JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Systems/Circuits

Anterior temporal lobectomy impairs neural classification of body emotions in right superior temporal sulcus and reduces emotional enhancement in distributed brain areas without affecting behavioral classification

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DOI: 10.1523/JNEUROSCI.0634-18.2018

Received: 7 March 2018

Revised: 30 August 2018

Accepted: 4 September 2018

Published: 18 September 2018

Author contributions: L.V.D.V., J.J., W.V.P., M.V., and J.V.d.S. designed research; L.V.D.V. performed research; L.V.D.V., Y.-A.H., and J.V.d.S. analyzed data; L.V.D.V. wrote the first draft of the paper; L.V.D.V., J.J., Y.-A.H., M.V., and J.V.d.S. edited the paper; L.V.D.V., M.V., and J.V.d.S. wrote the paper.

Conflict of Interest: The authors declare no competing financial interests.

The authors declare no competing financial interests. LV holds an aspirant fellowship granted by Fonds Wetenschappelijk Onderzoek (FWO)- Vlaanderen [11Z8917N]. JJ is a post-doctoral researcher supported by Fonds Wetenschappelijk Onderzoek (FWO)- Vlaanderen. JV is supported by FWO-Vlaanderen and a KU Leuven starting grant. We are grateful to all patients and healthy volunteers for their cooperation. We thank Dr. Kristof Vansteelandt for his advice on statistics and Jochen Weber for technical support.

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Cite as: J. Neurosci ; 10.1523/JNEUROSCI.0634-18.2018

Anterior temporal lobectomy impairs neural classification of body emotions in right superior temporal sulcus and reduces emotional enhancement in distributed brain areas without affecting behavioral classification

Abbreviated title: Processing body language in temporal lobectomy

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Number of pages: 29
Number of figures: 6
Number of Tables: 3
Number of multimedia: 3
Number of words abstract: 239
Number of words introduction: 631
Number of words discussion: 1493

Acknowledgement:
The authors declare no competing financial interests. LV holds an aspirant fellowship granted by Fonds Wetenschappelijk Onderzoek (FWO)- Vlaanderen [11Z8917N]. JJ is a post-doctoral researcher supported by Fonds Wetenschappelijk Onderzoek (FWO)- Vlaanderen. JV is supported by FWO-Vlaanderen and a KU Leuven starting grant. We are grateful to all patients and healthy volunteers for their cooperation. We thank Dr. Kristof Vansteelandt for his advice on statistics and Jochen Weber for technical support.

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Abstract

Humans with amygdalar lesions show proportional reductions of the emotional response to facial expressions in the fusiform face area as well as deficits in emotion recognition from facial expressions. While processing of bodily expressions shares many similarities with facial expressions, there is no substantial evidence that lesions of the amygdala result in similar behavioral and neural sequellae. We combined behavioral assessment with functional neuroimaging in a group of male and female humans with unilateral anterior temporal lobe (ATL) resections including the amygdala (right: n= 10; left: n=10) and 12 matched controls. The objective was to assess whether the amygdala is crucial for the recognition of body expressions and for modulatory effects on distant areas during perception of body expressions. The behavioral results revealed normal performance in both patient groups on emotion categorization of body expressions. The neuroimaging results showed that ATL patients displayed no enhanced activations in right FBA and left EBA and that left ATL patients additionally displayed no enhanced activations in right pSTS and right EBA respectively. Multi-voxel pattern analysis (MVPA) revealed altered categorization capacity between emotional and neutral stimuli in right pSTS in right ATL patients. In addition, we also found emotional enhancement in frontal, parietal, occipital and cingulate regions in controls. Taken together our data show that the amygdala and anterior temporal lobes are not necessary for recognition of dynamic body expressions, but suggest that amygdala lesions affect body emotion processing in distant brain areas.

Significance Statement

For humans information from emotional expressions of others is crucial to support social interactions. The majority of emotion studies has focused on facial expressions, however, in daily life, we also use information from body postures and body movement. Visual processing of body expressions relies on a brain network including body specific visual areas and visuomotor areas. Even though the importance of the amygdala and its modulatory effects on distant brain regions has been documented, it remains unclear whether the amygdala plays a crucial role in emotional body processing. By combining behavioral and neuroimaging data in patients with amygdalar lesions we provide further evidence for its modulatory effect on distant areas during the perception of body expressions.

Introduction

Converging evidence from functional imaging studies and neuropsychological studies in clinical cohorts indicate that the anterior-temporal lobe (ATL) and the amygdala in particular are key components of the 'emotional brain' (Adolphs, 2010; Adolphs, Tranel, Damasio, & Damasio, 1994; Bickart, Dickerson, & Barrett, 2014; Fusar-Poli et al., 2009; Haxby & Gobbini, 2011; Morris et al., 1996; Olson, Plotzker, & Ezzyat, 2007). The role of the amygdala in emotional face processing has been well established by means of functional imaging (Vuilleumier & Pourtois, 2007) and lesion studies. Patients with bilateral amygdalar lesions show impaired recognition of facial expression, particularly fear and this deficit appears more pronounced compared to unilateral lesions (Adolphs et al., 1994; Adolphs et al., 1999). Also, neurodegenerative disorders characterized by amygdala atrophy, like behavioural variant frontotemporal dementia (bvFTD), are associated with deficits in facial expression recognition and this deficit is proportional to amygdalar volume (De Winter et al., 2016; Kumfor, Hazelton, De Winter, Cleret de Langavant, & Van den Stock, 2017; Rosen et al., 2002). Unilateral anterior temporal lobectomy typically includes the amygdala and results in facial emotion recognition impairments (Adolphs et al., 1994; Monti & Meletti, 2015). Amygdalar modulatory effects at distance, especially in face-selective areas, further corroborate the central role of the amygdala in the brain's response to emotional faces. Activity in amygdala correlates with activity in FFA during perception of facial expressions (Diano et al., 2017; Herrington, Taylor, Grupe, Curby, & Schultz, 2011; Morris et al., 1998) and fMRI studies in patients with both unilateral and bilateral amygdalar lesions show reductions of emotion effects in FFA proportional to the lesion extent (De Winter et al., 2016; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), supporting the notion of a functional coupling between amygdala and FFA. Recent work on bodily expressions seems to confirm the importance of this region in the processing of emotional body actions as well (de Gelder, 2006; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Goldberg, Christensen, Flash, Giese, & Malach, 2015; Hadjikhani & de Gelder, 2003; Peelen, Atkinson, Andersson, & Vuilleumier, 2007; Pichon, de Gelder, & Grezes, 2008; Van den Stock, Hortensius, Sinke, Goebel, & de Gelder, 2015). Amygdala responses to body expressions correlate with responses in FBA and EBA (Peelen et al., 2007). Furthermore, the amygdala, as a node in the emotion network, has strong connections with the action observation network and functions primarily as a source region, i.e. it modulates activation in other regions (Huang et al., 2018; Jastorff, Huang, Giese, & Vandenbulcke, 2015). However, there is currently no evidence that the amygdala is directly involved in decoding or representing emotion-specific information independent of the mode of expression (e.g. Peelen et al., 2010; Skerry & Saxe, 2014) or correlations with emotion-recognition performance (Jastorff, Huang et al. 2015), although this may be related to MVPA limitations (Skerry & Saxe, 2014).

Activation patterns in other regions of the emotion or action observation network, such as the posterior STS (pSTS) reliably discriminate emotional expressions in body

postures and other modalities (Jastorff et al., 2015; Peelen, Atkinson, & Vuilleumier, 2010; Skerry & Saxe, 2014).

At the behavioral level, there is currently no strong evidence that lesions of the amygdala result in body expression recognition deficits (Atkinson, Heberlein, & Adolphs, 2007; de Gelder et al., 2014). To study the role of the amygdala in bodily emotion recognition and its modulatory effect on distant areas during the perception of body expressions, we performed a series of behavioural and neuroimaging experiments in patients with unilateral ATL resections and matched controls. The aims of the study were 1) to reveal whether intact amygdala are necessary for body expression recognition and 2) to reveal effects at distance in neural activity and decoding accuracy of ATL resections during body expression perception in body-responsive areas as well as at the whole brain level.

Materials and Methods

Participants

A total of 20 patients who had previously undergone unilateral surgical resection due to mesial temporal lobe epilepsy were recruited through the epileptic surgery database of University Hospitals Leuven, Belgium. Demographics are presented in Table 1. All patients had an extensive history of uncontrollable epilepsy before surgery with an average onset of seizure at 12.4 years of age (SD= 2.3). Ten (4 male and 6 female) and 7 (6 male and 1female) participants underwent respectively a left and right unilateral anterior temporal lobectomy. Two male participants underwent a right amygdalo-hippocampectomy. One female patient had a right-sided tumour resection including the amygdala and hippocampus. The lesion overlap map is displayed in Figure1. The time since surgery was variable with a mean length of 10.5 years (SD=0.9). All patients were seizure free at the time of scanning. Six patients were medication free at the time of scanning. The remaining patients were prescribed levetiracetam (n =7), valproate (n = 2), carbamazepine(n=7), lamotrigine (n=2),topiramate (n=1), pregabaline (n=1) and clonazepam (n=2). Exclusion criteria for patients were generalized cognitive impairment (IQ <80), major DSM axis I psychopathology, other neurological conditions than epilepsy or major somatic disorders. The healthy control group (5 male and 7 female) was recruited using the hospital co-workers internal advertisement service. Controls were matched for mean age and sex ratio with the patient group (Table 1), had no self-reported major DSM axis I psychopathology, neurological or somatic disorder and did not take any psychotropic medication.

