approach to previous studies (Colombo et al. 2019; Griffiths et al. 2019; https://github.com/milecombo/spectralExponent), we calculated the power spectral density (PSD) for each amygdala using Welch's method (Matlab function pwelch), with Hanning windows of 2 s and 50% overlap. The following 3 steps were performed in order to estimate the slope (i.e. spectral exponent $\alpha$) of the background PSD. The PSD background (i.e. nonoscillatory or aperiodic activity) decays approximately according to an inverse power law $\mathrm{PSD}(f) \sim 1/f\ \alpha$. First, a linear regression line was fit to the PSD using log–log axes. Secondly, frequency bins with positive residuals were considered as containing oscillatory activity and thus removed from subsequent analysis. Thirdly, another linear regression line was then fit on the remaining frequency bins (i.e. those consistent with a $1/f$ behavior). The slope/gradient of this second line was considered as the estimated spectral exponent $\alpha$ of the PSD background.

We considered for these analyses only the lower frequency band (6–30 Hz), where well-known oscillations are usually observed (e.g. theta, alpha, beta). We also confirmed the results of this analysis with another recently developed method suitable for iEEG (Donoghue et al. 2020), which is less susceptible to aperiodic influence biases (https://github.com/fooof-tools/fooof), by applying the same parameters as described above. Note, however, that the short time-window (i.e. lower frequency resolution) used for these analyses (−300 to 0 ms) may potentially be less sensitive to weaker effects in other frequencies. Applying the same method for the gamma band did not yield any positive results.

## Inter-trial phase coherence analysis

Phase synchronization across trials during prestimulus window is known to predict subsequent visual awareness (Harris et al. 2018). To complement our evoked power analyses, we specifically examined inter-trial phase coherence (ITPC) of amygdala activity time-locked to the onset of the CFS image inputs. This provides a more direct measure of neural synchrony at each time–frequency bin across trials, within the averaged evoked response (Makeig et al. 2004). Analysis was carried out after preprocessing (see above) and with the toolbox Fieldtrip (Oostenveld et al. 2011) implemented in Matlab (Mathworks, R2012), for the frequency bands 6–30 Hz, and over the full prestimulus window (−500 to 0 ms).

## iEEG statistics

Data were fitted into a general linear mixed-model (GLMM, function fitglme in Matlab, without assumption on the distribution) with a cluster permutation approach to identify, e.g. significant differences between detected and undetected trials. As permutation distribution is strictly data-driven and nonparametric by definition, no degrees of freedom are given (Zheng et al. 2017; Domínguez-Borràs et al. 2019). In a separate analysis, and to examine amygdala activity previous to the CFS stimulation (i.e. free of visual input), we also compared each condition (Detected and Undetected) with its corresponding baseline period from −500 ms to −300 ms. Both analyses were conducted without a priori assumptions (2-tailed). Both GLMM analyses were conducted for theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (30–150 Hz) bands. This statistical approach for our time-series data was used in order to avoid false-positive findings. We report only cluster-based corrected $P$-values obtained with 1,000 permutations (with cluster $\alpha$ threshold = 0.05, except when stated otherwise; Méndez-Bértolo et al. 2016; Zheng et al. 2017). The reported

*T*-scores ($t_{cluster}$) correspond to the sum values and *P*-values ($P_{cluster}$) correspond to the minimal values over the significant time-windows for all the tests in the time dimension and over the significant frequency windows when in the frequency dimension. Effect size (*d*) was again computed with Cohen's *d* (Cohen 1992) following the same procedure as above, but this time over the average values within significant clusters, and following standard practices for cluster-based permutation tests in EEG (Meyer et al. 2021). For comparisons of prestimulus activity (−300 to 0 ms) relative to the preceding baseline window (−500 to −300 ms), amygdala power values in the −300 to 0 ms window were compared, point by point, with average values of the baseline period. This was done for each condition (Detected, Undetected) and for each frequency band. Please note that our GLMM analyses included amygdala as the sole random factor, despite 2 patients having bilateral implants. We chose this approach due to the low number of observations regarding bilateral recordings in our dataset and following our methodology in a previous study (Domínguez-Borràs et al. 2019). However, an additional analysis of our data with 7 patients (i.e. after averaging left and right amygdalae in bilateral implants) revealed similar results for all statistical tests (See Supplementary Table S1). Finally, to further examine individual linear relationships between prestimulus amygdala activity and subsequent face detection, we performed Pearson correlations (2-tailed) between individual hit rates and individual mean amygdala power values, extracted from the time-window and frequency band where the most robust effects were observed in our initial Morlet wavelet analysis.

