Spatiotemporal Dynamics of Affective Picture Processing Revealed by Intracranial High-Gamma Modulations

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Abstract: Our comprehension of the neural mechanisms underlying emotional information processing has largely benefited from noninvasive electrophysiological and functional neuroimaging techniques in recent years. However, the spatiotemporal dynamics of the neural events occurring during emotional processing remain imprecise due to the limited combination of spatial and temporal resolution provided by these techniques. This study examines the modulations of high-frequency activity of intracranial electroencephalography recordings associated with affective picture valence, in epileptic patients awaiting neurosurgery. Recordings were obtained from subdural grids and depth electrodes in eight patients while they viewed a series of unpleasant, pleasant and neutral pictures from the International Affective Picture System. Broadband high-gamma (70–150 Hz) power was computed for separate 100-ms time windows and compared according to ratings of emotional valence. Compared to emotionally neutral or pleasant pictures, unpleasant stimuli were associated with an early and long-lasting (≈ 200 – $1,000$ ms) bilateral increase in high-gamma activity in visual areas of the occipital and temporal lobes, together with a late and transient (≈ 500 – 800 ms) decrease found bilaterally in the lateral prefrontal cortex (PFC). Pleasant pictures were associated with increased gamma activity in the occipital cortex, compared to the emotionally neutral stimuli. Consistent with previous studies, our results provide direct evidence of emotion-related modulations in the visual ventral pathway during picture processing. Results in the lateral PFC also shed light on the neural mechanisms underlying its role in negative emotions processing. This study demonstrates the utility of intracranial high-gamma

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Additional Supporting Information may be found in the online version of this article.

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modulations to study emotional process with a high spatiotemporal precision. *Hum Brain Mapp* 36:16–28, 2015. © 2014 Wiley Periodicals, Inc.

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INTRODUCTION

Fast and efficient processing of threatening and rewarding information is crucial for the individual's and its species' survival. How the brain specifically responds to emotionally laden information is a key issue in understanding the neural mechanisms underlying adaptive behaviour and affective processes. These mechanisms have been clarified in large part since the advent of functional brain imaging techniques [e.g., Dalglish, 2004; Damasio and Carvalho, 2013; Tamietto and de Gelder, 2010]. In the last decades, a substantial amount of electrophysiological and neuroimaging studies have examined the brain response to visual presentation of emotional scenes from the International Affective Picture System [IAPS, Lang et al., 2005], which is based on a two-dimensional model in which emotions are defined as a function of valence, that is, the level of pleasantness or unpleasantness experienced, and arousal, which corresponds to the intensity of the emotion [Lang et al., 1993].

The temporal dynamics of affective picture processing in the brain have been widely investigated using noninvasive scalp-recorded electroencephalography (EEG). Event-related potentials (ERPs) recorded during the presentation of affective pictures are typically characterised by an early posterior negativity (EPN; 150–300 ms), which is modulated by the emotional arousal value of the stimulus and is typically seen over temporo-occipital sites [Junghöfer et al., 2001; Leite et al., 2012; Schupp et al., 2004]. This early component is followed by a centroparietal late positive potential (LPP), which increases in response to unpleasant and pleasant images in comparison to emotionally neutral ones. The EPN has been interpreted as evidence of processing advantage of emotional stimuli during the initial stages of visual processing, whereas the LPP is thought to reflect the recruitment of selective attention processes related to the motivational signification of the stimuli. Studies using magnetoencephalography (MEG) have also found increased activity in occipitotemporal areas in relation to the arousing value of visual stimuli during the EPN time interval [Burgmer et al., 2013; D'Hondt et al., 2010], further supporting that early processing of visual stimuli along the ventral pathway is modulated by their affective value.

Oscillatory EEG activity has also been examined in association with affective picture presentation, and responses in the gamma band have been of particular interest [Güntekin and Başar, 2014]. Converging evidence from different studies suggest that affective pictures, and more

especially those of negative valence, are associated with higher gamma (>30 Hz) responses than emotionally neutral pictures over posterior regions [Keil et al., 2001; Martini et al., 2012; Matsumoto et al., 2006]. In two studies, this effect was prominent around 400–500 ms [Keil et al., 2001; Matsumoto et al., 2006], whereas Martini et al. [2012] found that the effect was long-lasting and peaked around 200 and 850 ms after stimulus onset. Earlier (<100 ms poststimulus) responses specifically associated with unpleasant images have also been reported in the lower gamma, sometimes extending to beta frequencies [Keil et al., 2001, 2007]. However, scalp-recorded EEG is limited by poor spatial resolution, making it unreliable for localizing the sources of activations, especially when they are located in medial brain regions.

