

Social Neuroscience

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/psns20>

The neural substrates of social emotion perception and regulation are modulated by adult attachment style

Pascal Vrtička ^{a b d}, Guido Bondolfi ^c, David Sander ^{a d} & Patrik Vuilleumier ^{a b}

^a Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

^b Laboratory for Neurology and Imaging of Cognition, Department of Neurology and Department of Neurosciences, University Hospital and Medical School, University of Geneva, Geneva, Switzerland

^c Department of Psychiatry, Geneva University Hospital, Geneva, Switzerland

^d Laboratory for the Study of Emotion Elicitation and Expression (E3 Lab), Department of Psychology, FPSE, University of Geneva, Geneva, Switzerland

Accepted author version posted online: 12 Dec 2011. Version of record first published: 05 Jan 2012.

To cite this article: Pascal Vrtička, Guido Bondolfi, David Sander & Patrik Vuilleumier (2012): The neural substrates of social emotion perception and regulation are modulated by adult attachment style, Social Neuroscience, 7:5, 473-493

To link to this article: <http://dx.doi.org/10.1080/17470919.2011.647410>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

The neural substrates of social emotion perception and regulation are modulated by adult attachment style

Pascal Vrtička^{1,2,4}, Guido Bondolfi³, David Sander^{1,4}, and Patrik Vuilleumier^{1,2}

¹Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

²Laboratory for Neurology and Imaging of Cognition, Department of Neurology and Department of Neurosciences, University Hospital and Medical School, University of Geneva, Geneva, Switzerland

³Department of Psychiatry, Geneva University Hospital, Geneva, Switzerland

⁴Laboratory for the Study of Emotion Elicitation and Expression (E3 Lab), Department of Psychology, FPSE, University of Geneva, Geneva, Switzerland

Adult attachment style (AAS) refers to individual differences in the way people experience and regulate their social relationships and corresponding emotions. Based on developmental and psychological research, it has been hypothesized that avoidant attachment style (AV) entails deactivating strategies in social contexts, whereas anxious attachment style (AX) involves hyper vigilance and up-regulation mechanisms. However, the neural substrates of differences in social emotion regulation associated with AAS have not been systematically investigated. Here we used fMRI in 19 healthy adults to investigate the effect of AAS on the processing of pleasant or unpleasant social and nonsocial scenes. Participants were asked either to naturally attend (NAT), cognitively reappraise (REAP), or behaviorally suppress (ESUP) their emotional responses. Avoidantly attached participants showed increased prefrontal and anterior cingulate activation to social negative scenes when making spontaneous emotion judgments. They also exhibited persistent increases in dorsolateral prefrontal cortex and left amygdala activity for the same stimuli during reappraisal, as well as additional activation in supplementary motor area and ventral caudate during the suppression of social positive emotions. These results suggest that AV may imply less efficient reappraisal strategies to regulate social negative emotions, and lead to higher conflict or effortful control when suppression cannot be employed. In contrast, anxiously attached participants showed differential increases in the right amygdala and left parahippocampal cortex for social negative and positive stimuli, respectively, but only when making spontaneous emotion judgments. No effect of AX was found during down-regulation conditions. This suggests heightened arousal to negative information without difficulty in down-regulating emotions through cognitive re-evaluation or suppression. Taken together, these findings reveal for the first time the neural underpinnings of attachment-related differences in social emotion regulation.

Keywords: Attachment style; Emotion perception; Emotion regulation; Reappraisal; Suppression; fMRI.

From early childhood to adulthood, the main function of the attachment system is to maintain proximity to significant others in times of stress, or, in other words, to regulate support-seeking behavior (Bowlby, 1969, 1982). Because such regulatory efforts of attachment

processes are tightly linked with general emotion regulation mechanisms, some researchers have argued that “the attachment system is, in itself, an emotion regulation device” (Mikulincer & Shaver, 2007, p. 190). Accordingly, attachment theory has led to the

Correspondence should be addressed to: Pascal Vrtička, Swiss National Center for Affective Sciences, 7, rue des Battoirs, 1205 Geneva, Switzerland. E-mail: pascal.vrticka@unige.ch

This research was supported by the National Center of Competence in Research (NCCR) Affective Sciences financed by the Swiss National Science Foundation (no. 51NF40-104897) and hosted by the University of Geneva, plus grants of the Swiss National Science Foundation to D.S. and P.V.

establishment of an elaborate framework to characterize how individual differences in adult attachment style (AAS) might influence emotion regulation strategies that people use in social situations. In the present study, we sought to clarify the effects of AAS on different emotion regulation mechanisms, such as re-appraisal and suppression (Gross, 2002), and to determine their neurobiological substrates.

AAS was originally defined following pioneer work in infants (Ainsworth, 1978), and is typically classified in four main categories (Bartholomew & Horowitz, 1991): secure, anxious, avoidant, and fearful-avoidant. Whereas individuals with a secure attachment style report positive and trusting interactions with others, those with attachment anxiety (AX) express strong need for closeness, worry about relationships, and fear of rejection. In turn, attachment avoidance (AV) implies greater self-reliance and emotional distance from others, while a disorganized style is characterized by contradictory tendencies such as a desire for proximity but simultaneous withdrawal and avoidance behaviors. More recent accounts of AAS (Brennan, Clark, & Shaver, 1998; Kurdek, 2002; Simpson, Rholes, & Nelligan, 1992) proposed bi-dimensional models of attachment in which these different personality categories are defined by two orthogonal axes of AV and AX (see also Vrtička, Andersson, Grandjean, Sander, & Vuilleumier, 2008). Accordingly, attachment security corresponds to individuals in whom both AV and AX are low, whereas disorganized traits involve a combination of both. Distinct patterns of emotion regulation have been associated with these individual differences (Mikulincer & Shaver, 2007).

In the case of secure attachment, emotion regulation can beneficially influence emotional processing through a cognitive re-evaluation of the meaning and impact of events with potentially threatening significance for interpersonal relationships. This strategy corresponds to "antecedent-focused" regulation or reappraisal (REAP; Gross, 2002), and allows the successful management of negative social emotions that are goal-incongruent and undesirable for securely attached individuals (Mikulincer & Shaver, 2007). In contrast, avoidantly attached people tend to deal with (social negative) emotions by reducing the recruitment of the attachment system, which cannot be achieved by REAP but is thought to involve deactivating strategies (Mikulincer & Shaver, 2007). Thus, emotion regulation strategies applied by these individuals may rely more on behavioral inhibition or expressive suppression (ESUP) of emotions, also termed "response-focused" regulation (Gross, 2002). Strategies associated with AV may therefore

include a reduction or masking of both verbal and nonverbal expressions of emotion (Mikulincer & Shaver, 2007). Conversely, anxiously attached individuals tend to intensify negative social events through *hyper-activating* strategies, which may be conceptualized as up-regulation of emotion (analogous to REAP)—in contrast to a down-regulation of negative affect as seen for secure attachment. This can involve increased vigilance to signs of rejection or support, and easier access to memories and ruminations about actual and potential threats (Mikulincer & Shaver, 2007). In addition, more general difficulties in inhibiting negative thoughts and emotions are also found in attachment-anxious people (Fraley & Shaver, 1997; Vrtička et al., in press).

Despite important theoretical links between attachment processes and emotion regulation, very little is known about their neural correlates. To our knowledge, only one functional magnetic resonance imaging (fMRI) study investigated the effects of individual differences in AAS on brain activity during emotion regulation, using a think/no-think paradigm that probed for the ability to suppress social negative thoughts (Gillath, Bunge, Shaver, Wendelken, & Mikulincer, 2005). Results showed that AX was associated with increased activation during thoughts of negative relationship scenarios in anterior temporal pole (previously implicated in sadness; Levesque et al., 2003), but decreased activation in orbitofrontal cortex (previously implicated in down-regulation of emotions; Kim & Hamann, 2007; Levesque et al., 2003; Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner et al., 2004; Phan et al., 2005). In contrast, AV correlated with less activity in subgenual cingulate and lateral prefrontal cortex during the suppression of negative thoughts—two regions also involved in emotion regulation (see Levesque et al., 2003)—suggesting that the ability to inhibit thoughts was less complete or efficient in avoidantly attached people (Gillath et al., 2005).

Although this pioneer study (Gillath et al., 2005) unveiled important effects of individual differences in AAS on brain activation during emotion regulation, it leaves several questions unresolved. Firstly, as the experimental design only included a suppression strategy in a think/no-think paradigm, no conclusions can be drawn on the distinction between the two major emotion regulation mechanisms associated with REAP and ESUP, as extensively studied in neuroscience (Goldin, McRae, Ramel, & Gross, 2008; Kim & Hamann, 2007; Levesque et al., 2003; Ochsner et al., 2002, 2004; Phan, et al., 2005). Moreover, recent fMRI studies have established that REAP and ESUP (regardless of any individual differences) have different neural

substrates in frontal cortical regions (Goldin et al., 2008; Vrtička, Sander, & Vuilleumier, 2011), produce differential modulatory effects on activity in perceptual and limbic systems (Vrtička et al., 2011), and act at different stages along emotional processing pathways (Goldin et al., 2008). Distinctive patterns of neural activity were also found for regulation of social and nonsocial emotional information (Vrtička et al., 2011). Furthermore, based on behavioral research suggesting different patterns of emotion regulation strategy as a function of AAS (Mikulincer & Shaver, 2007), these individual differences would be predicted to involve distinct effects of REAP or ESUP on the processing of socially relevant emotional stimuli. AV might be associated with greater use of behavioral suppression (ESUP) and/or reduced re-evaluation (REAP), whereas AX should more strongly involve cognitive up-regulation (REAP) and/or difficulties in the suppression (ESUP) of negative emotions. Moreover, AV is also associated with reduced attentional biases to attachment-related emotional information, but these effects are reversed by cognitive load, suggesting an active inhibitory control of attention requiring cognitive effort (Edelstein & Gillath, 2008).