To document any cognitive changes following ATL resection we performed a cognitive assessment including global cognitive ability (Mini Mental State Examination), verbal memory (Rey's Auditory Verbal Learning Test), categorical verbal fluency (animal verbal fluency) and visual divided attention and task shifting (Trail Making Test A and B). Participants also completed a mood (Beck Depression Inventory) and affect (Positive and Negative Affect Scale) questionnaire. All but 1 right resection patient and 1 control were right handed as assessed through the

Edinburgh handedness inventory. All participants had normal or corrected-to-normal visual acuity.

The study was conducted in accordance with the Declaration of Helsinki and all participants gave written informed consent. The ethical committee of University Hospitals Leuven approved the study.

Experimental design

Stimuli: The stimuli have been described in detail elsewhere (Jastorff et al., 2016; Jastorff et al., 2015). In short, they consisted of video clips displaying puppet-models of walking humans. They were constructed using motion capture data of emotionally expressive (angry, fearful, sad and happy) and neutral gaits. An animated custom-built volumetric puppet model was built and rendered in Matlab (for details, see Roether, Omlor, Christensen, & Giese, 2009). These stimuli served as prototypes for subsequent emotion morphing (Giese and Poggio, 2000; Jastorff et al. 2006). The complete set of prototypical stimuli contained 30 stimuli, six examples of 5 conditions (angry, happy, sad and fearful). We used a continuum of expressions ranging from 100% neutral prototype to 125 % emotional prototype. For frame examples of stimulus prototypes and different morph levels see Figure 2.

Scrambled versions of the stimuli were created by decomposing the figure and rearranging the individual geometric shapes. A constant random offset in horizontal or vertical direction was added to the original movement of the geometric shapes forming the puppet model. In half of the stimuli the shapes translated horizontally, while in the other half the shapes translated vertically. The speed of each shape was the average speed of all shapes in the original stimulus. Thus in both conditions, the global motion energy was matched. For stimulus examples, see Movies 1 to 3.

Behavioural experiments: Morphed stimuli were displayed on an LCD screen (60 Hz frame rate; 1,600 x 1,200 pixels resolution) that was viewed binocularly from a distance of 40 cm, producing a stimulus size of about 7 degrees visual angle. Stimulus presentation and recording of the participants' responses was implemented with the MATLAB Psychophysics Toolbox (Brainard,1997). The stimuli were shown against a uniform gray background (Figure 2).

A trial consisted of presentation of a stimulus at the center of the screen for 10s. No fixation requirements were imposed. Participants were instructed to categorize the stimulus as happy, angry, fearful, or sad by pressing 1 of four labeled buttons, indicating their choice for the corresponding emotion category. Participants were instructed to respond as soon as they had made their decision but we did not emphasize responding quickly. If the participant answered within 10s, stimulus presentation was terminated immediately, otherwise, it halted after 10 s and a uniform gray screen was shown until the subject entered a response. After a 1.5s inter-trial interval, the next trial started. The experiment started with a demonstration session where subjects were familiarized with the stimuli for a maximum of 12 trials (3 trials per emotion). No feedback regarding performance was provided during the entire experiment.

We used a 1-up-1-down staircase procedure to calculate individual emotion detection

thresholds for every emotion separately. The initial test level was set at 50% emotion for each staircase. Emotions were shown in a random order. When participants answered correctly, test level increased with 5% (a 5% less emotional stimulus was shown), when they answered incorrectly, test level decreased with 5% (a 5% more emotional stimulus was shown). The minimal test level for each emotion was 0% and the maximal test level was 125%. These motion morphs were derived from 6 different prototypical stimuli for each emotion category, as was described above. When the boundaries were hit 4 times for a particular emotion, the presentation of this emotion was stopped. Otherwise, it stopped after 10 reversals of the staircase or after 35 trials per emotion. Hence, the number of trials and selection of stimuli per emotion category was dependent on the responses of the participants. Individual emotion detection thresholds were calculated for each emotion based on the reversal values of the 4 staircases. Each threshold represents the mean of 10 reversals and is an estimate of the 50% correct performance level. In order to obtain a general emotion detection threshold, thresholds were averaged over the four emotions for each subject.

We added a control experiment similar to the emotion task in terms of stimuli and display parameters. Stimuli consisted of motion morphs derived from neutral walking and neutral running prototypes and the instruction stated to categorize the stimuli as walking or running. This task allows investigating the specificity of any emotion processing deficits (Jastorff et al., 2016; Van den Stock, 2018).

fMRI task (Fig. 2): Prototypical avatars (i.e. 100% emotional) expressing the four emotions and a neutral condition were presented against a black background in an event related oddball paradigm. As an oddball we added a neutral backwards-walking avatar. Stimuli appeared centrally on the screen for 1.5 to 5.0s followed by an inter-stimulus interval of variable length (2.3 -5.0s, determined by an exponential function (Dale, 1999)) displaying only a red fixation dot. In each run, each stimulus was presented at two different sizes. Two different sizes were used to minimize the effect of low-level features such as retinal position on the fMRI activations. Twelve null trials (baseline) were randomly interspersed presenting only the fixation dot for 3s. The oddball was shown 6 times. Participants were asked to press a button every time the oddball appeared. Four functional runs were recorded per participant. To familiarize with the stimuli, all participants watched some stimuli prior to the experiment. The order of experiments (behavioural/fMRI) was counterbalanced between participants.

Localizer experiment: In order to study emotion effects in independently defined body-responsive ROIs, we performed one localizer run for each participant in addition to the experimental runs. The localizer consisted of two stimulus conditions: intact prototypical (neutral and emotional) stimuli and scrambled versions of these prototypical stimuli, both organised in separate blocks with duration of 15s. The stimulus duration varied across stimuli but was matched between scrambled and intact blocks with a 500ms interstimulus interval. Blocks were separated by an ISI of 6-7s (baseline). The run consisted of 16 stimulation blocks, eight of every condition.

Participants were instructed to fixate a red fixation dot in the centre of the screen during the entire run.

MRI Data acquisition: Structural and functional images were collected on a 3T Philips achieva dstream scanner with a 32 channel receive only headcoil. A standard EPI sequence was used to acquire the functional runs (TR= 2s, TE= 30ms flip angle= 90°, 36 slices, 0.3mm interslice gap, 2.75mm x 2.75mm x 3.5mm voxel size). All functional scans were preceded by 4 dummy scans to allow for magnetization to reach equilibrium state. During the scan session a high resolution T1 weighted anatomical image (TR=9.7, TE=4.6, flip angle= 8°, 182 slices, matrix size 256 x256, 1 mm x 1 mm x 1 mm voxel size) was acquired.

Statistical analysis

Behavioural data analysis: Neuropsychological data as well as the data from the control task were analysed by means of one-way ANOVAs using IBM SPSS Statistics version 24. To assess group differences in emotion recognition, linear mixed models analyses with random intercept and fixed effects for group, emotion and group*emotion were performed on the emotion detection thresholds. All post-hoc tests were performed with a Bonferroni correction.

fMRI data analysis: All data were analysed using statistical parametric mapping (SPM12, Wellcome trust centre for neuroimaging London) within Matlab (Mathworks, inc.). Data were slice time corrected, motion corrected (aligned to the mean image across runs) and coregistred to the subject's high-resolution anatomical image. Images were then normalized to MNI space with a voxel size of 2mm x 2 mm x 2mm using New Segment with an extra prior (the mean of white matter and CSF TMP's (Ripolles et al., 2012)) and DARTEL. Data were smoothed using an 8mm isotropic Gausian Kernel.

For each participant, all conditions with durations and onsets were entered in a general linear model, yielding a design matrix containing 6 regressors modelling the 6 conditions (4 emotions + neutral + fixation (baseline)). Head movement parameters, obtained from the motion correction during preprocessing, were entered as a regressor-of-no-interest for each run. To exclude variance due to the oddball and the subjects' response, two additional regressors were added to model the appearance of the oddball and the subsequent button press during the ISI's. On the subject level, all regressors were convolved with the canonical haemodynamic response function. We calculated contrasts for each participant for each of the four emotional conditions versus neutral and the average of all four emotional conditions versus neutral. Data were further analysed at second level through analysis of variance (ANOVA) using a full factorial design. Factors consisted of group (3 levels: controls, right resection and left resection) and emotion (4 levels: angry vs. neutral, fear vs. neutral, sad vs. neutral, happy vs. neutral). Statistical threshold was set at $P_{height} < 0.05$, FWE corrected, cluster-extent of 20 voxels. The following effects were investigated: the effect of emotion (i.e. a one-sample t-test on each of the four emotions vs neutral contrasts) in

each group separately; effect of emotion in controls vs right resected patients (i.e. a two-sample t-test on each of the four emotions vs neutral contrasts between controls and right resected patients); effect of emotion in controls vs left resected patients; effect of emotion in left vs right resected patients. In addition, all inverse group effects were also investigated.