Insights on the neuroanatomical correlates of affective picture processing have mostly been provided by functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), which showed that several brain areas are differentially engaged according to the stimulus emotional valence and arousal value. These include the occipital and occipitotemporal regions, in concordance with EEG and MEG studies, but also the prefrontal cortex (PFC), the medial temporal lobe, the anterior cingulate cortex and the insula [e.g., Aldhafeeri et al., 2012; Anders et al., 2004; Garavan et al., 2001; Gerdes et al., 2010; Heinzel et al., 2005; Nielsen et al., 2009; Northoff et al., 2000; Phan et al., 2002; Sabatinelli et al., 2011; Viinikainen et al., 2010]. However, due to their poor temporal resolution, the precise timing and sequence of these brain activations cannot be inferred from these techniques. Furthermore, fMRI and PET provide only indirect measures of brain activity, relying on changes in cerebral blood flow to infer neural activity.

In recent years, invasive intracranial electroencephalography (iEEG) recordings, primarily performed for clinical purposes such as presurgical monitoring for refractory epilepsy, are being increasingly used in neuroscience as a functional brain imaging technique. These recordings provide direct measurements of neural activity, combining a spatial precision comparable to that of fMRI and PET, with the high temporal resolution of EEG [Lachaux et al., 2003], and thus offer a unique opportunity to study the neural processes underlying emotion processing. Recently, iEEG recordings in epileptic patients have been successfully used to study the intracranial ERP response associated with affective image processing [Brázdil et al., 2009]. Larger intracranial ERP amplitudes were found in response to unpleasant stimuli, in comparison to neutral and pleasant pictures, in the lateral and mesial regions of

TABLE I. Participant characteristics.

Patient	Gender	Age (years)	Seizure focus	Implanted regions	No. of bipolar contacts for analysis
Pt. A	F	38	Anterior insula (L)	L (F, T, I)	45
Pt. B	F	35	Posterior insula (R)	R (F, T, P, I)	47
Pt. C	F	32	Operculoinsular (R) + mesio-temporal (L)	L (T, O), R (F, T, P, I)	95
Pt. D	M	25	Not determined	L (F, T, P, I)	80
Pt. E	M	36	Temporal (L)	L (F, T, P, O, I)	73
Pt. F	F	26	Occipital (R)	L (T, P, O), R (T, P, O)	77
Pt. G	M	41	Anterior insula (R)	R (F, T, P, O, I)	59
Pt. H	M	49	Precuneus (R)	L (P, O), R (F, T, P, O)	64

L, left; R, right; F, frontal; T, temporal; P, parietal; O, occipital; I, insula.

the prefrontal and temporal cortices. On average, these differences peaked around 500 ms poststimulus in the lateral PFC, and occurred somewhat later in the other regions, although the results were heterogeneous across subjects. No specific response elicited by pleasant pictures was reported. Unfortunately, the occipital lobe was not covered in their participants, thereby missing the opportunity to examine congruence with previous scalp EEG and MEG findings.

In the last decade, evidence has accumulated that high-frequency (>40 Hz) iEEG activity allows the investigation of task-related neural processes with especially high functional, anatomical and temporal specificity [Lachaux et al., 2012]. Gamma-band responses (GBRs) have been observed in relation to sensory as well as motor, cognitive and affective processes, and with a remarkable level of congruence with fMRI BOLD signal and with electrocortical stimulation findings [Crone et al., 1998; Edwards et al., 2005; Jung et al., 2011; Koga et al., 2011; Lachaux et al., 2005, 2007; Mainy et al., 2007; Qian et al., 2013; Ray et al., 2008; Sederberg et al., 2007]. Advantages of GBRs over ERPs include the ability to distinguish between neural activity increases and decreases, and they are also thought to be more suitable to estimate the duration of neural activity [Lachaux et al., 2008, 2012]. The present study aims to further examine the spatiotemporal dynamics of affective picture processing in the human brain, by exploring the modulations of high-frequency activity of the iEEG recorded in epileptic patients during the presentation of emotional and neutral pictures from the IAPS.