## Results

### Behavior

As expected (see above), during binocular stimulation, face detection hit rate was above chance level (mean hit rate: 0.442 ± 0.21, $t_6 = 3.07$, $P = 0.021$, $d = 1.16$; Fig. 2), while during monocular stimulation hit rate was not different from chance level (mean hit rate: 0.35 ± 0.25, $t_6 = -1.81$, $P = 0.11$, $d = -0.68$; Fig. 2); moreover, hit rates were significantly higher during binocular stimulation in comparison with monocular stimulation ($t_6 = 3.07$, $P = 0.02$, $d = 1.16$; Fig. 2). Unlike our prediction, however, hit rates did not differ among emotion expressions for binocular stimulation (Fearful vs. Anger: $t_6 = 0.556$, $P = 0.597$, $d = 0.21$; Fearful vs. Neutral: $t_6 = 1.57$, $P = 0.167$, $d = 0.59$; Anger vs. Neutral: $t_6 = 0.83$, $P = 0.437$, $d = 0.31$) or for monocular stimulation (Fearful vs. Anger: $t_6 = 0.557$, $P = 0.597$, $d = 0.21$; Fearful vs. Neutral: $t_6 = -0.042$, $P = 0.967$, $d = -0.01$; Anger vs. Neutral: $t_6 = -0.519$, $P = 0.622$, $d = -0.19$). Given this lack of detection advantage for emotional compared to neutral faces in the current paradigm, all face conditions were pooled together and the emotional factor was disregarded from further analyses. Finally, *d'* analyses confirmed that faces presented during binocular stimulation were better detected than during monocular stimulation ($t_6 = 3.08$, $P = 0.021$, $d = 1.09$), while *d'* between emotions did not differ either for binocular stimulation (Fearful–Anger: $t_6 = 0.728$, $P = 0.493$, $d = 0.27$; Fearful–Neutral: $t_6 = 1.583$, $P = 0.164$, $d = 0.59$; Anger–Neutral: $t_6 = 0.89$, $P = 0.4$, $d = 0.33$) or for monocular (Fearful–Anger: $t_6 = 0.029$, $P = 0.977$, $d = 0.01$; Fearful–Neutral: $t_6 = -0.0647$, $P = 0.541$, $d = -0.24$; Anger–Neutral: $t_6 = -0.96$, $P = 0.373$, $d = -0.36$). In addition, response times were similar among monocular and binocular trials ($P = 0.8$). Furthermore, regardless of binocular or monocular presentation, response times did not differ for detected versus undetected faces (1,074 ± 280 ms, 1,101 ± 275 ms, $P > 0.86$, $d = 0.08$) or among emotional expressions (all $P > 0.74$).

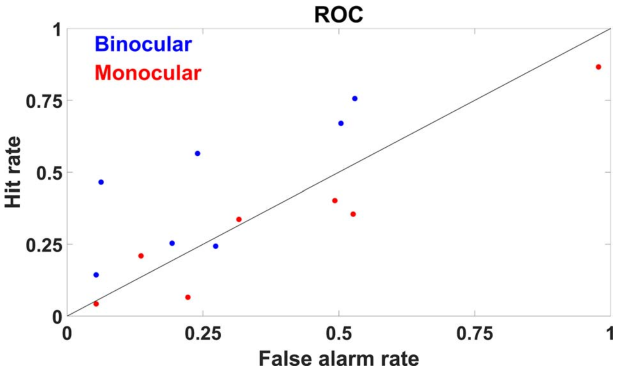

**Fig. 2.** Receiver operating characteristic (ROC) analyses of behavioral performance for the face detection task. Both during binocular stimulation, where detection was above chance level, and during monocular stimulation, where detection was at chance level.