Data from the localizer were preprocessed in a similar way to the data from the experimental runs, yielding a design matrix containing three regressors modelling the three conditions (bodies, scrambles, baseline). The contrast 'bodies vs. scrambles' was calculated for each subject. Subsequently a random effects analysis was performed on the parameter estimates of activity for this contrast across participants over the whole group (controls and patients) using a one-sample t-test. Threshold was set at $P_{height} < 0.001$, uncorrected with a minimal cluster extent of 100 voxels. Subsequently, ROI analyses by means of small volume corrected (SVC) contrasts were performed to investigate group differences in emotion response in the body-responsive ROIs defined by the localizer. The mean percent signal change (PSC) was calculated for the average of the four emotional conditions relative to baseline as well as for the neutral condition relative to baseline by averaging the PSC within each of these predefined ROIs using Marsbar (Brett, 2002). Group differences were investigated using a linear mixed model with random intercept and fixed effects for group, ROI and group*ROI. All post-hoc tests were performed with a Bonferroni correction.

To investigate functional coupling between amygdala and body-responsive regions, we correlated fitted responses in right and left amygdala with fitted responses in body-responsive ROIs in the healthy control group only. Fitted responses were computed for all contrasts at the peak voxels in the ROIs as derived from the localizer experiment. Consequently, we calculated Spearman correlations between the fitted responses in every ROI in order to investigate connectivity between the ROIs in healthy controls.

MVPA: In order to investigate whether body-responsive brain regions contain information for emotion categorization, MVPA analyses were performed in MNI space on unsmoothed data. We used 'The decoding toolbox (TDT) ' (Hebart, Gorgen, & Haynes, 2014) to assess performance in classification between emotional and neutral stimuli as well as between the four emotional conditions based on predefined t-contrasts and beta values respectively in the ROIs defined by the localizer.

To this end, we first calculated a contrast for the average of all four emotional conditions versus baseline and the neutral condition versus baseline per run per subject. The resulting t-maps were loaded into the toolbox, which then subsequently used all runs to test and to train on a leave-1-run-out basis. To assess classification between the four emotions, the parameter estimates of each emotional condition per run were loaded into the toolbox. The toolbox used these parameter estimates of all four runs to test and train in a leave-1-run out basis.

Subsequently we conducted a linear mixed models analysis with random intercept and fixed effects for group, ROI and group*ROI on the accuracy-minus-chance values. All post-hoc tests were performed with a Bonferroni correction.

Parametric testing of all non-voxelwise analyses always depended on the results of a normality check by means of Shapiro-Wilk test and visual inspection of the QQ-plot. These were either performed on the variables or on the unstandardized residuals of linear mixed models analyses. If homogeneity of variances could not be assumed based on Levene's test, a Welch test was performed and 95% confidence intervals (CI) are reported as an estimate of effect size.

Results

Neuropsychological testing

Results are presented in Table 1. There was a significant effect of group for MMSE ($F(2, 14.155)= 7.374$, $p = .006$), Boston Naming Test ($F(2, 13.338)=9.003$, $p =.003$), the Auditory verbal learning test (% Recall: $F(2, 14.191)=5.860$, $p=0.013$) and the Animal Verbal Fluency ($F(2, 28)=3.642$, $p=0.039$, $\eta^2= .206$). Post-hoc tests revealed that compared to controls, left ATL patients were moderately impaired on MMSE ($t(2)= 3.583$, $p= 0.01$,95%CI [0.4051, 2.7616] , Boston Naming Test ($t(2)=3.910$, $p= .008$, 95%CI [2.236, 13.152], Auditory Verbal Learning Test (% Recall: $t(2)=2.990$, $p= 0.032$, 95%CI [0.0324, 0.6746] and the Animal Verbal Fluency ($t(2)= 2.663$, $p =0.038$, 95%CI [0.2548, 11.3563]. These findings are in accordance with the function of the resected area (i.e. semantic memory) and were used as regressors of no interest in further analysis.

There was no significant group effect of BDI score ($F(2, 28)= .927$, $p=.408$), but a significant group effect on the PANAS for negative affect ($F(2.28) = 5.503$, $p= 0.10$, $\eta^2=.282$). Post-hoc tests revealed that patients with left ATL scored significantly higher on the PANAS for negative affect than patients with right ATL($t(2)=2.647$, $p= .04$, 95%CI[0.3412, 17.6810] and controls ($t(2)= 3.068$, $p=0.014$, 95%CI [1.6539, 17.8128]. This score was also used as a regressor of no interest in further analysis. Results are presented in Table 1.

Body emotion recognition experiment

Linear mixed model analysis on the emotion detection thresholds was performed with MMSE, AVLT, BNT,AVF and PANAS negative affect score as variables of no interest. This did not reveal a significant group effect in the emotion recognition task ($F(2, 96)=.195$, $p=.823$), nor any group* emotion interaction($F(6, 49)=.456$, $p=.837$). There was however a significant effect of emotion ($F(3, 49)= 11.522$, $p< .001$). Post-hoc tests revealed that better performance on 'happy' than on the 3 other emotions [happy vs. angry ($t(40.956)=-4.83$, $p< .001$, 95%CI [-29.753, -7.240]), happy vs. sad ($t(44.018)=-3.60$,$p=.004$, 95%CI[-23.761, -3.454]), happy vs. fear($t(44.451)=-4.29$,$p< .001$, 95%CI [-25.325, -6.060])]. Results are presented in Figure 3.

Imaging results

Due to technical failure one patient with a left sided resection was excluded from further analysis. For the oddball detection task, all subjects obtained a maximum of 6 hits (6 oddballs) per run.

Body-responsive regions:

Based on the localizer data of the entire sample, we defined bilateral EBA and right pSTS (Figure 4, yellow outline). A logical conjunction analysis (requiring significant activations in all groups) revealed that both bilateral EBA and right pSTS were activated in the 3 groups (P_{height} <0.01, uncorrected).

Within group emotion effects:

Control subjects

An emotion effect (i.e. a one-sample t-test on the average of the four emotions vs neutral contrasts) in healthy controls was observed in a large bilateral cluster in lateral occipito-temporal cortex, overlapping EBA and pSTS, in addition to smaller distributed clusters: bilateral inferior frontal gyrus, precuneus, superior parietal lobule, supplementary motor areas, right fusiform, postcentral and superior temporal gyrus, left insula and middle frontal gyrus. At the subcortical level, there was an effect in the amygdala bilaterally. As the cluster in the right fusiform gyrus overlapped with coordinates reported for FBA (Peelen & Downing, 2005), we selected this as an additional region of interest. Within the predefined body responsive regions we found large clusters in right EBA (x=46 y =-64 z =8, #Voxels =316), in left EBA (x=-52 y =-66 z =4, #Voxels=175) and rpSTS (x=62 y =-38 z =16, #Voxels =348). See Figure 4 and Table 2.

Amygdalar connectivity with body-responsive regions: We calculated the fitted responses in peak voxels of left and right amygdala and left and right EBA, right pSTS and right FBA. Spearman correlation analyses were performed and revealed a significant result for the mean of the four emotions compared to neutral between the right amygdala and right EBA (ρ=.783, N= 12, p= .0075, 1-tailed, Bonferroni corrected, 95%CI [0.333, 1]). Spearman correlation analysis between right amygdala and left amygdala (ρ=.615, N=12, p=.0825, 1-tailed, Bonferroni corrected) and between right amygdala and right FBA (ρ=.587, N=12, p = .1225, 1-tailed, Bonferroni uncorrected) were not significant. These results confirm previous findings (Peelen et al., 2007) and provide support for the paradigm as a valid tool to investigate modulatory influences between amygdala and body-responsive regions.

Right TLE

The effect of emotion (a one-sample t-test on the average of the four emotions vs neutral contrasts) in the right resection group revealed significant results in the left superior temporal gyrus, inferior frontal gyrus and right middle temporal gyrus. ROI analysis revealed only one small cluster in right EBA (x=56 y =-66 z =4, #Voxels =28), but not in the other two body-selective ROIs. See Figure 4, red outline.

Left TLE

In the left ATL group we found an effect of emotion in the left parahippocampal gyrus. We did not find any significant activation in the body-responsive ROIs. See Figure 4, blue outline.

Between group comparisons:

Controls vs right resection group (Figure 5, Table 3)

Compared to the right resection group, healthy controls showed a stronger emotion effect (i.e. a two-sample t-test on the average of each of the four emotions vs neutral contrasts) in the bilateral precuneus, the right fusiform, cingulate, parahippocampal and middle occipital gyrus, as well as in the right caudate nucleus, amygdala and superior parietal lobule. ROI analyses showed only a small cluster in left EBA (x=-50 y =-72 z =10, #Voxels =5).

The reverse contrast (right resection groups vs. controls) revealed no significant differences in activation.