MATERIALS AND METHODS

Subjects

Participants were eight patients (four women; all right-handed) awaiting neurosurgery for drug-resistant epilepsy and hospitalised for long-term extraoperative invasive iEEG monitoring to better delineate their epileptic focus at the Centre Hospitalier de l'Université de Montréal (CHUM)—Hôpital Notre-Dame. Testing occurred at least 3

days after intracranial electrode implantation. All patients gave their informed written consent to participate to the experiment. The study was approved by the CHUM ethics committee, and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki. Characteristics of the study participants are presented in Table I.

Stimuli and Procedure

Patients were tested in their hospital room and seated approximately 57 cm from a 17 in. display monitor (1280 × 1024 pixels), which projected the visual stimuli (E-Prime 2.0; Psychology Software Tools, Pittsburgh). Three sets of 100 pictures were selected from the IAPS [Lang et al., 2005]: unpleasant, pleasant and neutral. Given the documented differences between males and females in emotional reactivity [Bradley et al., 2001], pictures were selected according to gender. Each set contained a similar number of pictures depicting faces, animals, objects, landscapes and human beings, and were made equal (Image J Software) in terms of main physical characteristics: mean luminance, standard deviation of luminance (i.e., contrast index), and colour saturation (red, green and blue). Detailed procedure for picture selection and validation of the stimulus set has been described elsewhere [D'Hondt et al., 2010]. Complete lists of IAPS identification numbers for selected pictures are presented in Supporting Information. Pictures had an angular size of 12° (horizontal) and 8° (vertical) and were presented centrally with a black background.

The task was conducted in two steps. First, iEEG was acquired during the presentation of five blocks of 60 stimuli presented in a pseudorandomised order, each block containing 20 pictures of each set. During each trial, a central fixation cross was presented for 500–1,500 ms, alerting the participant to the imminent arrival of the picture, which was projected for 500 ms. The screen was left blank for 1,000 ms before the presentation of the next trial. Participants were asked to concentrate on the emotional content induced by the picture. A short pause was offered

Figure 1.

Distribution of the electrode contacts in our study participants ($N = 8$) according to the estimated Talairach coordinates, for lateral (top) and median (bottom) cortical sites. Different colors were used to represent each patient: Pt. A: cyan; Pt. B: magenta; Pt. C: yellow; Pt. D: purple; Pt. E: green; Pt. F: red; Pt. G: blue; and Pt. H: gray.

after each block. In the second step, each picture presented at the first step was presented again and participants were asked to rate it on emotional arousal and valence dimensions, using two five-point scales adapted from the Self-Assessment Manikin [Bradley and Lang, 1994]: a valence scale (from very unpleasant to very pleasant) and an arousal scale (from very calm to very arousing).

iEEG Recording and Analysis

Intracranial EEG acquisition was performed at 2 kHz using a Stellate Harmonie audio-video-EEG monitoring system (Natus Medical, San Carlos, CA), by means of subdural grids and depth electrodes (Ad-tech medical instruments, Racine, WI), with one mastoid used as reference and the other used as ground. All signals were downsampled offline to 500 Hz and were re-referenced to their nearest neighbour on the same electrode array, constituting a bipolar montage. For localization of electrode con-

tacts, postimplantation MRIs were registered to fit the Montreal Neurological Institute template [Bertrand et al., 2013]. From this, Stellate Gridview coordinates were transformed to Talairach coordinates, which allowed for the automatic localisation of electrodes according to the Talairach Daemon atlas [Lancaster et al., 2000]. The distribution of the electrode contacts from the eight patients is illustrated in Figure 1. A total of 540 bipolar contacts were analysed in the present study; 134 in the frontal lobe, 215 in the temporal lobe, 95 in the parietal lobe, 67 in the occipital lobe and 27 in the insula. There were 253 bipolar contacts in the left hemisphere and 287 in the right hemisphere. Definite localisation of each electrode showing a significant effect of our experimental manipulation was insured by manually reviewing the postimplantation MRI scan of the patient.