### Intracranial EEG

To determine whether amygdala activity differed during the prestimulus time-window (−300 ms to stimulus onset, i.e. during CFS stimulation) between trials where faces were detected or undetected, we first performed a time–frequency analysis across a broad frequency range (3–150 Hz). As predicted, increased spectral power for undetected (vs. detected) trials was observed in the ALPHA range from −280 to −80 ms prior to stimulus onset ($t_{cluster} = 68.93$, $P_{cluster} = 0.002$; at $\alpha = 0.01$, from −270 to −100 ms; $d = 0.87$; Fig. 3b). Interestingly, such increase was also observed in THETA from −300 to −130 ms ($t_{cluster} = 24.74$, $P_{cluster} = 0.003$; $d = 0.69$; Fig. 3a), BETA from −270 to −80 ms ($t_{cluster} = 28.21$, $P_{cluster} = 0.0053$; at $\alpha = 0.01$, from −140 to −110 ms; $d = 0.68$; Fig. 3c), and GAMMA from −210 to −140 ms ($t_{cluster} = 20.23$, $P_{cluster} = 0.008$; $d = 0.71$; Fig. 3d).

To complement these analyses, and to additionally examine amygdala activity free of CFS stimulation, we also compared prestimulus activity relative to the preceding baseline before CFS stimulation onset (−500 to −300 ms). For undetected faces, this showed higher power in all frequency bands (THETA: −300 to −170 ms, $t_{cluster} = 39.29$, $P_{cluster} = 0.004$, $\alpha = 0.01$: −270 to