Controls vs left resection group (Figure 5, Table 3)

Compared to the left resection group, healthy controls showed a stronger emotion effect (i.e. a two-sample t-test on the average of each of the four emotions vs neutral contrasts) in the left superior occipital, postcentral, middle frontal and superior temporal gyrus, as well as in the left precuneus and cerebellum. In the right hemisphere, there were significant differences in middle, medial and inferior frontal, precentral, middle temporal and fusiform gyrus and the superior parietal lobule. We observed one small cluster in left EBA (x=-50 y =-72 z =10, SVC, #Voxels =16), one small cluster in right EBA (x=48 y =-66 z =8, #Voxels =11) and one cluster in right pSTS (x=56 y =-42 z =4, #Voxels =20).

The reverse contrast (left resection group vs. controls) revealed no significant differences in activation.

Left vs right resection group (Figure 5, violet outline)

Compared to the right resection group, left ATL resection patients show a stronger emotion effect (i.e. a two-sample t-test comparing each of the four emotions vs neutral contrasts) in the left calcarine sulcus extending in the left occipital lobe and the precuneus. There were no significant differences in activation in the body-responsive ROIs.

The reversed contrast (right vs. left resection group) revealed no significant differences.

MVPA: within group results (Figure 6):

Control subjects

In the control group all three ROIs reliably categorized between emotional and neutral stimuli as was determined by permutation testing with 1000 permutations (right EBA: $t(11)= 5.897$, $p<.001$, $d= 1.702$; left EBA: $t(11)= 3.939$, $p = .002$, $d= 1.137$; right pSTS: $t(11)= 7.966$, $p< .001$, $d= 2.3$). For discriminating between the four emotions separately, the three ROIs performed significantly above chance level as well (right EBA: $t(11)= 4.451$, $p=.001$, $d= 1.285$; left EBA: $t(11)= 5.946$, $p< .001$, $d= 1.716$; right pSTS: $t(11)= 3.362$, $p = .006$, $d=0.970$).

Right TLE

In the right resection group all three ROIs reliably categorize between emotional and neutral stimuli as was determined by permutation testing with 1000 permutations (right EBA: t(9)= 5.514, p=<.0001, d= 1.744; left EBA: t(9)= 7.856, p =< .001, d= 2.484; right pSTS: t(9)=3.354, p = .008, d= 1.06). For discriminating between the four emotions separately, bilateral EBA ROIs performed significantly above chance level as well (right EBA: t(9)= 3.475, p=.007, d= 1.099; left EBA: t(9)= 3.926, p = .003, d= 1.241). However, right posterior STS does not reliably discriminate between the four emotions in this patient group (t(9)= 2.023, p = .222, uncorrected).

Left TLE

In the left resection group both right EBA and rpSTS reliably categorize emotional and neutral stimuli as was determined by permutation testing with 1000 permutations (right EBA: t(8)=3.578, p=.007, d= 1;192; right pSTS: t(8)=3.5, p = .008, d= 1.167). In left EBA categorization performance between emotional and neutral stimuli did not surpass chance level (t(8)= 2.412, p = .126, uncorrected). For discriminating between the four emotions, the left EBA performed significantly above chance level (t(8)= 4, p=.004, d= 1.333), unlike the other areas (right EBA: t(8)= 2.997, p = .051, uncorrected; right pSTS: t(8)= 2.667, p = .087, uncorrected).

MVPA: group differences (Figure 6)

Linear mixed model analysis on the accuracy minus chance values for the emotions vs. neutral categorization showed no effect of group (F(2.30)=1,811,p=.181) nor ROI (F(2.37)=1.632, p=.209). However the interaction group*ROI was significant (F(4.37)=4,845, p=.003). Post-hoc tests revealed a significant difference between the healthy controls and the right resection group in the right pSTS only (t(29.56)=3.112, p=.012, 95%CI [3.456, 34.044]).

For the categorization of four emotions linear mixed model analysis on the accuracy minus chance values showed no significant effect of group (F(2.78)=.549,p=.580) nor a significant interaction between group and ROI (F(4.63)=.155, p=.960). The effect of ROI was significant (F(2.63)=6.298,p=.003). Post-hoc tests revealed a significant difference between left EBA and right pSTS (t(53.143)=3.23, p=.005, 95%CI [2.176, 15.185), with better performance in right STS.

Discussion

To investigate body emotion processing, we used artificial stimuli expressing emotions conveyed through motion (Kruger, Sokolov, Enck, Krageloh-Mann, & Pavlova, 2013; Sokolov, Kruger, Enck, Krageloh-Mann, & Pavlova, 2011).

The first aim was to investigate whether the ATL and the amygdala in particular play a crucial role in the perception of emotional body expressions. The results reveal normal body emotion categorization performance in both patient groups. Hence, our data further challenge a key role for the amygdala in accurate interpretation of emotional body language. This is in line with neuropsychological evidence of preserved body expression recognition in patients with bilateral amygdalar atrophy due to Urbach-Wiethe disease (Atkinson et al., 2007; de Gelder et al., 2014). On the

contrary, another syndrome characterized by amygdalar atrophy, i.e. bvFTD, is associated with deficits in recognizing body expressions (Jastorff et al., 2016; Van den Stock, De Winter, et al., 2015). However, those studies also revealed that the deficits were not related to structural integrity of the amygdala, but rather to the volume of a region in the left temporal pole (not overlapping the amygdala) and the left inferior frontal gyrus (Jastorff et al., 2016). Interestingly, we observed in the same sample of bvFTD a facial emotion recognition deficit that was associated with structural integrity of the amygdala (De Winter et al., 2016). These results suggest a dissociation in the structural neuroanatomy underlying body and face emotion recognition deficits. This notion is supported by the finding that the sensitivity of the amygdala is higher to facial than to body emotions (Kret, Pichon, Grezes, & de Gelder, 2011) and suggests that while the amygdala is necessary to recognize facial expressions, it is not necessary to recognize body expressions. This is in line with a functional hypothesis of the amygdala as a personal relevance detector and modulator of brain processes underlying adaptive behaviour (Janak & Tye, 2015; Sander, Grafman, & Zalla, 2003). The amygdala is functionally connected to primary visual areas but also to motor structures and frontal cortices (Bickart et al., 2014; Bickart, Hollenbeck, Barrett, & Dickerson, 2012; Grezes, Valabregue, Gholipour, & Chevallier, 2014; Toschi, Duggento, & Passamonti, 2017). The disproportional effect of amygdalar lesions on processing facial compared to bodily expressions may thus relate to social stimulus proximity detection and regulating personal space (Kennedy, Glascher, Tyszka, & Adolphs, 2009). In particular, detailed perception of a facial expression typically implies closer proximity and hence higher personal relevance compared to perceiving a whole body. Similarly, our findings are in line with studies relating the amygdala to driving eye gaze and attention to the eyes of others (Adolphs et al., 2005; Gamer & Buchel, 2009).

The second aim of the study was to reveal whether amygdala lesions influence neural processes in distant areas, particularly body-sensitive regions.

Both patient groups showed decreased activation in left EBA and right fusiform gyrus. Additionally, the left resection group showed no emotional enhancement in right EBA and pSTS. The right resection group however shows an emotional response in the right EBA and STS. These findings support a central role for the amygdala in emotional enhancement of ventral (FBA) but not posterior lateral temporal cortex when perceiving body expressions. This is in line with facial expression recognition findings in patients with amygdalar lesions (De Winter et al., 2016; Vuilleumier et al., 2004) and structural connectivity studies in normal subjects reporting white matter tracts between amygdala and ventral posterior areas, but not STS (Gschwind, Pourtois, Schwartz, Van De Ville, & Vuilleumier, 2012; Smith et al., 2009).

On the other hand, the MVPA results in the right pSTS reveal a reduction in the right ATL patients in distinguishing emotional from neutral stimuli. This suggests that the ATL and amygdala directly or indirectly influence the function of the pSTS when processing body expressions. Reduced activation in pSTS in response to facial expressions has been observed in patients with ATL lesions (Ahs et al., 2014; Vuilleumier et al., 2004). While there is evidence that amygdala and pSTS are

functionally connected (Pitcher, Japee, Rauth, & Ungerleider, 2017; Sato, Kochiyama, Uono, Yoshikawa, & Toichi, 2017), body emotion processing in posterior lateral temporal cortices like EBA and right pSTS may rely primarily on non-amygdalar input, like cortical visual areas and motor areas (Erickson, Rauschecker, & Turkeltaub, 2017; Ewbank et al., 2011; Lahnakoski et al., 2012; Zimmermann, Mars, de Lange, Toni, & Verhagen, 2017). One could speculate that altered input from, e.g. FBA, due to absent amygdalar modulation, could explain the reduced emotion classification in the right pSTS.

The effects at distance we observe are not confined to the ipsilateral hemisphere. This is surprising since amygdala modulations have up until now been described predominantly ipsilateral to the lesion side (Vuilleumier et al., 2004). We speculate that these contralateral altered responses rely on altered input from the homotopic visual areas ipsilateral to the lesion side, which in turn receives diminished input from the lesioned amygdala. There is indeed evidence for corpus callosum deficits in TLE, which results in diminished interhemispheric transfer (Schneider et al., 2014).