EEG data were processed in Brain Vision Analyzer 2.0.1 (Brain Products, Munich, Germany). High and low pass filters were set at 0.1 and 200 Hz, respectively, and a notch filter was applied at 60 Hz. Automatic artefact rejection

TABLE II. Number of pictures identified as unpleasant, neutral and pleasant for each participant.

Patient	Unpleasant	Neutral	Pleasant
Pt. A	80	135	85
Pt. B	85	133	82
Pt. C	69	167	64
Pt. D	63	207	30
Pt. E	136	50	144
Pt. F	72	140	88
Pt. G	83	147	70
Pt. H	84	113	103

(± 250 μ V) and manual inspection of the data were performed to remove epochs containing noise and interictal activity. Channels localised in seizure focus areas, and those for which more than 15% of the signal had been rejected because of noise, were discarded. Data were segmented (−400 to 1,200 ms poststimulus onset) and grouped according to the patient's subjective valence ratings of the stimuli into the three following categories: unpleasant (ratings of 1 or 2 on a five-point scale), neutral, (ratings of 3) and pleasant (ratings of 4 or 5). Continuous time–frequency analysis over each trial was performed using complex Gaussian Morlet's wavelets in the frequency range of 70–150 Hz, in eight separate 10-Hz linear steps. Selection of this frequency band was based on previous works from the INSERM laboratory that used a 50–150 Hz band to study intracranial GBRs [Vidal et al., 2010]; we rejected the 50–70 Hz band from our analyses to limit the influence of 60-Hz power-line noise present in North America. The Morlet parameter was set at 13. The following resolution values at the time–frequency plane edges were obtained: at 70 Hz, the wavelet duration was 59 ms and the spectral bandwidth was 10.77 Hz; at 150 Hz the wavelet duration was 28 ms and the spectral bandwidth was 23.08 Hz. A baseline correction (−200 to −50 ms prior to stimulus onset) was applied.

Since event-related GBRs are generally broadband [Lachaux et al., 2012] and to limit the number of statistical comparisons, a broadband 70–150 Hz gamma-band power measure was computed, using a normalization method allowing for correction of the power decrease of the signal with increasing frequency inspired from previous work [Jung et al., 2011; Juphard et al., 2011]. For eight separate frequency layers (from [70–80 Hz] to [140–150 Hz]), power values for a given time interval were divided by the median value, on the same frequency layer, from all the prestimulus baseline epochs. Then, the broadband, 70–150 Hz, gamma-band power variable was computed by calculating the average of those eight normalised frequency layers. Epochs with outlying values (>3.29 S.D. from the mean) were excluded, since they were likely to reflect noise, which could not be accurately detected in the raw EEG. This procedure was repeated for each time interval, including the baseline (−200 to −50 ms) and every 100-ms

intervals from 0 to 1,000 ms poststimulus. The values obtained thus represent the mean broadband gamma power over a time interval of 100-ms duration, for each electrode of each participant and are expressed as percentage of power change relative to baseline level. This procedure was performed using MATLAB (version 7.9.1.705, The MathWorks, MA).

Statistical Analyses

Electrodes showing a significant response in the gamma band associated with presentation of the stimuli were identified using Wilcoxon signed-rank tests comparing gamma-band power during each poststimulus time interval to that of the prestimulus baseline period (−200 to −50 ms) on the same trial. This procedure was performed for the unpleasant and pleasant conditions separately. Because of the large number of comparisons for each condition (number of sites $\times$ 10 time intervals), responses were considered significant at $P < 0.001$. Then, for each significant GBR identified for a condition (i.e., each poststimulus 100-ms time interval different from its baseline at the same electrode), Mann–Whitney nonparametric tests were conducted to compare this GBR with the other two conditions [e.g., if an electrode showed significant activity at 300–400 ms in comparison to baseline, activity during this time interval was compared to the same interval for (1) neutral and (2) pleasant stimuli]. Valence-related gamma-band modulations were considered significant at $P < 0.025$, to correct for comparisons with two different conditions. Only brain regions for which the same experimental effect was observed in at least two patients (regardless of the hemisphere) were reported, thereby decreasing the probability of reporting chance findings. All analyses were conducted in MATLAB 7.9.1.705. Gamma-band activity was not analysed according to arousal ratings because they were missing for a significant part of the sample (37.5%) and because they could hardly be dissociated from valence ratings (i.e., unpleasant pictures were overrepresented among highly arousing pictures).