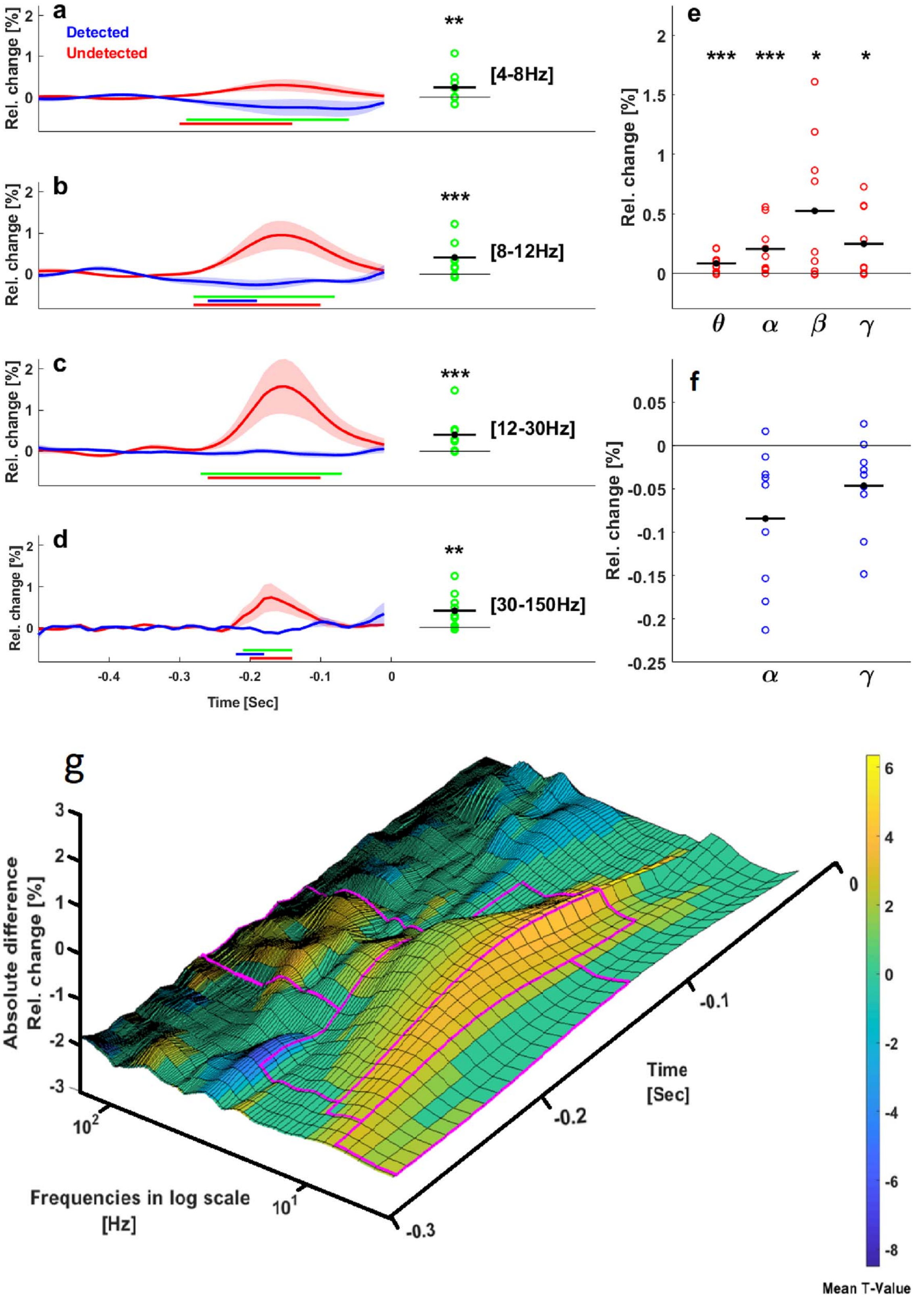

**Fig. 3.** Prestimulus amygdala ($n = 9$) broadband spectral power is associated with visual face detection. [Left inset] Percent change (mean ± SEM) for undetected and detected trials showing significant difference in (a) the theta, (b) the alpha, (c) the beta, and (d) the gamma bands. Colored lines below waveforms indicate significant temporal clusters of power differences, green for detected versus undetected, blue for detected versus baseline, and red for undetected versus baseline. Scatterplots depict the average power difference between undetected and detected conditions over the significant time interval. [Right inset] Scatterplots of mean power values for undetected trials in red (e) and detected trials in blue (f) relative to baseline period before CFS stimulation. (g) $T$-value map showing a continuum of differential activity in amygdala across frequency bands during the prestimulus period, when faces were undetected versus detected computed as an absolute difference between the 2 conditions, peaking around −150 ms prior to stimulus onset. Colors correspond to $T$-values, with yellow indicating higher activity when faces were undetected (vs. detected) and blue depicting the opposite. Magenta lines indicate significant temporal clusters.

$-240$ ms, $d = 1.02$; ALPHA: $-270$ to $-90$ ms, $t_{\text{cluster}} = 52.51$, $P_{\text{cluster}} = 0.005$, $\alpha = 0.01$: $-270$ to $-230$ ms, $d = 1.04$; BETA: $-250$ to $-90$ ms, $t_{\text{cluster}} = 12.7$, $P_{\text{cluster}} = 0.015$, $d = 0.81$; GAMMA: $-190$ to $-130$ ms, $t_{\text{cluster}} = 9.82$, $P_{\text{cluster}} = 0.02$, $d = 0.76$; Fig. 3e). However, and more critically, for detected faces, both ALPHA and GAMMA showed a selective reduction in power relative to baseline, suggesting that a selective suppression of activity in these 2 bands was permissive for subsequent visual detection (ALPHA: $-250$ to $-180$ ms, $t_{\text{cluster}} = -19.44$, $P_{\text{cluster}} = 0.002$ and $-140$ to $-80$ ms, $t_{\text{cluster}} = -22.17$, $P_{\text{cluster}} = 0.002$, and, at $\alpha = 0.01$, from $-110$ to $-90$ ms, $d = 0.85$; GAMMA: $-210$ to $-160$ ms, $t_{\text{cluster}} = -12.55$, $P_{\text{cluster}} = 0.013$, $d = 0.81$; Fig. 3f).