Interestingly, we also observed strong distant effects of ATL resections beyond body responsive visual areas, i.e. in frontal, parietal, occipital and cingulate regions, which showed emotional enhancement in the control group. Widespread activation during body motion perception (Pavlova et al., 2017) and emotional body expression perception has consistently been reported (de Gelder, 2006; de Gelder et al., 2004; Grezes, Pichon, & de Gelder, 2007; Kret et al., 2011; Pichon et al., 2008; van de Riet, Grezes, & de Gelder, 2009). The present results suggest that these activations may also be primarily amygdala-dependent.

The notion that specific emotions can be mapped to specific brain circuits has been increasingly challenged by psychological constructionist theories. These models hypothesize that processing of emotions relies on distributed brain networks and processing of specific emotions relies on co-activation patterns within and between those networks (Barrett, 2013; Huang et al., 2018; Jastorff et al., 2015; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). The amygdala is considered a ‘core affect’ region in constructionist accounts, adding to the representation of emotional events in concert with other areas and networks. Indeed, the amygdala is strongly connected to other regions of the social brain. It is considered to be involved in multiple processes with a common ground of detecting arousal and salience in multiple types of stimuli (i.e. emotional, novel, rewarding stimuli) (Adolphs, 2010; Sander et al., 2003). As a ‘relevance detector’, it seems to modulate several of these social brain regions in order to facilitate adaptive behaviour (Bickart et al., 2014). There is indeed evidence that the amygdala is both structurally and functionally linked to (pre)motor areas such as the supplementary motor area and pre- and postcentral gyri (Grezes et al., 2014; Pichon et al., 2008; Toschi et al., 2017).

Several limitations of the present study need to be addressed. The normal performance of body emotion recognition in the clinical groups may be related to insufficient sensitivity of our behavioral task, although the sensitivity of psychometric function modelling may surpass conventional accuracy measures (Biotti & Cook, Cortex 2017). Second, TLE is associated with ATL sclerosis and deficits in emotion

recognition (Monti & Meletti, 2015), also before surgery. As we did not include pre-surgical data, nor patients with active temporal lobe epilepsy, we cannot conclude that the group differences are due to the resection of the anterior temporal lobe.

A related issue to consider is the neural plasticity that may have taken place after the resection but also before, possibly compensating for the amygdala and ATL. While functional compensation may occur in contralateral amygdala, we did not find any evidence for increased responses to emotional stimuli in patients compared to healthy controls. Furthermore in neither patient group did we observe an emotion effect in the intact amygdala, suggesting no compensatory activation from contralateral amygdala.

There is evidence that emotion recognition in TLE depends on intellectual capacity (Monti & Meletti, 2015) and we excluded patients with total IQ <80. While this exclusion criterion benefits the validity of comparisons with the control group, it may also reduce the sensitivity to reveal IQ-dependent behavioural effects.

Our sample size is rather small and may negatively influence statistical power. To compensate for this, we applied a conservative statistical threshold (FWE-correction) to maximize the reliability of the significance of the group differences. It should however be noted that this stringent control for Type I errors increases the probability of Type II errors, which we considered less relevant for the present study purpose.

Finally, anti-epileptic medication in a part of the patient group, while absent in the control group, might also have influenced the results.

In summary, the findings reveal that unilateral ATL resection does not reduce recognition of body emotions despite the indications that it plays a central role in enhancing activation in the right fusiform gyrus during body emotion perception. Furthermore, the enhanced activity in a widely distributed set of regions during body emotion perception supports the role of the amygdala as a hub in the emotional brain.

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Legends

Figure 1. Lesion overlap in patients with unilateral resection of anterior temporal lobe.

Figure 2. (A) Static frames of prototypical and (B) morphed stimulus examples. Panel (B) displays different morph levels between neutral and emotional (sad) gaits as used during the behavioral experiment. (C) Schematic overview of imaging procedure: 4 functional emotion scans were interspersed by a high resolution anatomical scan and followed by a functional localizer scan. Bottom: event-related experimental fMRI design. Trials consisted of 1.5-5 sec clips with an inter-stimulus interval between 2.3 and 5s. The oddball stimulus was a neutral backwards-walking avatar. ISI = inter-stimulus interval.

Figure 3. Behavioral results. Detection thresholds are displayed per group for the emotion task (A) and Control task (B). Detection thresholds reflect an estimate of the emotional intensity required to obtain a 50% correct performance level. The average detection threshold is calculated over emotions to represent a general emotion detection threshold.

Figure 4. Emotion effect (i.e. a one-sample t-test on the average of each of the four emotions vs neutral contrasts) as a function of group. The statistical map displays the emotion effect in the control group while the red and blue outlines delineate the significant clusters in the right and left anterior temporal lobe resection groups respectively. The yellow outlines delineate body-sensitive regions defined by means of the localizer in the total sample.

Figure 5. Group comparisons of the emotion effect (i.e. two sample t-tests on the average of each of the four emotions vs neutral contrasts). Statistical maps displaying stronger emotion effects in the control group on the one hand compared to the right (yellow to red color-coding) and left (blue to green color-coding) anterior temporal lobe resection group on the other hand. The pink outlines display the areas showing stronger emotion effects in the left compared to the right anterior temporal lobe resection group. The yellow outlines delineate body-sensitive regions defined by means of the localizer in the total sample (Top). The bar charts represent the percent signal change (PSC) for the contrast emotions vs. baseline and neutral vs. baseline as a function of group and body-sensitive ROI (bottom). LH= Left hemisphere; RH= right hemisphere; SFS= Superior Frontal Sulcus; IFS= Inferior Frontal Sulcus; CS= Central Sulcus; STS= Superior Temporal Sulcus; ITS= Inferior Temporal Sulcus; IPS= Intraparietal Sulcus; EBA= Extrastriate Body area; FBA= Fusiform Body Area.

Figure 6. MVPA results showing classification performance levels for discriminating between (A) emotional and neutral stimuli as well as (B) between the four emotions in all 3 groups in right EBA, left EBA and right pSTS. Only in right pSTS there is a

significant difference in classification performance for emotion vs. neutral between controls and right ATL patients (purple delineation). Classification between emotional and neutral stimuli was not significant in left EBA (p= .042) in the left resection group, nor was classification of the 4 emotions in the left resection group in both right EBA (p = .017) and right pSTS (p =.029) and in the right resection group in rpSTS (p=.074) (red delineation).

Table 1. SAH = Selective amygdalohippocampectomy; ATL = Anterior Temporal Lobectomy; BDI = Beck Depression Inventory; PANAS = Positive and Negative Affect Scale; MMSE = Minimental State Examination; RAVLT = Rey's Auditory Verbal Learning Test; BNT = Boston Naming Test; AVF = Animal Verbal Fluency; TMT = Trail Making Test; * Left ATL patients had significantly higher scores on PANAS for negative affect than both controls and right ATL patients. $ Left ATL patient performed significantly worse than controls on MMSE, RAVLT (% Recall) and Boston Naming Test.

Table 2. Whole Brain fMRI results of emotion effect (i.e. a t-test comparing each of the four emotions vs neutral contrasts against zero) in healthy controls. Coordinates are mm in MNI space.

Table 3. Whole brain fMRI group differences for the emotion effect (i.e. two-sample t-tests on the average of each of the four emotion vs neutral contrasts).

Movie 1. Stimulus example of a prototypical anger expression.

Movie 2. Stimulus example of a prototypical neutral expression.

Movie 3. Stimulus example of a scrambled stimulus.

922 **Tables**
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924 **Table 1. Demographic and neuropsychological test results**

		Controls		Right ATL		Left ATL	
		Mean	(STD)	Mean	(STD)	Mean	(STD)
Age		54.3	8.0	52.3	10.6	52.3	8.3
Sex(M/F)		5/7		8/2		4/6	
Resection type (SAH/ATL)		n/a		2/7		0/10	
Seizure onset		n/a		13	9.8	11.9	11.5
Time since surgery		n/a		9.8	4.7	11.2	3.2
BDI		4.9	4.8	4.6	6.1	8.0	7.7
Panas	Negative Affect	16.2	5.2	16.9	7.6	25.9*	9.3
	Positive Affect	37.3	7.8	34.7	8.0	32.4	4.5
MMSE		29.6	0.8	27.7	2.8	28.0$	1.1
RAVLT	A1-A5	50.1	9.9	45.0	13.1	36.9	11.9
	% recall	88.8	11.7	71.6	22.9	53.5$	35.8
	Recognition	14.4	1.2	13.8	2.8	13.4	2.2
BNT		57.9	1.9	54.3	4.8	50.2$	5.7
AVF		25.9	5.6	22.6	5.3	20.1	3.1
TMT	A (secs)	27.6	8.0	30.8	15.1	29.5	8.0
	B(secs)	55.3	18.0	65.9	53.3	55.6	15.9

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Table 2. Whole brain fMRI results for the emotion effect (i.e. a one-sample t-test on the average of each of the four emotion contrasts) in healthy controls