RESULTS

Behavioural Results

For all participants, analyses of variance (ANOVAs) confirmed that the subjective ratings of emotional valence significantly differ according to a priori categories of the pictures in the expected direction (i.e., unpleasant $<$ neutral $<$ pleasant; all P 's < 0.001). Mean (SD) ratings of valence, on the five-point-scale, according to a priori categories were: unpleasant = 1.98 (0.16); neutral = 3.00 (0.11); and pleasant = 3.70 (0.19). For three patients, arousal ratings were invalid because of confusion with the concept of emotional arousal; for the remaining five

participants, mean (SD) ratings of arousal according to a priori categories were: unpleasant = 3.04 (0.91); neutral = 1.58 (0.84); and pleasant = 2.45 (0.97). The number of trials per condition (i.e., number of stimuli identified as unpleasant, neutral and pleasant according to valence ratings) for each participant is presented in Table II.

Gamma-Band Modulations Associated with Stimulus Valence

Figure 2 depicts the distribution of contacts showing significant valence-dependent modulations, across time, for (a) unpleasant versus neutral, (b) unpleasant versus pleasant and (c) pleasant versus neutral contrasts. Significant broadband gamma power modulations associated with emotional pictures are listed in Table III.

Early- and long-lasting valence-dependent modulations of GBRs were first observed bilaterally in the occipital pole and in the lateral occipital cortex. More specifically, unpleasant pictures were associated with increased gamma-band activity in comparison to both neutral and pleasant pictures in most patients and in a large proportion of contacts implanted in these areas. This effect appeared up to 1,000 ms after stimulus onset. Pleasant pictures were also associated with early increases in GBRs in these regions compared to neutral stimuli. Representative cases of valence-dependent effects on gamma activity in the occipital pole and lateral occipital cortex are illustrated in Figure 3a. Activity recorded at occipital sites is characterised by a large, early increase in high-gamma power peaking around 220 ms in the occipital pole (minimum value $\approx$ 155 ms) and around 250 ms in the lateral occipital cortex (minimum value $\approx$ 200 ms), and a later increase peaking at 500–600 ms, which may be linked to the end of the stimulus presentation. These responses are stronger for the unpleasant stimuli.

As can be seen in Figure 3b, GBRs recorded in the occipitotemporal gyrus, which forms the fusiform gyrus, are similar to those recorded in the occipital pole and in the lateral occipital cortex. Large GBRs peaking around 220 ms in the occipital part of the fusiform gyrus (minimum value $\approx$ 155 ms), and around 250 ms in the temporal part (minimum value $\approx$ 190 ms) are observed. Modulations of GBRs by unpleasant images observed in this region are also similar to those described above. Increased activity in comparison to both neutral and pleasant stimuli was observed in all participants with electrodes in this region. However, in contrast to what was found in the lateral parts of the occipital cortex, pleasant stimuli did not induce higher activity in this region, and even showed decreased activity compared to neutral stimuli in two patients. A later ($\approx$ 400 ms) and shorter increase in high-gamma power was also observed in the lateral part of the inferior temporal gyrus of two patients in response to unpleasant versus neutral pictures.

Contrary to what was observed in the occipital and temporal lobes, most of the patients implanted in the frontal cortex had at least one electrode displaying transient reductions in high-gamma power in response to unpleasant stimuli in the lateral PFC. These reductions were generally observed at 400–900 ms and were more consistently observed in the anterior part of the inferior frontal gyrus, when unpleasant pictures were contrasted with neutral pictures. Differences between unpleasant and pleasant pictures were also observed, and two patients also displayed such gamma-band suppressions in response to unpleasant pictures in the middle frontal gyrus. As illustrated in Figure 3c, PFC sites show an abrupt reduction in high-gamma activity peaking between 500 and 800 ms after unpleasant stimulus onset and reaching lower activity compared to baseline level, suggesting suppression of neural activity.