To further complement our time–frequency analyses, we also applied a classic Fourier transform, over the time-window $-300$ to 0 ms, which again revealed higher ALPHA activity for undetected versus detected trials ($t_{\text{cluster}} = 7.93$, $P_{\text{cluster}} = 0.04$, $d = 0.57$; Fig. 4a). Finally, we verified whether amygdala spectral modulations were oscillatory in nature by removing the scale-free background activity (i.e. $1/f$; Colombo et al. 2019), over the same time-window as above. This analysis indicated higher residual (i.e. oscillatory) activity for undetected versus detected trials that was again restricted to ALPHA ($t_{\text{cluster}} = 12.61$, $P_{\text{cluster}} = 0.018$, $d = 0.85$; Fig. 4b), confirming the robustness of our previous observations for this frequency band. Furthermore, we found no differences between the exponents (i.e. slopes) of the $1/f$ background, nor between its intercepts, for detected versus undetected trials (respectively, $t = 1.96$, $P > 0.08$ and $P > 0.11$, $t = -1.78$), suggesting that the scale-free iEEG background may have been similarly modulated for both conditions. We also corroborated this analysis using the FOOOF method (Donoghue et al. 2020), recently proposed to be less susceptible to aperiodic biases, which revealed similar results over the ALPHA band ($t_{\text{cluster}} = 11.5$, $P_{\text{cluster}} = 0.031$, $d = 0.73$; Fig. 4c), again over the time-window $-300$ to 0 ms. However, given that the lower frequency resolution of the methods used to remove scale-free activity may have overlooked smaller effects in frequencies other than alpha, we estimated equally important to report our observations in broadband activity after more standard analyses, which confirm, moreover, previous findings on EEG spectral activity linked to CFS stimulation (del Río et al. 2018). In sum, these complementary analyses rather confirmed that at least prestimulus alpha activity was oscillatory in nature and highlighted the strength of the effects in this band.

We also tested phase-synchronization across trials (ITPC) time-locked to the CFS visual inputs during the prestimulus window and found consistent higher phase coherence for undetected versus detected trials from $-250$ to $-185$ ms, restricted to the ALPHA band ($t_{\text{cluster}} = 18.3$, $P_{\text{cluster}} = 0.012$, $d = 0.82$; Fig. 5). This further supports a role for dynamic fluctuations of alpha activity in modulating subsequent stimulus awareness in the amygdala.

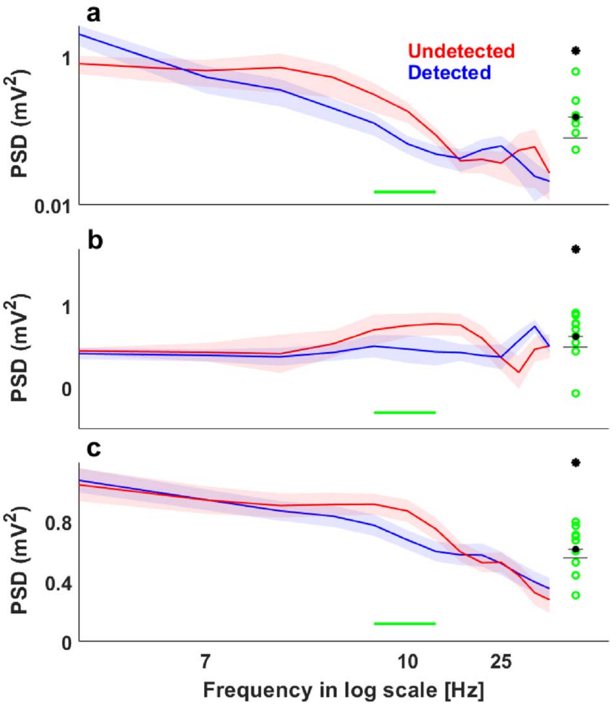

**Fig. 4.** Modulation of alpha amygdala oscillations prior to face onset during undetected and detected trials. Different analyses support the robustness of the effects in this frequency band. a) Fast Fourier transform. b) Oscillatory activity obtained with a classical method (Colombo et al. 2019). c) Oscillatory activity obtained with the FOOOF method (Donoghue et al. 2020). PSD stands for power spectral density. Same color and display codes as in Fig. 3.