Secondly, the study by Gillath et al. (2005) used negative relationship scenarios exclusively (such as conflict, breakup, or death of a partner), but did not take into account positive emotions. Even though negative attachment-related scenarios are probably the most potent activators of the attachment system, positive social emotions are also relevant to and reinforcing for attachment processes. Accordingly, neuroimaging research on maternal and romantic love has consistently emphasized a major role of reward-related circuits in the formation and regulation of interpersonal bonds (e.g., Fisher, Aron, & Brown, 2006). In addition, behavioral work on attachment style that investigated the perceptual processing of positive (happy) and negative (angry, sad) facial expressions in dynamic displays showed that insecurely attached individuals tend to perceive the offset of both happy and angry faces later than securely attached individuals (Fraley, Niedenthal, Marks, Brumbaugh, & Vicary, 2006; Niedenthal, Brauer, Robin, & Innes-Ker, 2002). This finding suggests a differential sensitivity to *both* positive *and* negative social cues. AV is also associated with a more negative view of others (Bartholomew & Horowitz, 1991), making avoidantly attached people more likely to distrust supportive social signals. This predisposition might increase the vigilance to positive social cues in AV, because the latter tend to be perceived as deceptive and thus more negative. Moreover, in a recent fMRI study, we found diminished activation

in reward-related brain areas as a function of AV during situations representing positive social support (Vrtička et al., 2008). Similarly, in a behavioral investigation where participants had to rate the pleasantness of positive/negative and social/nonsocial images, we found a selective negative correlation between pleasantness ratings for social positive images and AV (Vrtička et al., *in press*). It therefore seems important to extend the findings of Gillath et al. (2005) by not only using standard emotion regulation manipulations but also including both negative and positive attachment-related stimuli when considering the modulation of emotion processing by AAS.

To address these issues, we designed an fMRI study where participants were presented with both positive and negative attachment-relevant (i.e., social) emotional scenes while being instructed to use different emotion regulation strategies. We also included positive and negative nonsocial (attachment-irrelevant) emotional scenes as control conditions, resulting in four stimulus categories of interest (social or nonsocial, pleasant or unpleasant). Importantly, social versus nonsocial image categories were matched for pleasantness, intensity, and control ratings (see Methods). Note that our social stimuli were not intended to refer to specific attachment figures (e.g., parents or romantic partners) or attachment concepts (e.g., love or trust), but depicted scenes including interpersonal interactions between unfamiliar people and were thus indirectly attachment-relevant. However, because social scenarios are strong activators of the attachment system (Mikulincer & Shaver, 2007), comparing the processing of social and nonsocial scenes allowed us to probe for the recruitment of “internal working models” of interpersonal interactions (Bartholomew & Horowitz, 1991) and test any modulation thereof by individual attachment style in different regulation contexts.

Our fMRI data analysis focused first on the general response to social stimuli (by contrasting all social versus nonsocial scenes regardless of emotion content and regulation strategy), and then tested for more specific effects of either pleasant or unpleasant social scenes, as a function of individual scores in AV and AX. Specifically, we asked whether these individual differences might affect emotion processing (1) during spontaneous emotional judgments, and (2) during specific emotion regulation conditions; i.e., cognitive reappraisal (REAP) and emotion suppression (ESUP). First, we expected AV to modulate brain activity in response to social scenes (pleasant or unpleasant) in areas mediating cognitive control and inhibition (such as ACC and PFC), but also additional decreases in areas associated with reward and reinforcement for

pleasant social stimuli. Conversely, AX was expected to entail increased activations in limbic regions for unpleasant social scenes. Second, we predicted distinct effects of emotion regulation strategies as a function of attachment style, with AV showing predominant differences during ESUP and AX predominant differences during REAP.

METHODS

Participants

We recruited 19 healthy paid volunteers (all right-handed women, mean age 24.82 ± 4.0 years), who all had normal or corrected to normal vision, had no history of neurological or psychiatric disease, and gave informed, written consent according to the local ethics committee regulation. Only female participants were recruited in order to avoid any gender differences regarding emotion perception and regulation (see Fujita, Diener, & Sandvik, 1991; Kim & Hamann, 2007), or any difference in attachment style distribution as a function of gender (see Mikulincer & Shaver, 2007). This also ensured consistency between this sample and the group of volunteers (women only) who was tested in other preliminary experiments to determine emotional ratings on a range of pictures including those subsequently selected for our fMRI study (see also Vrtička et al., in press).

Psychological questionnaires

Adult attachment style

We assessed individual AAS with a validated French version (Guédeney, Fermanian, & Bifulco, 2010) of the original Relationships Scales Questionnaire (RSQ; Griffin & Bartholomew, 1994). Following recent recommendations (Kurdek, 2002), we analyzed the RSQ according to the bi-dimensional model of AAS (Simpson et al., 1992), in which scores for attachment (avoidance) (AV) and anxiety (AX) were calculated for each subject by taking into account 13 items (8 for AV and 5 for AX) out of the total 30 items contained in RSQ. This approach has been shown to provide a reliable and stable indicator of AAS in comparison with the attachment interview (Kurdek, 2002) and was already used in our previous studies (Vrtička et al., 2008, in press). Individual scores were then mean-centered (using z -scores) in order to reduce effects of multi-collinearity (Aiken & West, 1991).

General use of emotion regulation

We obtained a measure of the preferred emotion regulation strategy generally used by participants in their everyday life, by using a French version of the Emotion Regulation Questionnaire (ERQ; Gross & John, 2003). The ERQ includes 6 items for reappraisal, and 4 items for suppression.

Self and other models

We also administered a French version (translated and validated by N. Guédeney, 2005) of the Relationships Questionnaire (RQ) (Bartholomew & Horowitz, 1991), which can be used to calculate estimates of the positivity and/or negativity of self and other perception.

General anxiety

To differentiate AX from more general anxiety traits, we also distributed the State-Trait Anxiety Inventory, Trait version (STAII-T; Spielberger, 1983; Spielberger, Sydeman, Owen, & Marsh, 1999). This questionnaire includes 20 items assessing how participants generally feel in conditions associated with various anxiety dimensions.

Stimuli, experimental conditions, and procedure

Stimuli

A total of 360 emotional pictures were initially chosen either from the International Affective Pictures System (IAPS) or searches on the Internet, and adjusted in size and resolution. Half of the pictures displayed scenes with a clear social implication, such as two people fighting or a mother interacting with her baby. The other half represented objects or landscapes (nonsocial), such as a dead bird covered in oil or a tropical island scene. All 360 pictures were rated in a separate behavioral study by 54 female, second-year psychology students (Vrtička et al., in press) on three continuous rating scales (ranging from 0 to 100), including pleasantness (from very negative to very positive), arousal (from low to high arousal), and control (from absence to full presence). The judgment of control (or dominance) was defined as the degree to which the observer feels in control of emotions induced by a given scene (e.g., Bradley & Young,

1994). Based on mean ratings obtained for this sample, 240 pictures were finally chosen for the fMRI study and sorted according to social content (either social or nonsocial) and valence (either positive or negative). This gave rise to four stimulus categories (60 pictures each): social and nonsocial, pleasant and unpleasant. The final distribution of pictures in these four categories was such that unpleasant images had significantly lower pleasantness scores than pleasant images, negative = 20.67 ± 6.02 and positive = 72.14 ± 10.19 ; $F(1, 59) = 3919, p < .001$, but higher arousal, negative = 70.08 ± 8.05 and positive = 44.06 ± 7.14 ; $F(1, 59) = 1554, p < .001$, and lower degree of control, negative = 35.91 ± 8.14 and positive = 55.49 ± 9.25 ; $F(1, 59) = 452, p < .001$. However, more importantly, there were no significant differences for all three rating dimensions between social versus nonsocial images, $Fs(1, 59) < 1.36, ps > .25$, and no significant valence \times social content interactions, $Fs(1, 59) < 2.65, ps > .11$, as verified by 2 (valence) \times 2 (social content) repeated-measure ANOVAs. Finally, another set of 40 neutral images was also chosen from the IAPS database (20 including humans, 20 with no humans) to provide a baseline control condition (see below); their average valence rating was 49.7 ± 1.7 (on the same scale of 1 to 10). All images in the final stimulus set were also checked to show no difference in luminance across conditions, $Fs(1, 59) < 2.83; ps > .098$ in a 2 (valence) \times 2 (social content) ANOVA, and all social images had a similar number of human characters per picture, $Fs(1, 59) = .468; p = .497$, one-way ANOVA for social pleasant versus social unpleasant.