DISCUSSION

We studied the spatiotemporal dynamics of affective picture processing in the human brain by examining modulations of high-gamma iEEG activity in eight epileptic patients. We found that emotional pictures were associated with replicable modulations of the high-frequency signal in the occipital, temporal and frontal lobes. More specifically, compared to the emotionally neutral and to pleasant pictures, unpleasant stimuli elicited a stronger high-frequency response in lateral occipital and medial occipitotemporal areas associated with visual processing. This effect began around 200 ms after presentation of the stimulus and lasted for several hundreds of milliseconds. Contrasts between the pleasant and the emotionally neutral stimuli yielded less congruent findings, with replicable effects being found solely in the occipital lobe as increased and decreased activity were found in the lateral occipital cortex and in the fusiform gyrus, respectively. By contrast, in the lateral PFC, unpleasant images were associated with a late and transient reduction in high-gamma activity.

As expected from earlier neurophysiological studies, our results indicated that emotional pictures, whether unpleasant or pleasant, are associated with increased brain activity in the occipital visual areas when compared to emotionally neutral pictures, and this effect began around 200 ms after stimulus onset. The timing of this effect concords with scalp-recorded studies describing an early negative component that emerges 150–200 ms after emotionally laden pictures over occipitotemporal sites [Junghöfer et al., 2001; Schupp et al., 2004]. Affective pictures presented during a visual oddball paradigm have also been associated with a modulation of ERP segments starting at the P200 component [Olofsson and Polich, 2007]. Our group had also previously used the same protocol using MEG, and the main finding was the observation of a greater activity for emotional compared to neutral pictures at 180 ms in occipitotemporal regions, which correlated with the magnitude of

Figure 2.

Distribution of the electrode contacts showing significant high-gamma modulation across time, for each contrast. Values represent the ratio in broadband gamma activity for the following comparisons (a) unpleasant versus neutral; (b) unpleasant versus pleasant; and (c) pleasant versus neutral. Although analyses were

conducted with 100-ms time intervals, results are presented for 200-ms intervals for illustrative purposes: when effects were found during the entire 200-ms interval, values from the 100-ms interval showing the largest effect were shown.

TABLE III. Location of electrodes showing gamma-band modulations by emotional valence.

Brain area	Effect	# Patients	% Patients	# Contacts	% Contacts	Timing (ms)
Occipital pole	U > N	4	100	9	69	100–1,000
	U > P	3	75	7	54	300–800
	P > N	2	50	3	23	300–700
Lateral occipital cortex	U > N	3	75	8	42	200–1,000
	U > P	3	75	5	26	200–1,000
	P > N	3	75	6	32	200–1,000
Fusiform gyrus	U > N	5	100	20	43	200–1,000
	U > P	5	100	17	37	200–1,000
	N > P	2	40	9	20	100–800
Inferior frontal gyrus	N > U	5	83	6	13	500–900
	P > U	2	33	2	4	500–700
Middle frontal gyrus	N > U	2	33	3	11	400–600
	P > U	2	33	3	11	400–600
Lateral inferior temporal gyrus	U > N	2	33	4	11	400–800

Note: Only brain areas for which the same effect was seen in at least two participants are presented. Percentage values indicate the proportion of patients/contacts showing the effect among all patients/contacts implanted in this region (occipital pole: 4 patients, 13 contacts; lateral occipital: 4 patients, 19 contacts; fusiform: 5 patients, 46 contacts; inferior frontal gyrus: 6 patients, 46 contacts; middle frontal gyrus: 6 patients, 27 contacts; lateral inferior temporal gyrus: 6 patients, 35 contacts). Timing values indicate the time intervals in which the effects were observed across all patients/contacts.

N, Neutral; P, Pleasant; U, Unpleasant.

the skin conductance response [D'Hondt et al., 2010]. As was found in a previous scalp-EEG study [Martini et al., 2012], the modulation of gamma activity associated with emotional pictures is long-lasting, in some cases being still found hundreds of milliseconds after the stimulus disappeared. That this effect was more salient for negative than for positive stimuli may be attributable to the fact that the former were more emotionally arousing for our study participants. The localisation of this effect is also congruent with findings from fMRI and PET studies [e.g., Bradley et al., 2003; Lang et al., 1998; Nielen et al., 2009; Paradiso et al., 1999; Phan et al., 2002]. Intracranial recordings obtained from the primary cortex of nonhuman primates have revealed object-based attentional modulations of neural activity about 235 ms after the onset of stimulus presentation [Roelfsema et al., 1998]. Taken together, these results provide converging evidence for a processing advantage of emotionally laden stimuli during the very initial stages of visual processing [Vuilleumier, 2005].