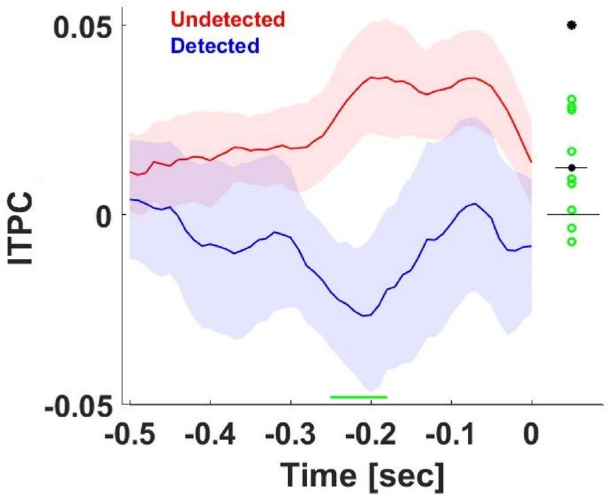

**Fig. 5.** Modulation of alpha ITPC in amygdala, prior to face onset during undetected and detected trials. Scatterplots depict the average ITPC difference between undetected and detected trials over the significant time interval. Same color and display codes as in Fig. 3.

Moreover, a functional link between prestimulus alpha activity in amygdala and face detection was also supported by a significant negative correlation between ALPHA power for detected faces (extracted from the time-window $-280$ to $-80$ ms where differences between detected and undetected trials were observed) and individual detection rates ($r_7 = -0.78$; $P = 0.012$; Fig. 6).

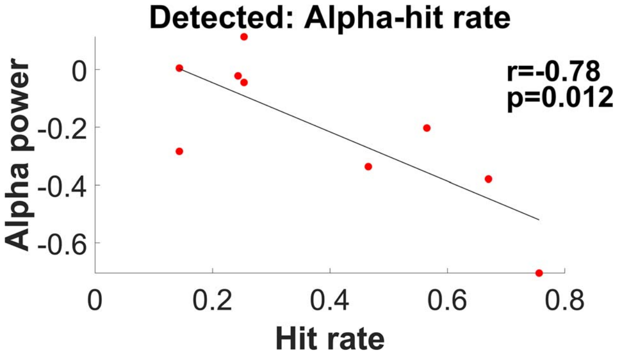

**Fig. 6.** Negative correlation between amygdala prestimulus alpha power for detected trials and patient hit rates. Intersubject correlation between alpha power during detected trials, as extracted from the time-window −280 to −80 ms, where main effects were observed, and individual hit rates.

For completeness, despite our main focus on prestimulus oscillations, we conducted an additional analysis on the poststimulus window alone to compare activity evoked by detected and undetected faces (see Supplementary Fig. S1). In brief, amygdala spectral power following the onset of a face target was selectively increased in the gamma band for detected versus undetected trials, whereas there was no significant difference in any other frequency band. This is consistent with the well-known role of poststimulus gamma activity in visual encoding and attention, widely reported in the cortex (Tallon-Baudry and Bertrand 1999; Fell et al. 2003). Moreover, gamma in its higher frequency range (e.g. 80–150 Hz) provides a reliable index of local neuronal spiking (Buzsáki et al. 2012) and has previously been found to be evoked in the amygdala in response to attended faces (Zheng et al. 2017). Similar gamma increases were also described for nonsuppressed targets in visual cortices during CFS (del Río et al. 2018).

Finally, given that detection rates in monocular trials were shown to be no different from chance level, and above chance level for binocular trials, we performed control analyses to ensure that amygdala activity would not differ across monocular and binocular trials for each of the conditions of interest (i.e. Detected and Undetected, separately). Statistical comparisons revealed no such differences for any of the conditions or for any frequency band (all $P > 0.05$ uncorrected; see Supplementary Fig. S2). This allowed us to rule out potential confounds derived from the inclusion of monocular trials (with overall poor detection) especially in the Detected condition or from differences in the number of monocular (versus binocular) trials included in each of the conditions compared.