Experimental conditions

Participants were instructed that the goal of the study was to investigate how the brain reacts to different types of images (e.g., real scenes, TV or movie scenes) and to which degree people can regulate the emotional impact of these images. Accordingly, the experimental layout comprised four different viewing conditions, in which pictures were presented with different task instructions to induce different emotion regulation strategies.

The first condition served a control baseline, and was introduced to the participants as a “photography” judgment, where they had to indicate on each trial (by button press, using a 4-point scale—see below) whether the image was of good quality (e.g., well focused or properly lighted). All images in this condition were neutral, but could display either scenes with humans (i.e., social content) or inanimate settings and landscapes (i.e., nonsocial content). This condition

served as a baseline for general differences in brain activation to social versus nonsocial stimuli, irrespective of emotional processing demands and valence. It was presented as the first block of the first scanning run and the last block of the last run.

The three other viewing conditions constituted the main experimental design and included emotional images only. To assess brain responses during “natural” viewing (Kim & Hamann, 2007; Ochsner et al., 2004), participants were asked to watch and experience the depicted emotional scenarios as if they were living them for real (NAT). To assess the effect of cognitive re-evaluation (REAPPRAISAL condition; REAP), participants were instructed to view the depicted emotional scenes as parts of a movie clip or TV show that displayed fake or artificially set up situations created to give rise to emotions. The latter strategy (“pretend unreal”) has been one of the most often used to down-regulate emotional reactions to negative and positive images (Kim & Hamann, 2007). Finally, to assess the effect of behavioral (expressive) inhibition (SUPPRESSION condition; ESUP), the participants were instructed to watch the pictures similarly to the NAT condition, but with the important difference that they were told not to display any felt emotions that could become visible on the outside (e.g., through breathing frequency, heart rate, skin conductance responses, and facial expression, which were pretended to be recorded via electrodes attached to the body and an eye-tracker camera). After each picture, participants were shown a rating display and asked to report the feeling state evoked by the preceding stimulus (“How did you feel while seeing the last image?”), using a 4-point scale (see below).

All emotional images were counterbalanced across participants, so that the same images seen in one viewing condition by a given subject were seen in the other viewing conditions by different subjects.

Procedure

The fMRI session was divided into three successive scanning runs. Each run included two of the three experimental viewing conditions, presented in blocks of 40 emotional images (duration = 294 s per block), whereas the first and the last run also included an additional block of 20 neutral images (baseline condition, duration = 151 s). Within each block, images were pseudo-randomized and equally probable for the different stimulus categories (social versus nonsocial content, pleasant versus unpleasant valence). The first and the third runs lasted approximately 13 min, and the middle run 10 min.

Each block began with an instruction display (7 s), followed by images in pseudo-randomized order. Every individual trial started with a fixation cross at the screen center (average duration = 1125 ms jittered between 790 and 1485 ms), followed by an emotional or neutral image for 2 s, and then a response display probing for emotion ratings (4 s; see Figure 1). Ratings were made on a 4-button response box, according to a 4-point scale ranging from very and slightly negative (buttons 1 and 2, respectively), to slightly and very positive (buttons 3 and 4, respectively).

MRI acquisition. MRI data were acquired on a 3 T whole-body scanner (Siemens TIM TRIO, Erlangen, Germany), using standard head-coil configuration. For each participant, a structural image was obtained with a MPRAGE T1-weighted sequence (TI/TR/TE/flip = 900/1900/2.32/9°, parallel acquisition (GRAPPA) with acceleration factor 2, FOV = 230 × 230 × 173 mm³, matrix = 256 × 246 × 192). Functional images (TR/TE/flip = 2200 ms/30 ms/85°, parallel acquisition (GRAPPA) with acceleration factor 2, FOV = 235 × 235 mm, matrix = 128 × 84, resulting voxel size = 2.8 × 1.8 × 3.4 mm³) covered the whole brain, composed of 36 contiguous, 4-mm axial slices parallel to the inferior edge of the occipital and temporal lobes, and they were acquired continuously for a total of 975 images per participant (two sessions with 350 and one session with 275 images). Image quality was verified to exclude prominent signal drop-out in orbitofrontal and mediotemporal areas.

MRI analysis. Image processing was performed with SPM2 (www.fil.ion.ucl.ac.uk), using standard

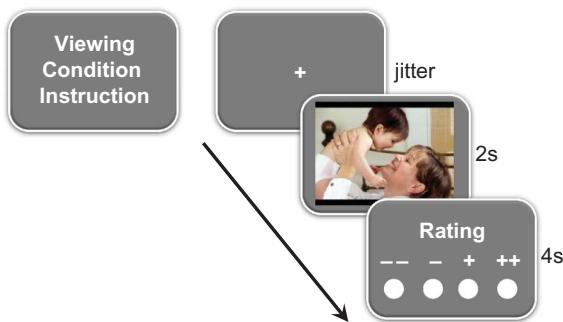


Figure 1. Illustration of the fMRI paradigm. Each block began with an instruction slide (7 s) presenting the task—spontaneous emotion experience (NAT), reappraisal (REAP), or expression suppression (ESUP). Trials began with a central fixation cross (jittered between 790 and 1485 ms, average 1125 ms), followed by a visual scene (2 s) that could be either pleasant or unpleasant, and with or without social content. Participants were subsequently asked to rate the image during a 4-s display.

procedures for realignment of the time series, slice-timing correction, normalization to a standard brain template in MNI space, and smoothing with an 8-mm FWHM Gaussian kernel. Statistical analysis was performed by the general linear model implemented in SPM2, with a separate regressor for each event type convolved with a canonical hemodynamic response function. Twelve event types from the emotion regulation task (four image categories: social and nonsocial, pleasant and unpleasant, for each of the three viewing conditions: NAT, REAP, and ESUP), plus two additional event types (social and nonsocial) from the baseline condition (BASE) were modeled for each participant, using the three scanning runs in a fixed-effect analysis at the single-subject level. Movement parameters from realignment corrections were entered as additional covariates of no interest for each scanning run, in order to account for residual movement artifacts after realignment. Statistical parametric maps were then generated from linear contrasts between the different conditions in each participant.

A first second-stage, random-effect (RFX) analysis was performed, using one-sample *t*-tests on contrast images obtained in each subject for each comparison of interest. Contrasts were performed across the whole brain with a standard threshold criteria (Worsley et al., 1996) of $p < .001$ uncorrected at voxel-level (except for bilateral amygdala, $p < .005$ given a priori predictions), and cluster size greater than 5 voxels (135 mm³). Note that all reported effects also passed the criteria of $p < .005$ and cluster > 10 voxels, as recommended by Lieberman and Cunningham (2009) to obtain an appropriate balance between types I and II error rates, and survived a false discovery rate (FDR) correction of $p < .05$ at the voxel level. Results concerning the main effects of different emotion regulation strategies on different categories of emotional stimuli, unrelated to attachment, have been described in details in a separate report (Vrtička et al., 2011).

For regions of interest (ROIs), parameter estimates of activity (betas) for each condition were extracted and averaged from all voxels within clusters showing significant effects in the group analysis ($p < .001$, except for bilateral amygdala, $p < .005$ given a priori predictions). These beta values were then submitted to additional repeated-measure ANOVAs and *t*-tests in SPSS (Chicago, Illinois, USA) with the factors of stimulus content, valence, and viewing condition, when appropriate.

Statistical correlations with AAS and other personality traits were examined by two different approaches. First, we tested for a relation between extracted beta values (cluster average) from activated ROIs in the main contrast social versus nonsocial (highlighting

responses to attachment relevant information) and scores obtained from standardized questionnaires (AAS from RSQ, plus ERQ, RQ, and STAI-T), across all individuals. These correlations were assessed by using two-tailed Pearson product moment coefficients in SPSS 17.0 (SPSS). Second, we performed a whole-brain, multiple-regression analysis on contrast images of interest (see below), using individual AV and AX scores as linear parametric factors in SPM—this allowed us to test for any voxels throughout the brain where activation in the given contrast varied as a function of behavioral measures (Phan et al., 2004). Because our goal was to determine how AAS modulates the brain response to social scenes with different affective values, these whole-brain parametric analyses focused on the two contrasts of interest, namely, “social pleasant versus nonsocial pleasant” and “social unpleasant versus nonsocial unpleasant” for each viewing condition. By entering AV and AX scores into the same multiple-regression analysis, we controlled for possible cross-correlations between the two attachment dimensions, even though the scores were not significantly correlated (see Questionnaire data below). Significant effects in this regression analysis were identified by a statistical threshold of $p < .001$ at the voxel level (uncorrected) and cluster size of ≥ 5 voxels (see Results). To check for the direction of correlations found in these whole-brain contrasts (e.g., positive parametric modulation of responses to social pleasant versus social unpleasant images during NAT as a function of AV scores), we then computed post-hoc regressions on the beta values extracted from significant clusters (averaged across voxels) and plotted these correlation for each condition separately (i.e., social pleasant \times AV and nonsocial pleasant \times AV), using SPSS. For illustrative purpose, such relations are plotted in correlation graphs and median split graphs (Figures 3–5), depicting differential effects according to high versus low attachment (AV or AX) scores, respectively. No further statistical test was directly performed on the median split data (except for the amygdala).