Gamma-band modulations associated with stimulus valence were also consistently observed in the occipitotemporal (fusiform) gyrus, within both its temporal and its occipital parts. A clear distinction between unpleasant and pleasant stimuli was observed as the former elicited stronger activity and the latter sometimes elicited weaker activity, in comparison to neutral stimuli. Involvement of the fusiform gyrus in negative picture processing is supported by fMRI [Aldhafeeri et al., 2012; Radua et al., 2014; Simpson et al., 2000] and PET [Lane et al., 1997; Paradiso et al., 1999] studies. The fusiform gyrus is involved in high-level, complex visual information processing and has been shown to play a major role in object recognition and visually guided action [Joseph, 2001; Konen et al., 2011; Shein-

berg and Logothetis, 1997]. Function of the fusiform gyrus has also been associated with face processing, as it is the seat of the fusiform face area [Barton et al., 2002; McCarthy et al., 1997]. Increased activity for emotional faces, in comparison to neutral faces, has also been reported in the fusiform gyrus [Fusar-Poli et al., 2009]. Since our visual stimuli contained both types of stimuli, we cannot conclude that the observed modulation of gamma activity was specific to images of faces, or if it extended to scenic stimuli. Nevertheless, a recent fMRI study has reported activation of the fusiform gyrus in response to nonfacial unpleasant stimuli, along with deactivation for photographs eliciting happiness or sadness [Radua et al., 2014], which is congruent with our findings with gamma activity (i.e., unpleasant > neutral > pleasant).

Recently, an iEEG study in humans has revealed broadband and high-gamma modulations in the fusiform gyrus associated with target detection [Bansal et al., 2014]. In this study, participants had to indicate whether a cued category was present or absent on a subsequent image. Increased activity for the target-present trials started around 250 ms after stimulus onset and lasted hundreds of milliseconds, similar to what was found in our study and was observed for various types of objects. The authors concluded that, rather than just containing passive representations of visual objects, the human inferior temporal cortex is actively modulated by task demands. Our findings further suggest that even in the absence of any active task, this brain region is modulated by the emotional content of the visual stimuli. This effect may reflect the outcome of a top-down process allowing a better identification of visual objects that constitute potential threats in our environment.

Figure 3.

Representative illustrations of valence-dependent high-gamma activity across time at (a) occipital pole and lateral occipital sites, (b) in the fusiform gyrus and (c) in the prefrontal cortex. Each image represents time-dependent change (%) in high-gamma activity, relative to baseline, at a given electrode contact, for unpleasant (red), pleasant (blue) and neutral (green) stimuli. Bold lines depict significant differences between conditions.

The most intriguing result in our study is the transient decrease in high-gamma activity found in response to unpleasant pictures in the lateral PFC. This effect appeared highly replicable and was found at similar latencies across patients, around 500–800 ms poststimulus onset, that is, after the stimulus has been consciously perceived and recognized. This finding appears, at least at first glance, contradictory with the vast majority of functional imaging studies reporting increased BOLD signal in the ventrolateral and dorsolateral PFC associated with arousing and unpleasant pictures [e.g., Aldhafeeri et al., 2012; Grimm et al., 2006; Kensinger and Schacter, 2006; Viinikainen et al., 2010]. Nevertheless, a few studies have provided some support for a deactivation of the lateral PFC in response to negative emotional pictures [Northoff et al., 2000; Paradiso et al., 1999]. Northoff et al. [2000] have reported negatively correlated intensity-weighted volumes in the lateral PFC in response to negative emotional pictures. It was proposed that these results reflected either a decrease in activity associated with neural inhibition, a steal effect on the regional blood circulation, or an alteration of a coupling mechanism between oxygen consumption and regional cerebral blood flow. Our direct recordings of neural activity in the lateral PFC may provide support for their first hypothesis.