## Discussion

These results provide, for the first time, evidence for intrinsic spectral activity in the amygdala with fluctuations that are associated to conscious detection of subsequent face stimuli. These findings suggest that prestimulus activity in this subcortical region may contribute to neural processes controlling the access of face information into awareness (Vuilleumier 2005). Specifically, we show that amygdala prestimulus broadband spectral activity, driven by the CFS stimulation, is higher when faces are undetected versus detected, which supports previous results showing that CFS stimulation impacts visual detection across a large range of frequencies (del Río et al. 2018). Moreover, we found predominant and consistent effects in the alpha band, in agreement with observations previously reported for cortical areas with surface EEG in various paradigms manipulating sensory awareness (Romei et al. 2010; Baumgarten et al. 2016; Kayser et al. 2016; Sadaghiani and Kleinschmidt 2016; Bagherzadeh et al. 2020), also when directly examining inter-trial phase synchronization (Busch et al. 2009). Here, selective prestimulus decreases in the alpha and gamma bands were associated with higher rates of subsequent face detection. Whereas a link between lower alpha and higher target detection is well known in cortical areas and accords with a pulsed gating mechanism (Sadaghiani and Kleinschmidt 2016), our finding of lower gamma activity during the prestimulus window may reflect weaker processing of the Mondrian masks in the amygdala, rendering the masks less effective in suppressing detection later in the trial. Indeed, gamma activity in the cortex is known to facilitate visual encoding and attention (Tallon-Baudry and Bertrand 1999; Fell et al. 2003). Moreover, high gamma (80–150 Hz) is a reliable index of local neuronal spiking (Buzsáki et al. 2012) and reflects stimulus encoding in the amygdala (Zheng et al. 2017). This again supports a direct link between ongoing amygdala activity and target detection.

Furthermore, amygdala prestimulus alpha power correlated negatively with the patients' hit rate for detected faces, indicating that stronger activity in this frequency range was associated to poorer detection performance. This strongly supports a functional link between amygdala activity and face detection (Vuilleumier 2005), even when peaking about 150 ms prior to face onset. Our findings therefore go beyond previous work on sensory cortical areas by demonstrating that conscious detection of faces may not be determined solely by modulations of activity in visual cortex (Romei et al. 2010) or cortical attentional networks (Sadaghiani and Kleinschmidt 2016) and by establishing that a "pulsed inhibition" mechanism in alpha-range governing perception may extend to a subcortical structure sensitive to multimodal inputs and involved in the detection of socially or emotionally significant information (Vuilleumier 2005; Pessoa and Adolphs 2010).

Our bipolar electrode analysis, for which we re-referenced each channel to its nearby white matter channel within the same electrode, ensured a reliable localization of intra-amygdala activity, by optimally canceling external signal influences and signal spillover from remote sources (Lachaux et al. 2012; Yao et al. 2019). However, one potential limitation in our study is that we cannot fully rule out that alpha oscillations in amygdala were driven by distant (e.g. visual) cortical areas. As electrode implantation in our patients was guided solely by clinical indications, no data were available from extratemporal lobe regions in our patients. However, even if we had observed similar alpha modulations outside the amygdala, we would not necessarily be able to determine the primary sources of these oscillations, as these might involve more distributed networks or additional subcortical regions (e.g. pulvinar; Saalmann et al. 2012). Further research will be critical to obtain more complete mapping of these neural dynamics and to understand the role of perceptual suppression in the amygdala. In any case, our data do reveal for the first time a link between face awareness and prestimulus activity in the amygdala, an effect that might contribute to differences in neural activity for conscious and nonconscious face perception observed at slower temporal scale with fMRI (Pourtois et al. 2013).

Another potential limitation is that we used only faces in this study, due to the well-known amygdala reactivity to these socially relevant stimuli (Vuilleumier and Pourtois 2007), which precludes any generalization over other object categories (e.g. abstract shapes; Guex et al. 2020), an important issue that should also be further investigated in the future. Moreover, unlike our expectations, we did not observe any detection advantage for emotionally negative faces as reported in other paradigms (De Martino et al. 2009), precluding a more detailed analysis of any differential effect of neural oscillations within the amygdala on its responsivity to emotional signals.

On the other hand, we note a discrepancy between our time–frequency analyses, where broadband increases were observed similarly as in previous scalp-EEG studies (del Río et al. 2018), and the oscillatory analyses, where only periodic alpha modulation was observed prior to face onset, which might raise the question about the functional significance of these broadband (potentially nonoscillatory) increases in the context of subliminal perception. Although our results do not allow us to fully conclude on this apparent discrepancy, it seems reasonable to speculate that CFS stimulation might not only entrains a steady-state response in the alpha range, and thus induces a neurophysiological state well-known to decrease sensory sensitivity, but also evokes broadband activity, as previously observed across the whole scalp with surface EEG (del Río et al. 2018).