RESULTS

Questionnaire data

Avoidant (AV) and anxious (AX) attachment style measures obtained by the RSQ were not correlated, $r = .283$, $p = .24$, consistent with the assumption of independent traits. We also examined any relation with individual differences in habitual emotion regulation strategies as assessed by the ERQ. For AV, we found a marginally significant positive relation between

employment of suppression, $r = .404$, $p = .096$, implying that the higher subjects scored on AV, the more they tended to use suppression to regulate emotions in everyday conditions. By contrast, AX scores showed a marginally negative relation with reappraisal use, $r = -.433$, $p = .073$. AX was also associated with marginally higher anxiety on the STAI-T, $r = .411$, $p = .09$, and significantly lower scores for the self model derived from the RQ, $r = -.630$, $p = .004$. These trends accord with previous behavioral research on AAS (Mikulincer & Shaver, 2007). As a result, there was also a highly significant negative correlation between general anxiety and self model, $r = -.770$, $p < .001$.

Behavioral data

During fMRI scanning, participants rated all scenes on a 4-point pleasantness scale from very negative to very positive (see Methods and Figure 1). As expected, ratings were higher for pleasant images and lower for unpleasant images compared to neutral images during all three viewing conditions and for all stimulus categories, $ts(18) > 6.24$, $ps < .001$; paired t -tests. There was no effect of social content, pleasant images: $ts(18) < 1.84$, $ps > .083$; unpleasant images: $ts(18) < 1.47$, $ps > .16$. Changes in ratings due to regulation instruction were stronger during REAP than during ESUP (when compared to NAT) across all four stimulus categories, $ts(18) > 2.72$, $ps < .014$. However, the decreases in ratings were significant for all scene categories during REAP, $ts(18) > 4.35$, $p < .001$, but only for positive scenes during ESUP, pleasant: $ts(18) > 2.56$, $p < .020$; unpleasant: $ts(18) < 1.45$, $ps > .17$, consistent with the view that REAP is a more efficient strategy to reduce emotion experience (Gross, 2002).

We did not find any effect of AV on rating scores, $rs < .347$; $ps > .15$, but we found a positive correlation between AX and ratings of nonsocial pleasant images during ESUP, $t(18) = .555$; $p = .014$.

fMRI data

ROI analysis of social brain networks

Two distinct analyses of fMRI data were performed to assess how individual differences in AAS modulate brain activity during the regulation of social information and emotions. In the first step, we defined ROIs showing differential responses to social versus nonsocial scenes (across all emotion and regulation conditions), allowing us to delineate brain systems

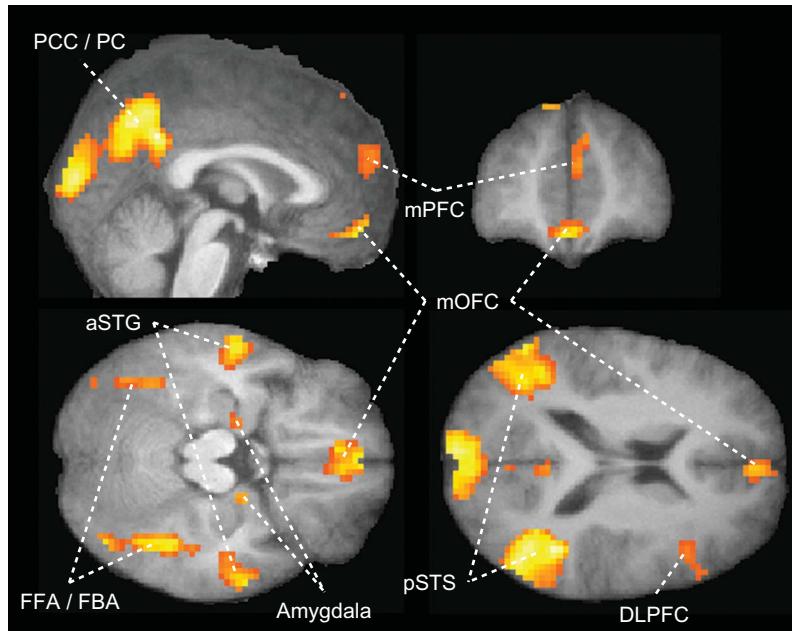


Figure 2. Brain networks involved in social processing. Depicted is the contrast comparing activations to all social versus nonsocial scenes ($p < .005$ for illustrative purposes), highlighting ROIs whose activity was sensitive to social scene content irrespective of emotional valence and emotion regulation condition. For abbreviations, please refer to Table 1.

generally implicated in the processing of social material and attachment-relevant information. As shown in Figure 2 and Table 1, this contrast (social versus nonsocial) identified several regions associated with social cognition such as the amygdala, medial and orbital prefrontal cortices, superior temporal sulcus (STS), and extrastriate visual areas in fusiform and lateral occipital cortex. We then correlated the extracted activation values of each of these ROIs with individual AAS scores (AV and AX), using parameter estimates (beta values averaged over all significant voxels in the cluster) for each social stimulus condition (pleasant and unpleasant) and each emotion regulation condition (NAT, REAP, ESUP). Correlations were tested with Pearson coefficients in SPSS.

For AV, we found a significant positive correlation with responses to social pleasant scenes in medial orbitofrontal cortex (mOFC) (see Figure 3a–c and Table 1), which was selective for the NAT condition. Hence, the higher individuals scored on AV, the stronger their mOFC responded to social pleasant scenes during the “spontaneous” viewing condition, $r = .48$, $p = .038$, with no such difference when they voluntarily regulated their emotions.

In contrast, for social unpleasant scenes, there was a positive correlation between AV scores and bilateral amygdala activity during REAP, left: $r = .56$,

TABLE 1
Main effects of social versus nonsocial scenes

Region	BA	Voxel	t-value	x, y, z
Amygdala left**		13	3.55	-21, -9, -18
Amygdala right**		26	4.21	21, -6, -18
mOFC**	11	40	5.26	-3, 54, -18
mPFC	10	28	4.36	3, 57, 15
PCC/PC	23 / 7	393	7.32	0, -51, 33
FFA/FBA right	37	98	6.59	42, -42, -27
DLPFC right	44	16	4.15	51, 21, 27
Temporal inferior left	20 / 21	109	6.85	-57, -3, -27
Temporal inferior right	21	111	6.29	60, -6, -24
pSTS/occipital left	19	458	7.82	-45, -84, 0
pSTS/occipital right	19	711	7.07	45, -48, 18
Occipital left	17	331	7.74	-6, -102, 9
Fusiform gyrus left	18	18	6.5	-15, -60, -6
FFA/FBA left	19 / 37	25	4.43	-42, -63, -21
Fusiform gyrus left	20	10	4.4	-42, -33, -24

Notes: **Regions showing correlations with AV scores (see text). None of these regions showed correlations with AX scores. Peak coordinates are given in MNI space and listed with best estimates of anatomical location. $p < .001$ for all regions except the amygdala ($p < .005$). All areas (including bilateral amygdala) survived a whole-brain FDR correction of $p < .05$ at the voxel level. BA = Brodmann's area, AV = avoidant attachment style, mOFC = medial orbitofrontal cortex, mPFC = medial prefrontal cortex, PCC = posterior cingulate, PC = pre-cuneus, FFA = fusiform face area, FBA = fusiform body area, DLPFC = dorso-lateral PFC, pSTS = posterior superior temporal sulcus.