		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
LOC	L	-54	-64	4	10.16	1636	>0.001
		-52	-74	8	8.64		
		-62	-50	8	8.39		
	R	46	-64	8	9.17	1831	>0.001
		50	-54	0	7.72		
		62	-38	16	7.52		
IFG	R	54	30	8	8.91	453	>0.001
		56	32	22	6.46		
FG	R	46	-48	-18	7.93	349	>0.001
SPL	R	22	-50	66	6.98	220	>0.001
		34	-34	56	5.87		
		32	-46	60	5.87		
Precun	R	18	-76	54	6.62	75	>0.001
IFG	R	44	12	30	6.53	156	>0.001
MFG	L	-48	32	36	6.25	49	0.001
IFG	L	-38	32	2	6.17	312	>0.001
SOG	L	-36	-86	26	5.92	51	0.001
Amygdala	R	26	-2	-12	5.91	28	0.004
OFC	R	32	38	-10	5.88	79	>0.001
		24	36	-10	5.19		
Amygdala	L	-20	-6	-16	5.75	54	0.001

SMA	R	10	-4	68	5.74	36	0.003
Insula	L	-44	-30	18	5.72	33	0.003
STG	R	68	-16	8	5.71	22	0.006
SMA	L	-14	-6	70	5.61	40	0.002
PoCG	R	64	-16	46	5.36	23	0.006
SPL	L	-30	-50	66	5.23	20	0.007

LOC= lateral occipitotemporal cortex; IFG= inferior frontal gyrus; FG=fusiform gyrus; SPL= superior parietal lobule; Precun= precuneus; MFG= middle frontal gyrus; SOG= superior occipital gyrus; OFC= orbitofrontal cortex; SMA= supplementary motor area; STG= superior temporal gyrus; PoCG= postcentral gyrus

Table 3. Whole brain fMRI group differences for the emotion effect (i.e. two-sample t-tests on the average of each of the four emotion vs neutral contrasts).

Controls vs. Right ATL Resection Patients							
		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
Precun	L	-2	-82	46	6.32	205	>0.001
	R	10	-88	40	5.15		
Cingulum	R	18	0	36	6.17	85	>0.001
LOC	L	-54	-64	2	5.95	38	0.003
Nc	R	30	-30	2	5.89	44	0.002
SPL	R	22	-52	68	5.62	20	0.007
Precun	R	18	-78	54	5.61	25	0.005
MOG	R	34	-74	20	5.58	35	0.003
FG	R	48	-50	-18	5.57	126	>0.001
		50	-50	-26	5.48		
PHG/	R	26	4	-22	5.42	44	0.002
Amygdala		26	-2	-12	5.27		
Controls vs. Left Resection Patients							
		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
Precun	R	18	-78	54	7.85	200	>0.001
SOG	L	-36	-86	26	6.88	454	>0.001
		-48	-72	12	6.26		
		-54	-60	6	6.23		
MFG	L	-48	32	36	6.67	67	0.001

PoCG	L	-30	-34	70	6.2	144	>0.001
		-42	-32	64	5.92		
PrCG	R	26	0	32	6.2	187	>0.001
		26	6	26	5.79		
Precun	L	-16	-80	56	6.1	38	0.003
MeFG	R	10	-8	52	5.94	35	0.003
MFG	R	54	38	26	5.92	81	>0.001
SPL	R	20	-50	68	5.84	24	0.006
IFG	R	56	30	10	5.67	30	0.004
Precun	L	-2	-84	50	5.63	30	0.004
Cereb, pyramis	L	-12	-74	-38	5.6	32	0.004
STG	L	-62	-48	8	5.49	20	0.007
FG	R	44	-48	-16	5.49	36	0.003
MTG	R	60	-42	0	5.39	50	0.001
LOC	R	40	-70	12	5.33	40	0.002
		48	-66	8	4.85		

933 Precun= precuneus; LOC= lateral occipitotemporal cortex; Nc= caudate nucleus;

934 SPL= superior parietal lobule; MOG= middle occipital gyrus; FG= fusiform gyrus;

935 PHC= parahippocampal gyrus.

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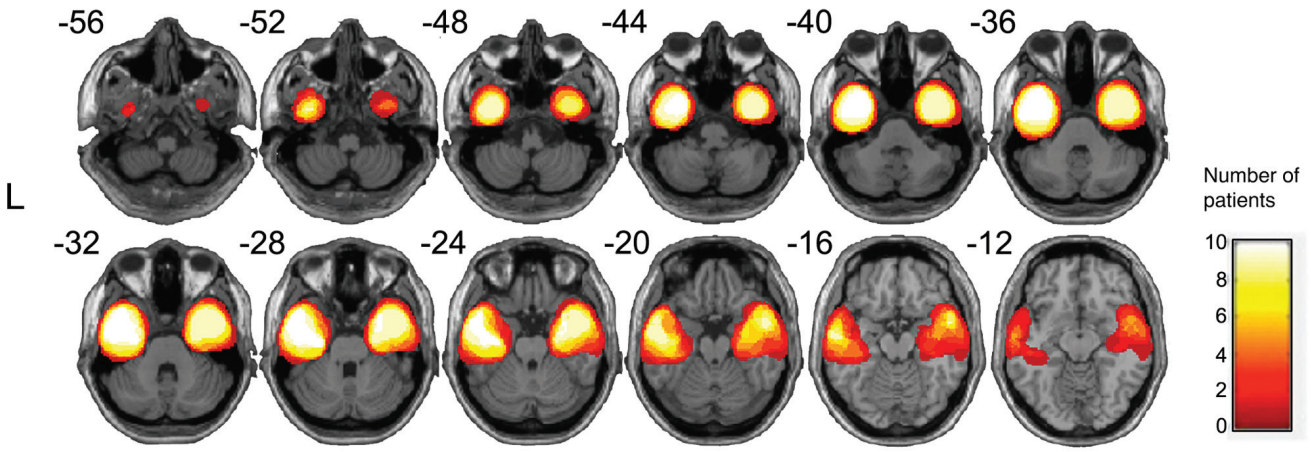