In any case, these findings provide novel support to the notion that states of increased spectral power and phase coherence, highly centered in alpha, play a key role in suppressive gating processes that control the flow of incoming sensory inputs (Romei et al. 2010; Baumgarten et al. 2016; Kayser et al. 2016; Sadaghiani and Kleinschmidt 2016). Accordingly, fluctuations in internal states (Baumgarten et al. 2016; Kayser et al. 2016; Sadaghiani and Kleinschmidt 2016) or task demands (Romei et al. 2010; Sadaghiani and Kleinschmidt 2016; Bagherzadeh et al. 2020) linked to attentional state may act through specific oscillatory neurophysiological mechanisms in order to modulate vigilance level and sensory awareness (Romei et al. 2010; Bagherzadeh et al. 2020), e.g. with more prominent alpha oscillations during spontaneous EEG states at rest than during active stimulus processing (Romei et al. 2010; Baumgarten et al. 2016; Kayser et al. 2016; Sadaghiani and Kleinschmidt 2016). More generally, by pinpointing a role for subcortical nodes in brain circuits gating sensory awareness during prestimulus activity, our results contribute to current debates of the localization of the neuronal correlates of (Vuilleumier 2005; Dehaene et al. 2006; Pessoa and Adolphs 2010; Koch et al. 2016; Boly et al. 2017; Odegaard et al. 2017) and models of face awareness (Williams et al. 2006).

The amygdala, specifically, has been long associated with reinforced representations of salient signals through its anatomical feedback projections to the sensory systems (Freese and Amaral 2005; Vuilleumier 2005), with a loss of such enhancing effects after damage to this structure (Vuilleumier et al. 2004; Hadj-Bouziane et al. 2012). Accordingly, stimulus-driven amygdala activity in fMRI has been associated with facilitated detection of salient stimuli in visual search tasks (Mohanty et al. 2009) or in tasks where attentional resources are limited (Schwabe et al. 2011; Fu and Rutishauser 2018). Thus, under binocular rivalry conditions, increased detection of (emotional) stimuli correlates with stronger functional connectivity between amygdala and ventral visual areas, supporting a direct amygdala contribution to stimulus detection in this task (Amting et al. 2010). In turn, amygdala lesion may impair such facilitated detection (Anderson and Phelps 2001; Domínguez-Borràs et al. 2020; but see Tsuchiya et al. 2009). Finally, amygdala response is also associated to the facilitation of awareness (and unconscious responses) to stimuli (predominantly emotional) presented within the blind spot of cortically blind patients (Morris 2001) or within the nonattended hemifield of patients suffering from spatial neglect (Pegna et al. 2005; see Domínguez-Borràs et al. 2012 for review). Here, however, we did not observe any difference in detection performance for emotional faces and therefore could not assess whether intrinsic amygdala oscillations might also influence the emotional facilitation of perception. Together, wide research converges to suggest that amygdala function may indeed play a modulatory role in stimulus awareness, although this issue has been subject to debate (Tsuchiya et al. 2009; Pessoa and Adolphs 2010). Our results therefore add novel and more direct insights on such amygdala contribution to stimulus detection, and importantly, beyond the context of affective salience. They also unveil the functional relationship of these processes to specific neural oscillation frequencies, extending previous data traditionally focused on cortical activity.

Further, by characterizing the spectral dynamics involved in this process, our data may also provide important information to guide neuromodulation techniques aiming to measure and/or regulate attentional states with enhanced resistance to distractors (Romei et al. 2010; Sitaram et al. 2019; Bagherzadeh et al. 2020). In sum, we show that spectral activity of the human amygdala during prestimulus time intervals may have direct or indirect functional impact on subsequent face visual awareness, particularly during conditions with degraded inputs.

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## Supplementary material

Supplementary material is available at *Cerebral Cortex Journal* online.

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*Conflict of interest statement*. The authors declare no competing interests.

## Data availability

The dataset analyzed in the current study is available from the corresponding author on reasonable request.

## Author contributions

RG, JD-B, and PV designed the study. PM and MS administered clinical evaluation. RG, LS, and JD-B recorded the data. RG and TR performed the analyses. RG, TR, PV, and JD-B wrote the report.

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