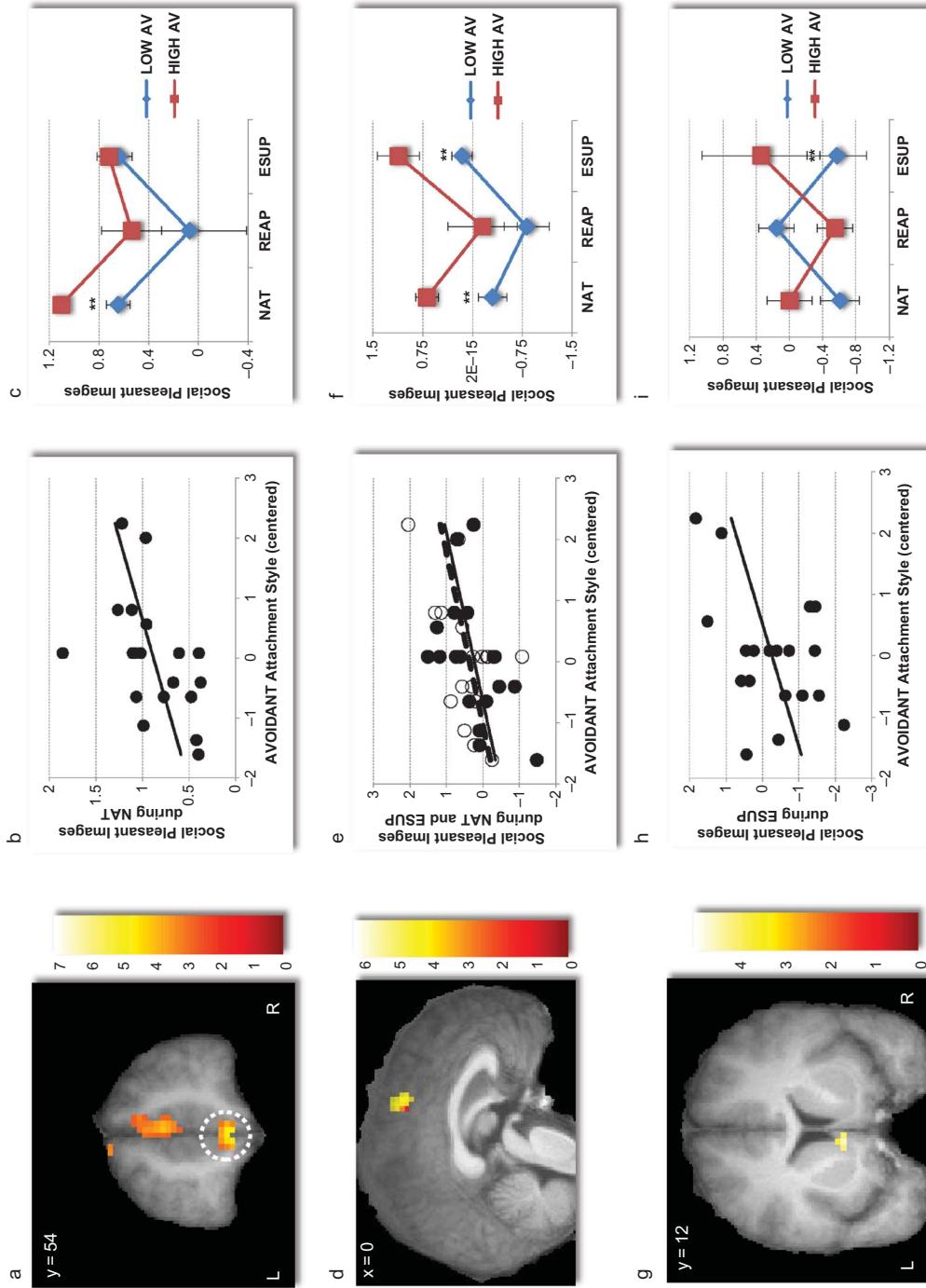


Figure 3. Brain activations to social pleasant scenes modulated by avoidant attachment style (AV). (a) Whole-brain activation map for the initial contrast social versus nonsocial ($p < .005$ for illustrative purposes), showing increases in medial orbitofrontal cortex (mOFC; $x, y, z = -3, 54, -18$). (b) Correlation between AV and parameter estimates (beta values) extracted from the mOFC cluster for social pleasant images during NAT (averaged across voxels). (c) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in mOFC, showing higher activity for social pleasant images during NAT in those with higher AV scores (asterisks indicate the differential response accounting for significant effects in the correlation analysis). (d) Statistical parametric map ($p < .001$) for the whole-brain, multiple-regression analysis (social pleasant versus nonsocial pleasant scenes, in the NAT—yellow—and ESUP—red—viewing conditions), showing a positive correlation with AV in the supplementary motor area (SMA); yellow cluster: $x, y, z = -3, -3, 54$. (e) Illustration of the correlation between AV scores and response to social pleasant stimuli in the SMA cluster (beta values, averaged across voxels) during NAT (filled circles and solid line) and ESUP (empty circles and dashed line) conditions. (f) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in SMA (yellow cluster in (d), showing higher activity for social pleasant images during NAT and ESUP with higher AV scores (asterisks indicate the differential response accounting for significant effects in the whole-brain correlation analysis). (g) Statistical parametric map for the whole-brain, multiple-regression analysis (social pleasant versus nonsocial pleasant images during ESUP), showing a positive correlation with AV in the left ventral caudate ($x, y, z = -6, 12, -6$). (h) Illustration of the correlation between AV and response to social pleasant images in the ventral caudate during ESUP. (i) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in the whole-brain correlation analysis. BOLD signal is depicted in arbitrary units, and error bars represent $\pm 1 SEM$.

$p = .012$; right: $r = .48, p = .040$, but not during NAT or ESUP (see Figure 4a–c), indicating a relative failure to dampen amygdala activation when instructed to re-evaluate the affective meaning of unpleasant social stimuli. This correlation was slightly stronger for the left than the right amygdala.

For AX, we found no correlation within any of these ROIs. In addition, no ROI showed a *negative* correlation with either AV or AX scores. Moreover, there was no relation to general anxiety measures (STAI-T; see below). Altogether, these data suggest that the effects above were specific for the avoidance dimension.

Whole-brain regression analysis

In a second step, we performed a complementary analysis by computing whole-brain, multiple-regression models in SPM. This whole-brain approach allowed us to identify brain regions modulated by AAS that responded specifically to either pleasant or unpleasant social information, outside brain networks with more general social responses as identified in the previous section. Individual AV and AX scores were entered as parametric modulators of the two contrasts of interest (i.e., social pleasant versus nonsocial pleasant, social unpleasant versus nonsocial unpleasant) and for each of the three viewing conditions (NAT, REAP, ESUP). By doing so, we could also avoid any confounding effect due to intrinsic differences in arousal and perceived control between pleasant and unpleasant images, since the social and nonsocial conditions were perfectly matched on valence, arousal, and perceived control scores, and were always compared across similar valence and task demands.

For avoidant attachment, this analysis showed a positive correlation ($p < .001$) of responses to social pleasant (versus nonsocial pleasant) stimuli in the left supplementary motor area (SMA; BA 6) during both NAT and ESUP (see Figure 3d–f and Table 2), and in the left ventral caudate nucleus during ESUP only (see Figure 3g–i and Table 2).

Furthermore, AV scores also correlated positively with differential activation to social unpleasant (versus nonsocial unpleasant) stimuli during NAT in several areas of the dorsolateral prefrontal cortex (DLPFC) and in both the dorsal and ventral anterior cingulate cortex (ACC) (see Figure 4d and g and Table 2). Post-hoc tests regarding the direction of these effects confirmed that they all reflected a positive relation between AV and response to social unpleasant scenes in the NAT condition (Figure 4e–i), with no relation to the nonsocial stimuli (data not shown). In addition, one LPFC (x, y, z = -54, 27, 21) cluster also showed a significant positive association between activity to

social unpleasant images and AV during the REAP condition (see Table 2), suggesting a persistent effect of AV despite a general reduction in activation during the REAP condition (as further indicated by inspection of median split data; see Figure 4f). There was no correlation during ESUP.

Finally, for anxious attachment, the whole-brain, multiple-regression analysis revealed a significant ($p < .001$) modulation of responses to both pleasant and unpleasant scenes, but only during the NAT condition. For social pleasant (versus nonsocial pleasant) scenes, activity in the left parahippocampus was found to increase proportionally to higher AX scores (see Figure 5a–c and Table 3). For activations to social unpleasant (versus nonsocial unpleasant) scenes, there was a highly significant correlation with AX in the right amygdala (see Figure 5d and Table 3). However, the post-hoc assessment of directionality revealed that this effect was predominantly caused by an inverse relation, as AX correlated negatively ($r = -.48, p = .039$) with the response to nonsocial unpleasant scenes in this condition (see Figure 5e), whereas the positive correlation with social stimuli did not reach significance ($r = .09$).

To clarify these differences in amygdala, we split the data for unpleasant stimuli during NAT at the median between low ($n = 9$) and high ($n = 8$) anxiously attached participants (see Figure 5f), and compared the different stimulus conditions between each group. These data revealed that the right amygdala responses to unpleasant stimuli were significantly stronger for social than nonsocial scenes in participants with high AX scores, but tended to be stronger for nonsocial scenes in those with low AX scores (Figure 5f). Accordingly, a 2×2 ANOVA with Social Content as within-subject and AX score as between-subject factors confirmed a significant interaction, $F(1, 15) = 6.37, p = .023$. Post-hoc *t*-tests comparing these different conditions demonstrated that (1) low and high anxiously attached participants did not significantly differ in amygdala activation to social unpleasant scenes, $t(7) = 1.47, p = .18$, but did differ for nonsocial unpleasant scenes, $t(7) = 2.31, p = .05$; and (2) this effect was primarily driven by significantly higher amygdala activation to social (as compared to nonsocial) unpleasant scenes in high anxiously attached individuals, $t(7) = 2.34, p = .05$, whereas there was no such difference in low anxiously attached individuals, $t(7) = 0.09, p = .93$. Overall, these analyses indicate that only high anxiously attached participants showed significantly greater activity in the right amygdala for social than nonsocial unpleasant images (Figure 5f), and that this effect was the source of the negative correlation of AX with activity for nonsocial unpleasant scenes (Figure 5e).