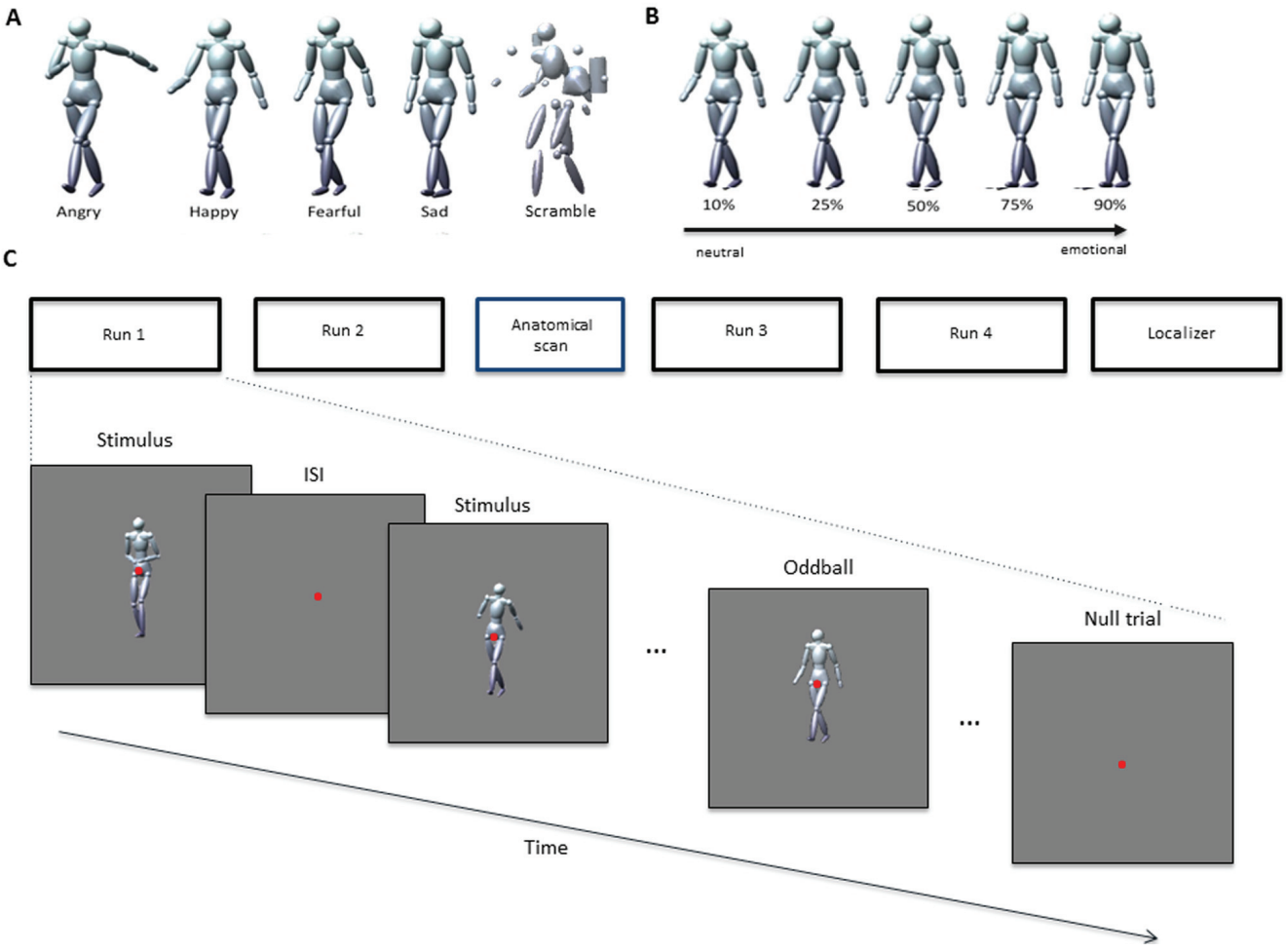

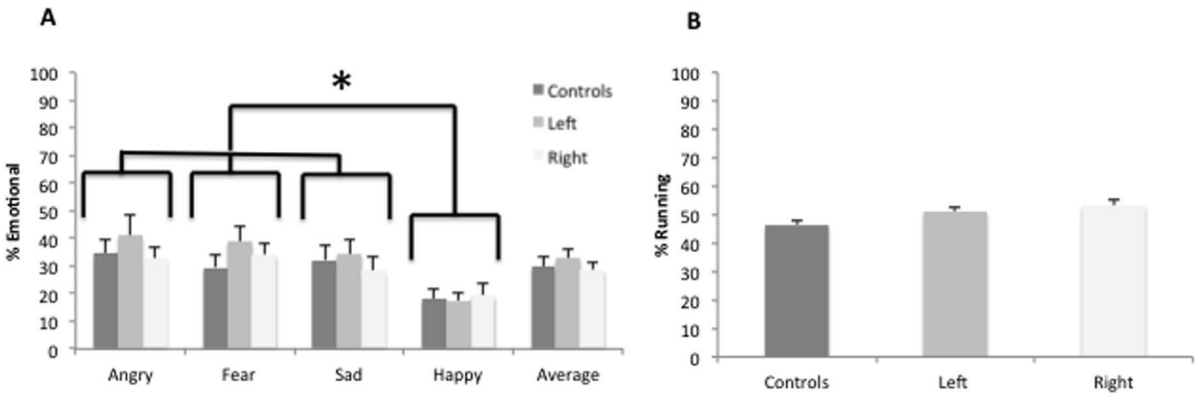

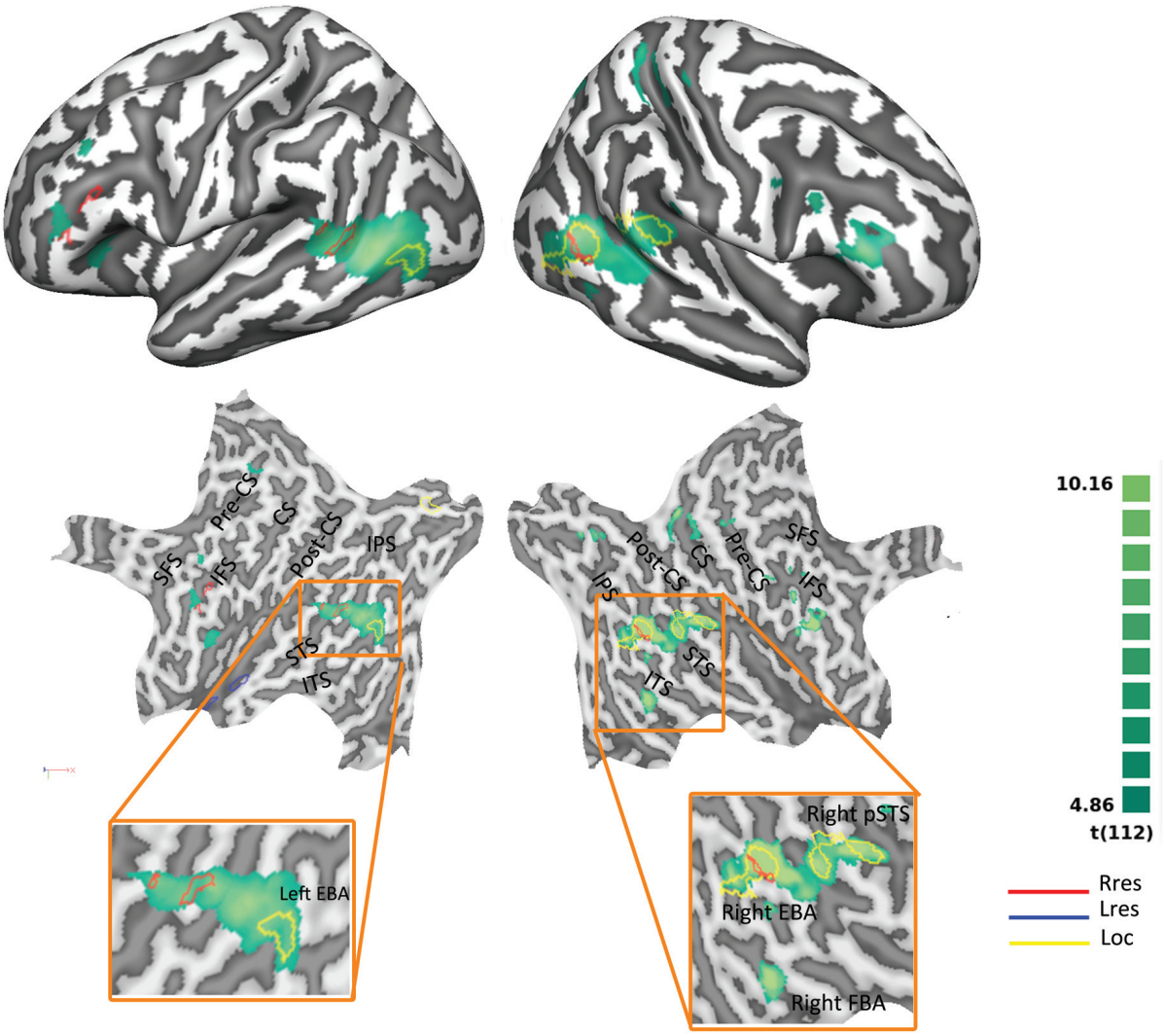

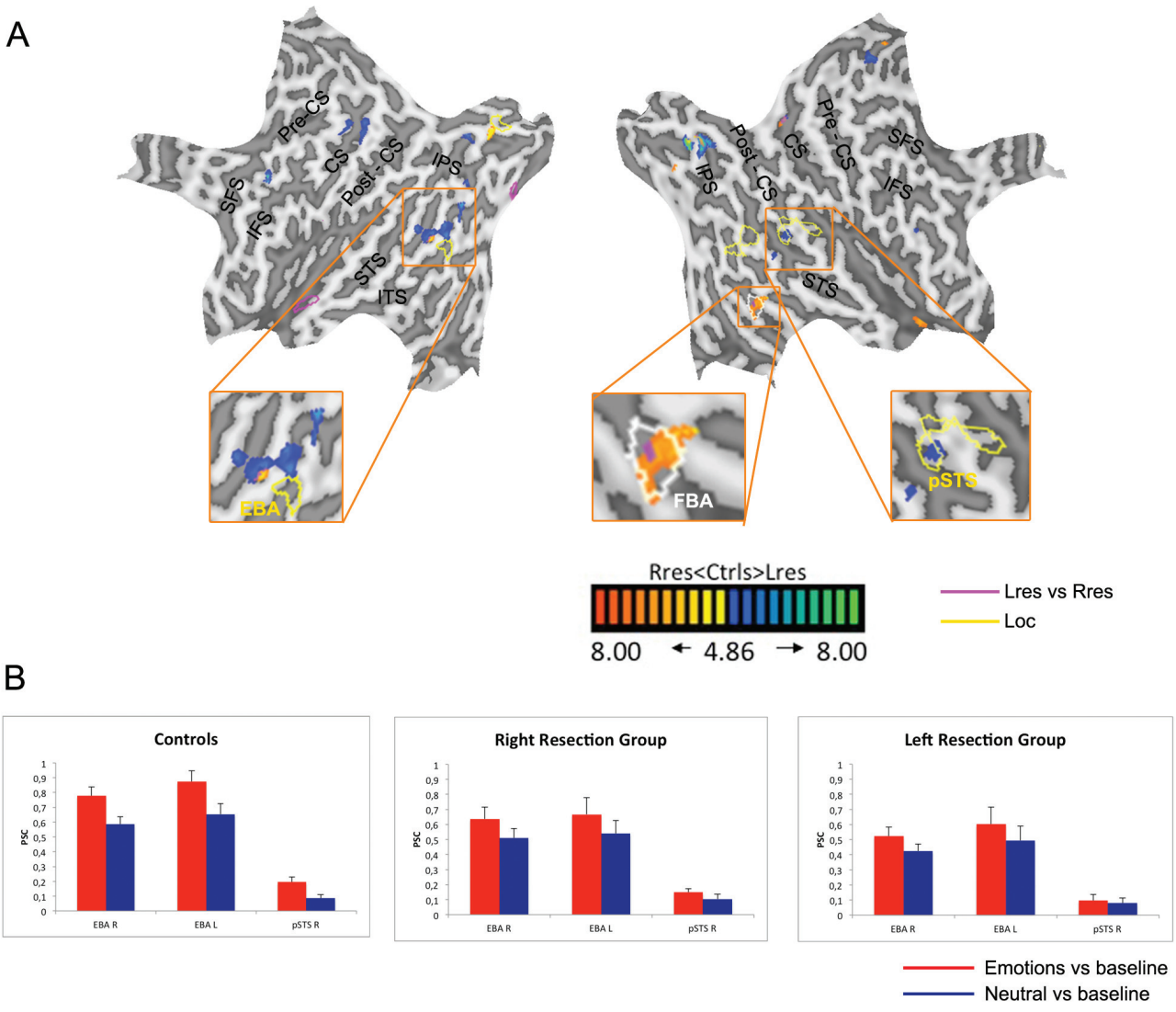

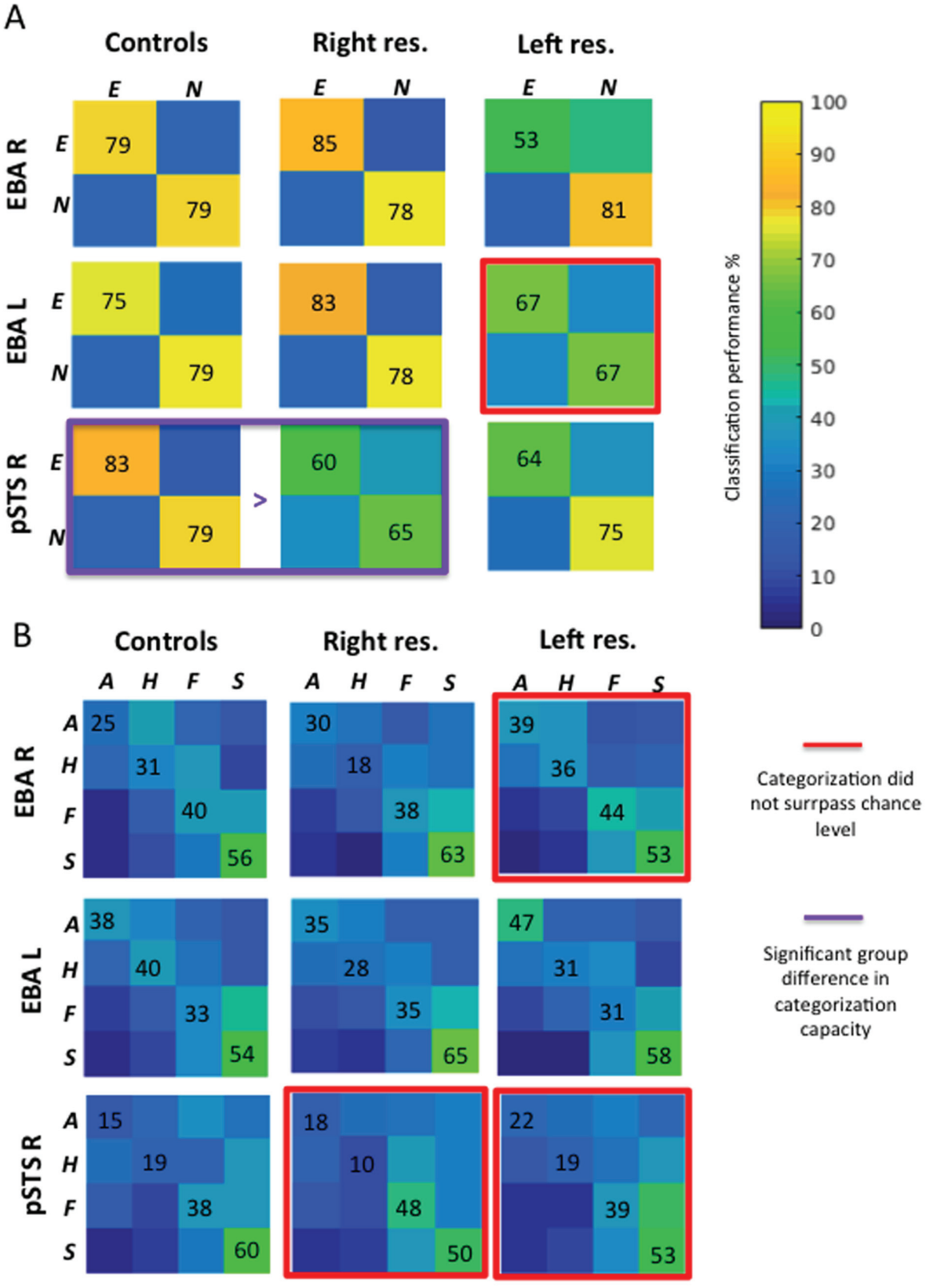

Table I. Demographic and neuropsychological test results

		Controls		Right ATL		Left ATL	
		Mean	(STD)	Mean	(STD)	Mean	(STD)
Age		54.3	8.0	52.3	10.6	52.3	8.3
Sex(M/F)		5/7		8/2		4/6	
Resection type (SAH/ATL)		n/a		2/7		0/10	
Seizure onset		n/a		13	9.8	11.9	11.5
Time since surgery		n/a		9.8	4.7	11.2	3.2
BDI		4.9	4.8	4.6	6.1	8.0	7.7
Panas	Negative Affect	16.2	5.2	16.9	7.6	25.9*	9.3
	Positive Affect	37.3	7.8	34.7	8.0	32.4	4.5
MMSE		29.6	0.8	27.7	2.8	28.0$	1.1
RAVLT	A1-A5	50.1	9.9	45.0	13.1	36.9	11.9
	% recall	88.8	11.7	71.6	22.9	53.5$	35.8
	Recognition	14.4	1.2	13.8	2.8	13.4	2.2
BNT		57.9	1.9	54.3	4.8	50.2$	5.7
AVF		25.9	5.6	22.6	5.3	20.1	3.1
TMT	A (secs)	27.6	8.0	30.8	15.1	29.5	8.0
	B(secs)	55.3	18.0	65.9	53.3	55.6	15.9

Table II. Whole brain fMRI results for the emotion effect (i.e. a one-sample t-test on the average of each of the four emotion contrasts) in healthy controls

		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
LOC	L	-54	-64	4	10.16	1636	>0.001
		-52	-74	8	8.64		
		-62	-50	8	8.39		
	R	46	-64	8	9.17	1831	>0.001
		50	-54	0	7.72		
		62	-38	16	7.52		
IFG	R	54	30	8	8.91	453	>0.001
		56	32	22	6.46		
FG	R	46	-48	-18	7.93	349	>0.001
SPL	R	22	-50	66	6.98	220	>0.001
		34	-34	56	5.87		
		32	-46	60	5.87		
Precun	R	18	-76	54	6.62	75	>0.001
IFG	R	44	12	30	6.53	156	>0.001
MFG	L	-48	32	36	6.25	49	0.001
IFG	L	-38	32	2	6.17	312	>0.001
SOG	L	-36	-86	26	5.92	51	0.001
Amygdala	R	26	-2	-12	5.91	28	0.004
OFC	R	32	38	-10	5.88	79	>0.001
		24	36	-10	5.19		