The lateral PFC, which plays a crucial role in high-order control of cognition and behaviour [Petrides, 2005; Steele et al., 2013; Wagner et al., 2001], is also thought to be involved in top-down regulation of emotion and shows increased BOLD activity when emotion regulation strategies are employed such as reappraisal and attention deployment [Johnstone et al., 2007; Kanske et al., 2011; Kim and Hamann, 2007; Ochsner et al., 2004; Phan et al., 2005; Ray and Zald, 2012]. Differential activity of this brain region with regards to stimulus valence may be related to such top-down regulation processes that the participants engage automatically when faced with unpleasant pictures. Mitchell [2011] also points out that the ventrolateral PFC is involved in negative feedback encoding and in attention to behaviourally significant stimuli and proposed that this region plays a role in modulating behavioural and emotional output according to contextual demands. The comprehension of the gamma-band suppression in the lateral PFC would benefit from further investigations examining how this response is modulated by overt task demands, such as attention allocation and employment of emotion regulation strategies.

Nevertheless, it still remains unclear why suppression, rather than an enhancement, of high-gamma activity in the lateral PFC was observed in response to unpleasant stimuli. Interestingly, Lachaux et al. [2008] observed a similar decrease in gamma-band power in the ventrolateral PFC during active reading. As the authors pointed out, although gamma-band activations have been shown to be positively correlated with BOLD activations, it is still unclear whether gamma-band activity decreases would be associated with BOLD deactivations: “this putative sym-

metry may be wrong if gamma suppression is an active mechanism associated with metabolic demands” [Lachaux et al., 2008, p. 447]. Another interpretation is that suppression of high-frequency activity may reflect deactivation of the “default-mode network,” which is active when the individual is not focused on external stimuli [Lachaux et al., 2012; Ossandón et al., 2011]. In the context of our study, this would indicate that perceiving unpleasant images provokes a deactivation of this network, resulting in increased attentional allocation to these potentially relevant stimuli [e.g., Sreenivas et al., 2012]. However, if our results in the lateral PFC reflected deactivation of the default-mode network, we would expect simultaneous deactivations in other and more central regions of the network, which was not the case in the present study. Of course, we cannot exclude the possibility that these regions (e.g., parietal cortex, medial PFC and posterior cingulate) were not sufficiently covered by the intracranial electrode maps of our patients to reliably assess gamma-band deactivations in response to unpleasant stimuli.

Surprisingly, we found no consistent valence-dependent responses in brain regions well known for their involvement in emotion processing, namely the amygdala, the insular cortex and the orbitofrontal cortex [i.e., Aldhafeeri et al., 2012; Britton et al., 2006; Gerdes et al., 2010; Northoff et al., 2000; Pessoa and Adolphs, 2010]. Previously, Oya et al. [2002], who recorded iEEG activity in the amygdala of four patients, found increased power in the lower-gamma band (30–60 Hz) in relation to aversive images, but not to pleasant or neutral images, 200–400 ms after stimulus presentation. Differences in frequency bands might account for the absence of consistent effect in our study. The small number of electrodes implanted in the orbitofrontal cortex is a likely explanation for the absence of significant findings in this region. Concerning the insula, three of our patients had contacts in the anterior portion of the insular cortex, which is thought to be more specifically involved in emotion processing [Kurth et al., 2010]. For two of these three patients, the focus of epileptic seizures was found to be localised in the anterior insula, leading to electrode rejection, and the other one had a posterior insular seizure focus, which may have affected the functional integrity of the entire insula.

This study is limited by factors that are inherent to the use of presurgical intracranial recordings in epileptic patients as a mean to study brain function. These include the incomplete coverage of the brain by intracranial electrodes, the possible influence of epilepsy on the functional organization of the brain and on neuropsychological performance, and the possible influence of analgesic medication on neural activity. Nevertheless, replication of the results across patients, together with the congruent findings from prior brain imaging studies with healthy participants, gives further confidence that these factors had a minimal impact on our results and do not alter our conclusions.

CONCLUSION

To our knowledge, this study is the first to examine the spatiotemporal dynamics of affective pictures processing by exploring gamma-band modulations of iEEG activity in distributed brain regions. Our findings in the occipital and temporal lobes replicate previous results obtained from indirect functional brain imaging techniques relying on regional changes in cerebral blood flow to infer neural activity, and provide information on the timing of activations that is compatible with previous scalp-EEG and MEG findings, but with increased spatial precision. The suppression of gamma-band activity observed in the lateral PFC in response to unpleasant stimuli may represent top-down emotion regulation processes, although further investigations will be necessary to elucidate its actual function.

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