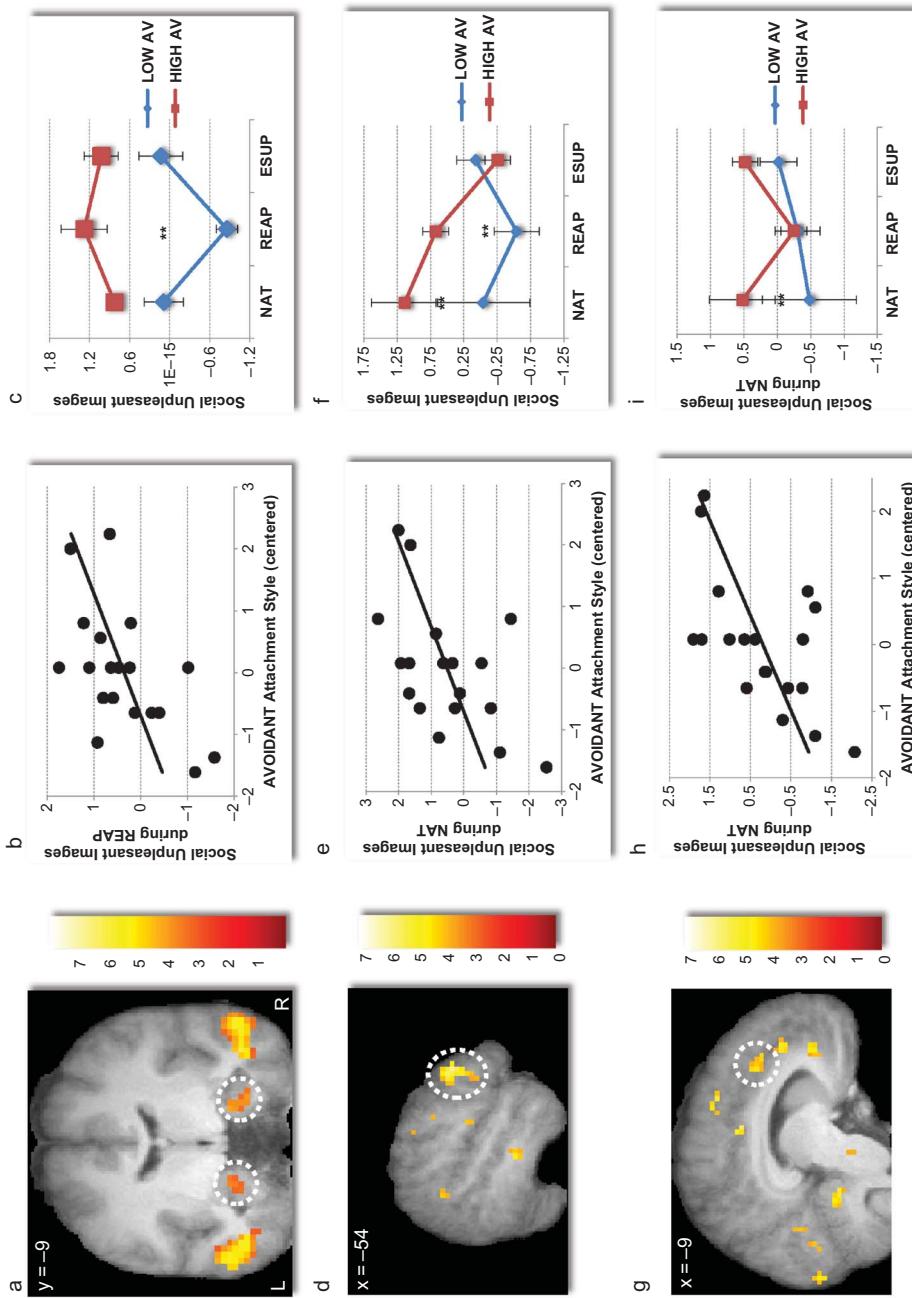


Figure 4. Brain activations to social unpleasant scenes modulated by avoidant attachment style (AV). (a) Whole-brain activation map ($p < .005$) for the initial contrast of social versus nonsocial, showing increased activity in bilateral amygdala (left: $x, y, z = -21, -9, -18$; right: $x, y, z = 21, -6, -18$). (b) Correlation between AV and parameter estimates (Beta values) extracted from left amygdala for social unpleasant images during REAP (averaged across voxels). (c) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in left amygdala, showing a decrease in activity to social unpleasant images during REAP for the low but not high avoidant (asterisks indicate the differential response accounting for significant effects in the correlation analysis). (d) Statistical parametric map for the whole-brain, multiple-regression analysis (social unpleasant versus nonsocial unpleasant during NAT), showing a positive correlation with AV in the left LPFC ($x, y, z = -54, 27, 21$). (e) Illustration of the correlation between AV and responses to social unpleasant stimuli for the left LPFC during NAT (Beta values, averaged across voxels). (f) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in left lateral PFC, showing higher activity to social unpleasant images during NAT and REAP with higher AV scores (asterisks indicate the differential response accounting for significant effects in the whole-brain correlation analysis). (g) Statistical parametric map for the whole-brain, multiple-regression analysis (social unpleasant versus nonsocial unpleasant during NAT), showing a positive correlation with AV in different regions of the anterior cingulate cortex (ACC). (h) Illustration of the correlation for social unpleasant images extracted from the left dorsal ACC: $x, y, z = -9, 42, 18$, circled in white in (h) during NAT. (i) Median split illustrating data for high (red; $n = 5$) versus low (blue; $n = 8$) avoidantly attached participants in left dorsal ACC, showing higher activity to social unpleasant images during NAT with higher AV scores (asterisks indicate the differential response accounting for significant effects in the whole-brain correlation analysis). BOLD signal is depicted in arbitrary units, and error bars represent ± 1 SEM.

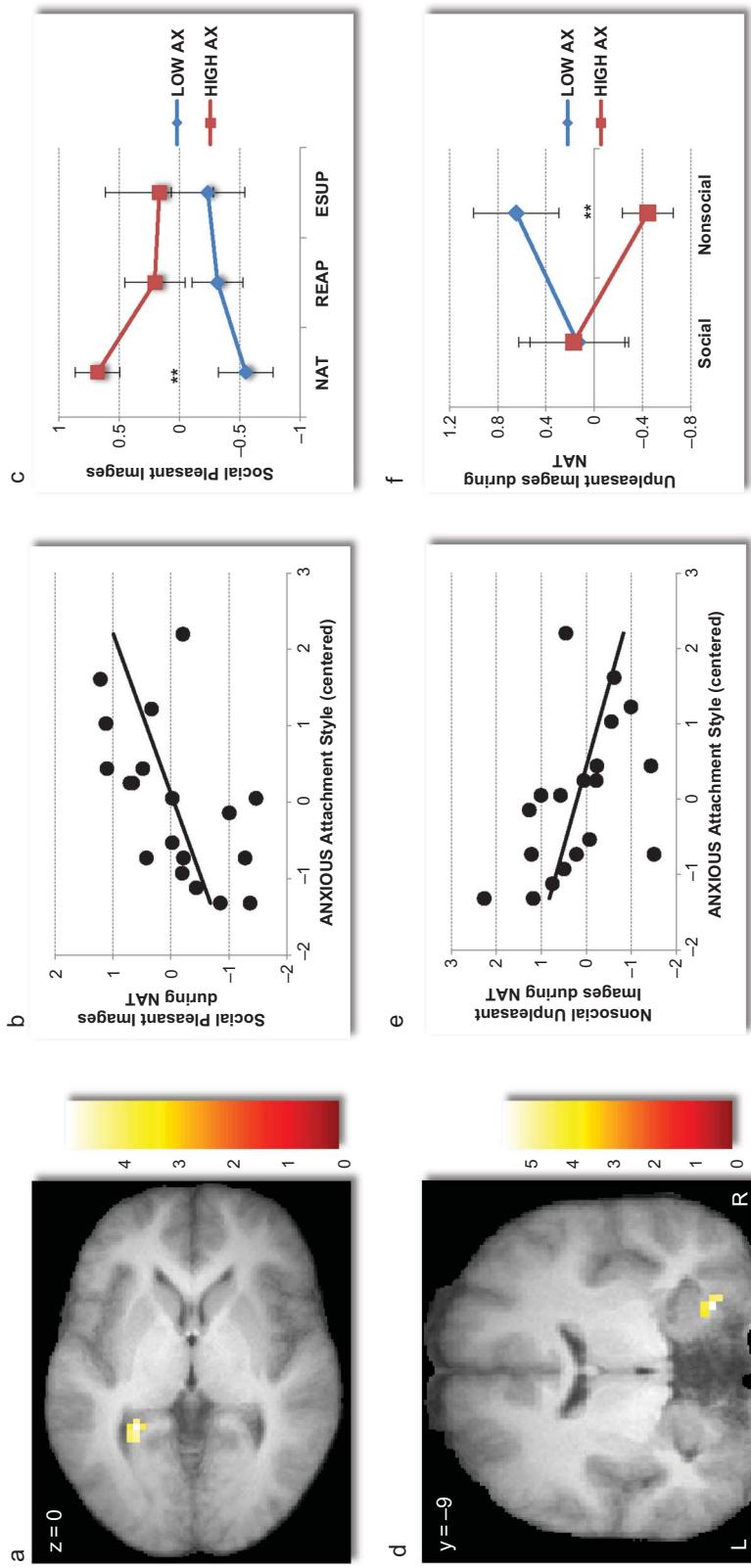


Figure 5. Brain activation to social stimuli modulated by anxious attachment style (AX). (a) Statistical parametric map for the whole-brain, multiple-regression analysis (social pleasant versus nonsocial pleasant during NAT), showing a positive correlation with AX in the left parahippocampus ($x, y, z = -27, -45, 0$). (b) Correlation between AX and parameter estimates (beta values) for social pleasant images extracted from the left parahippocampus during NAT (averaged across voxels). (c) Median split illustrating data for high (red; $n = 8$) versus low (blue; $n = 9$) anxiously attached participants in the parahippocampus, showing higher activity to social pleasant images during NAT with higher AX scores (asterisks indicate the differential response accounting for significant effects in the whole-brain correlation analysis). (d) Statistical parametric map for the whole-brain, multiple-regression analysis (social unpleasant versus nonsocial unpleasant during NAT), showing an effect of AX in the right amygdala ($x, y, z = 27, -9, -33$). (e) Illustration of the negative correlation between AX and response to nonsocial unpleasant images in the right amygdala during NAT (beta values, averaged across voxels). (f) Median split illustrating data for high (red; $n = 8$) versus low (blue; $n = 9$) anxiously attached participants in right amygdala, showing that activation to unpleasant scenes was greater for nonsocial content in those with higher AX scores (asterisks indicate the differential response accounting for significant effects in the whole-brain correlation analysis). BOLD signal is depicted in arbitrary units, and error bars represent ± 1 SEM.