Amygdala	L	-20	-6	-16	5.75	54	0.001
SMA	R	10	-4	68	5.74	36	0.003
Insula	L	-44	-30	18	5.72	33	0.003
STG	R	68	-16	8	5.71	22	0.006
SMA	L	-14	-6	70	5.61	40	0.002
PoCG	R	64	-16	46	5.36	23	0.006
SPL	L	-30	-50	66	5.23	20	0.007

LOC= lateral occipitotemporal cortex; IFG= inferior frontal gyrus; FG=fusiform gyrus; SPL= superior parietal lobule; Precun= precuneus; MFG= middle frontal gyrus; SOG= superior occipital gyrus; OFC= orbitofrontal cortex; SMA= supplementary motor area; STG= superior temporal gyrus; PoCG= postcentral gyrus

Table III. Whole brain fMRI group differences for the emotion effect (i.e. two-sample t-tests on the average of each of the four emotion vs neutral contrasts).

Controls vs. Right ATL Resection Patients

		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
Precun	L	-2	-82	46	6.32	205	>0.001
	R	10	-88	40	5.15		
Cingulum	R	18	0	36	6.17	85	>0.001
LOC	L	-54	-64	2	5.95	38	0.003
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MOG	R	34	-74	20	5.58	35	0.003
FG	R	48	-50	-18	5.57	126	>0.001
		50	-50	-26	5.48		
PHG/ Amygdala	R	26	4	-22	5.42	44	0.002
		26	-2	-12	5.27		

Controls vs. Left Resection Patients

		Coordinates					
Region	Hem.	X	Y	Z	t	#voxels	p-value
Precun	R	18	-78	54	7.85	200	>0.001
SOG	L	-36	-86	26	6.88	454	>0.001
		-48	-72	12	6.26		
		-54	-60	6	6.23		
MFG	L	-48	32	36	6.67	67	0.001
PoCG	L	-30	-34	70	6.2	144	>0.001
		-42	-32	64	5.92		
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MTG	R	60	-42	0	5.39	50	0.001
LOC	R	40	-70	12	5.33	40	0.002
		48	-66	8	4.85		

Precun= precuneus; LOC= lateral occipitotemporal cortex; Nc= caudate nucleus; SPL= superior parietal lobule; MOG= middle occipital gyrus; FG= fusiform gyrus; PHC= parahippocampal gyrus.