TABLE 2
Whole-brain correlations with avoidant attachment style

Region	BA	Voxel	t-value	p-value	x, y, z
<u>Natural viewing (NAT), positive correlations</u>					
<i>Social pleasant versus nonsocial pleasant</i>					
SMA	6	37	6.15	<i>p</i> < .001	0, 0, 57
<i>Social unpleasant versus nonsocial unpleasant</i>					
LPFC left	45	59	5.6	<i>p</i> < .001	-54, 27, 21
DLPFC left	6	51	5.48	<i>p</i> < .001	-39, -3, 42
DLPFC left	9	12	4.86	<i>p</i> < .001	-45, 9, 45
LPFC right	45	10	4.48	<i>p</i> < .001	45, 30, 24
DLPFC right	44	17	4.43	<i>p</i> < .001	36, 21, 27
dACC right	32	26	5.54	<i>p</i> < .001	15, 30, 30
dACC left	32	12	4.94	<i>p</i> < .001	-9, 42, 18
dACC right	24	34	4.78	<i>p</i> < .001	3, 27, 27
vACC left	11	12	4.71	<i>p</i> < .001	-9, 39, -3
<u>Reappraisal (REAP), positive correlations</u>					
<i>Social pleasant versus nonsocial pleasant</i>					
None					
<i>Social unpleasant versus nonsocial unpleasant</i>					
DLPFC left	45	15	3.61	<i>p</i> < .001	-51, 27, 21
<u>Suppression (SUP), positive correlations</u>					
<i>Social pleasant versus nonsocial pleasant</i>					
Caudate left	7	4.44	<i>p</i> < .001		-6, 12, -6
SMA	7	3.95	<i>p</i> = .001		-3, -3, 54
<i>Social unpleasant versus nonsocial unpleasant</i>					

Notes: Negative correlations were not significant for the same contrasts. Peak coordinates are given in MNI space and listed with best estimates of anatomical location. BA = Brodmann's area, SMA = supplemental motor area, DLPFC = dorso-lateral prefrontal cortex, dACC = dorsal anterior cingulate cortex, vACC = ventral ACC.

TABLE 3
Whole-brain correlations with anxious attachment style

Region	BA	Voxel	t-Value	p-value	x, y, z
<u>Natural viewing (NAT), positive correlations</u>					
<i>Social pleasant versus nonsocial pleasant</i>					
Parahippocampus left	8	4.92	<i>p</i> < .001		-27, -45, 0
<i>Social unpleasant versus nonsocial unpleasant</i>					
Amygdala right	6	5.49	<i>p</i> < .001		27, -9, -33
<u>Reappraisal (REAP) and Expressive Suppression (ESUP), positive correlations</u>					
<i>Social pleasant > nonsocial pleasant</i>					
None					
<i>Social unpleasant > nonsocial unpleasant</i>					
None					

Notes: Negative correlations were not significant for the same contrasts. Peak coordinates are given in MNI space and listed with best estimates of anatomical location. BA = Brodmann's area.

Other questionnaires: General anxiety, ERQ, and RQ self and other

All effects in ROIs responding to social (versus nonsocial) stimuli, as well as the whole-brain regression results in SPM showed no relation to STAI-T scores, suggesting that the findings above were independent of general anxiety. Similar results were found when adding both attachment and anxiety scores in the same regression design.

Likewise, we did not find any significant effect on fMRI data associated with general emotion regulation strategy employment (as assessed by ERQ), or with models of self and other (as assessed by RQ).

DISCUSSION

Our fMRI study aimed to elucidate the relation of AAS to brain activity during the perception and regulation of social emotions. By including both cognitive re-evaluation (REAP) and inhibition of emotional expression (ESUP) as different regulation strategies, and both pleasant and unpleasant social (versus nonsocial) emotions, we were able to identify the neural correlates of individual differences in emotion processing associated with attachment style.

Importantly, our questionnaire data revealed that the two different measures of avoidance (AV) and anxiety (AX) derived from the RSQ were not correlated with each other, as expected on the basis of current bi-dimensional models of attachment style (Kurdek, 2002). In addition, AX was negatively associated with the self model as defined by the RQ. Such a relation is well documented, linking the hyperactivating strategies of AX with intensification of doubts about self-worth and self-efficacy, and intensification of a person's sense of vulnerability to rejection or abandonment (Mikulincer & Shaver, 2007). Interestingly, the personality questionnaires also indicated that participants scoring high on AV tended to report more frequent use of suppression to regulate emotions, a finding which accords with attachment theory associating AV with deactivating strategies that allow the individual to keep the attachment system in a low engagement state, mainly through inhibition processes (Mikulincer & Shaver, 2007). On the contrary, AX was associated with a trend to reporting less use of REAP to down-regulate emotions. This may seem at first sight to contrast with attachment theory, which has linked AX with an intensification of evaluation processes and a tendency to up-regulate negative emotions (Mikulincer & Shaver, 2007). However, if anxiously attached subjects tend to overuse reappraisal

to up-regulate emotions, they would indeed be less likely to apply this strategy for the opposite effect, namely to down-regulate affect, in keeping with our findings. Taken together, these data confirm the consistency of differences in emotion regulation associated with attachment style and the reliability of our measures. There were no significant associations between attachment style and other questionnaire measures.

During fMRI scanning, as expected, emotion ratings of the visual scenes showed a global and stronger decrease during REAP as compared to ESUP, replicating previous findings on the impact of these two regulation strategies on negative emotion processing (Goldin et al., 2008). However, these changes in emotion ratings were not affected by differences in AAS, except for a positive correlation between AX and ratings of nonsocial pleasant images during ESUP. This relation between AX and perception of pleasant stimuli during ESUP is not typically predicted by attachment theory, but might be consistent with previous findings that AX correlates with greater emotional arousal in response to both pleasant and unpleasant stimuli (Vrtička et al., in press). More generally, the emotional ratings during fMRI indicated that our participants correctly followed regulation instructions and that differences in AAS were not associated with overt changes in rating behavioral performance in our task.

However, our fMRI results revealed profound influences of individual differences in AAS on brain responses, particularly for avoidance. Interestingly, most effects of AAS were observed during the "spontaneous" emotion experience condition (NAT), where participants were asked to rely on their personal feelings, rather than during the instructed regulation conditions. These results cannot be explained by ineffective task designs, as the same regulation strategies were already shown to produce significant modulations in several brain regions (Ochsner et al., 2002, 2004; Vrtička et al., 2011). Instead, our findings suggest that attachment-related differences essentially concerned the most "natural" or habitual responses of participants to social emotions, whereas many aspects of regulation could still be successfully implemented in our experimental conditions, regardless of attachment style. Because AV is associated with deactivating strategies to prevent strong emotions (Mikulincer & Shaver, 2007), avoidantly attached participants were most likely to be emotionally aroused and experience greater difficulty in "naturally attending" to social emotional scenes (NAT). On the other hand, AX is associated with hyperactivating strategies, and thus dovetails with heightened responses to social

emotional information during NAT. Below, we will discuss these findings in relation to each dimension of AAS and each emotion condition separately.

Attachment style and unpleasant social emotions

According to attachment theory, AV is associated with the employment of deactivating strategies to regulate the experience and expression of (particularly) social unpleasant emotions, and this is mainly achieved through suppression mechanisms because REAP may require the activation of the attachment system to a certain degree (Mikulincer & Shaver, 2007). We therefore hypothesized that avoidantly attached subjects should (1) display increased limbic and frontal activations to social unpleasant stimuli when instructed not to use inhibitory strategies, and (2) exhibit inefficient use of REAP to reduce the impact of these emotions. We also expected these subjects to show enhanced activity (increased effort) in cortical regions involved in behavioral control and inhibition.

In keeping with these predictions, our fMRI data revealed that high scores on AV were associated with increased activation in several areas of DLPFC, which were specifically recruited by social unpleasant emotions during NAT (but not generally activated by social stimuli across all conditions in the main effect social versus nonsocial). This activation pattern accords with previous studies showing that LPFC and DLPFC are implicated in emotion regulation, including REAP (down- and up-regulation) as well as ESUP, for both unpleasant and pleasant material (Goldin et al., 2008; Kim & Hamann, 2007; Levesque et al., 2003; Ochsner et al., 2002, 2004; Phan et al., 2005). The inferior lateral PFC has also been implicated in executive control and behavioral inhibition (Cojan et al., 2009; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Sagapé, Schwartz, & Vuilleumier, 2011). Our new fMRI results therefore suggest that high avoidantly attached participants, when asked to naturally experience emotions elicited by social unpleasant scenes, might already recruit particular regulation mechanisms mediated by the lateral PFC, as compared with securely or anxiously attached participants. This in turn might be consistent with the notion that avoidantly attached individuals normally attempt to regulate their experience and expression of social emotions (e.g., via ESUP) even in "spontaneous" viewing conditions (Mikulincer & Shaver, 2007). Furthermore, a region in left inferior LPFC (x , y , z = -54 , 27 , 21) was found to exhibit persistent increases to social unpleasant images during REAP in

avoidantly attached subjects, suggesting that they had to use more regulatory resources or executive control when trying to cognitively re-evaluate such information, consistent with the notion that reappraisal strategies are less efficient (Mikulincer & Shaver, 2007). This would accord with behavioral research showing greater attentional control in subject with high AV tendencies (Gillath, Giesbrecht, & Shaver, 2009).

Moreover, the same positive relation between AV and activation to social unpleasant scenes during NAT was also observed in several subregions of the ACC (see Figure 4). The ACC is commonly divided according to a dorsal-ventral anatomical distinction (Bush, Luu, & Posner, 2000) and associated with conflict detection and control efforts (Amodio & Frith, 2006). Thus, activity in dorsal ACC has been related to cognitive, and that in ventral ACC to emotional conflict (Carter & van Veen, 2007; Eger, Etkin, Gale, & Hirsch, 2008; Mohanty et al., 2007). Moreover, ventral ACC has strong connections with the amygdala, which plays an important role in the regulation of fear responses and in mood disorders (Pezawas et al., 2005). Recent fMRI studies also showed that ventral ACC is selectively recruited during the evaluation (Somerville, Heatherton, & Kelley, 2006) or implicit memory (Vrtička, Andersson, Sander, & Vuilleumier, 2009) of situations involving social rejection. In our study, both the dorsal and ventral ACC divisions were modulated by AV in the processing of social unpleasant scenes during NAT. Our results therefore suggest that avoidantly attached individuals might experience both cognitive and emotional conflict when asked to naturally evaluate social unpleasant emotions, as reflected by increased activity in dorsal and ventral ACC in the NAT condition, in keeping with their tendency to normally avoid emotion experience and close relationships (see above). In general, these results on PFC and ACC activations converge with those of Gillath et al. (2005), who found changes in both cingulate and lateral prefrontal cortices in avoidantly attached individuals, which were interpreted as reflecting less efficient inhibition of negative thoughts about personal relationships.

In agreement with the hypothesis of inefficient re-evaluation of unpleasant social events in avoidantly attached individuals, we also found that AV correlated with higher amygdala activity to social unpleasant scenes during REAP (see Figure 4). The amygdala is known to play a central role in social as well as non-social emotion processing, and it responds not only to threat but also more generally to information that is appraised as self-relevant, based on the individual's needs, values, goals, or concerns (Hsu & Pessoa, 2007; Sander, Grafman, & Zalla, 2003; Vuilleumier

& Sander, 2008). Because social stimuli have a major intrinsic value in guiding human behavior, they typically activate the amygdala more strongly than comparable nonsocial stimuli (Balderston, Schultz, & Helmstetter, 2011; Britton et al., 2006; Goossens et al., 2009; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002; Vrtička et al., 2011), as demonstrated by the main effect comparing social and nonsocial scenes in our study (see Figure 2). Furthermore, amygdala responses to emotional stimuli have been found to be significantly reduced by REAP in several fMRI studies (Kim & Hamann, 2007; Ochsner et al., 2002, 2004). Our findings that amygdala responses to social unpleasant emotions were significantly increased in high compared to low avoidantly attached subjects during REAP demonstrate a relative failure of high avoidantly attached subjects to down-regulate emotions through cognitive re-evaluation. This pattern is highly consistent with attachment theory, since AV has been linked to preferential use of suppression to regulate social emotions (as also shown by our questionnaire data), but also to inefficient use of reappraisal (see above). On the contrary, securely attached individuals more commonly and successfully apply cognitive re-evaluation strategies to regulate their emotions (Mikulincer & Shaver, 2007). Thus, our new data provide for the first time direct evidence that negative affective responses induced in the amygdala by social unpleasant emotions are successfully reduced by REAP in low, but not in high avoidantly attached individuals. Moreover, they add to previous observations that cognitive reappraisal may affect left more than right amygdala (Vrtička et al., 2011), as the differential effect of AV on REAP predominated on the left side. Importantly, no similar correlation was observed for AX during REAP, suggesting that this effect is specific to the avoidance dimension of attachment style.

Avoidant attachment style and pleasant social emotions

Attachment theory has generally focused on emotion and its regulation in response to potential threats, i.e., as related to unpleasant attachment-related scenarios, but has less often investigated responses to pleasant affect. However, AV can also modulate the processing of pleasant facial expressions (Niedenthal et al., 2002; Strathearn, Fonagy, Amico, & Montague, 2009) and social rewards (Vrtička et al., 2008). Moreover, because AV is characterized by a more negative model of others (Bartholomew & Horowitz, 1991) and increased distrust of affective social signals

(Mikulincer & Shaver, 2007), avoidantly attached individuals might perceive pleasant social scenes as less engaging and more unpleasant than securely attached individuals. Accordingly, pleasantness ratings for social stimuli have been found to be reduced in avoidantly (but not anxiously) attached individuals (Vrtička et al., 2008, *in press*). We therefore expected differential brain activity in response to pleasant social scenes, particularly in areas associated with reward and reinforcement. In keeping with these predictions, our fMRI data revealed that AV modulated activity to social pleasant stimuli in mOFC, SMA, and left ventral caudate nucleus. These effects again arose during “natural” emotion judgments (NAT) for the two former areas, but also during ESUP in the two latter areas (see Figure 3).

Activity in mOFC has been linked to hedonic evaluations and reinforcement-guided decision making, especially in terms of context-sensitive evaluation of outcomes and reversal (Kringelbach & Rolls, 2004; Rushworth, Behrens, Rudebeck, & Walton, 2007). In addition, the OFC is critically involved in encoding attachment-relevant stimuli such as one’s own infants, mother, or romantic partners (Minagawa-Kawai et al., 2009; Nitschke et al., 2004). In our study, such increase in mOFC activation to social pleasant stimuli during NAT in avoidantly attached subjects may reflect a greater recruitment of valuation systems in order to rate emotions elicited by these stimuli, due to their reduced intrinsic pleasantness, or greater recruitment of “ambivalent” affective associations during these judgments. Such ambivalence might result from the fact that, in avoidantly attached individuals, positive social scenes could activate representations of closeness and intimacy but also undesired and thus aversive situations. As these individuals are characterized by negative models of others, they should have greater difficulty in evaluating the potential outcome value of scenes depicting positive emotion-inducing interactions between people, and may therefore differentially recruit valuation processes in mOFC during the NAT condition. This was not necessary in the REAP and ESUP conditions, where emotions had to be down-regulated rather than subjectively appraised.

SMA increases are particularly interesting and consistent with a role of this region in motor inhibition and response suppression in emotional contexts (Sagaspe et al., 2011; Voon et al., 2010). Moreover, in a previous positron emission tomography (PET) study investigating the neural substrates of facial movements associated with laughing and smiling, activity in the SMA was selectively related to voluntary, but not spontaneous, facial displays of happiness (Iwase et al., 2002). Our data might thus suggest that avoidantly

attached subjects exert stronger inhibitory control over facial activity (and perhaps other motor or bodily reactions) in response to pleasant social scenes, specifically during the NAT and ESUP conditions. This would accord with attachment theory and observations that avoidantly attached individuals tend to express pleasant emotions in social contexts to a lesser degree because they prefer not getting involved in close positive interactions with others (Dozier & Kobak, 1992). Moreover, such inhibitory control of motor expressions would be expected to be stronger in the "natural" viewing situation (NAT) and during an explicit requirement to inhibit pleasant emotions (ESUP), as we found, since these corresponded to experimental conditions where participants could predominantly use this strategy.

Caudate activation has also been reported to increase during successful inhibition of responses to happy expressions (Hare, Tottenham, Davidson, Glover, & Casey, 2005). Because happy faces are associated with pleasant affect and reward (O'Doherty et al., 2003), and activity in ventral striatum (including caudate) usually reflects reward signals and positive prediction error (Montague & Berns, 2002), this inhibitory activity in caudate was attributed to the successful overcoming of prepotent tendencies to respond to positively valenced facial expressions. Therefore, in our study, increased caudate activity to social pleasant scenes during ESUP in avoidantly attached subjects might also reflect greater inhibitory control and reward-related representations of successful avoidance of social emotions.

Note that no such associations were found for AX, implying that AV more strongly affects the appraisal and regulation of pleasant emotions, as suggested by previous behavioral work (Niedenthal et al., 2002; Strathearn et al., 2009; Vrtička et al., 2008, in press).

Overall, these findings extend our knowledge of the neural substrates of deactivating strategies associated with AV. On the one hand, they provide new evidence for the assumption that response-focused emotion regulation (ESUP) is associated with AV and could represent a "default" strategy employed by avoidantly attached individuals in spontaneous conditions (NAT). On the other hand, they also explain why these individuals may become highly emotional when required to use another antecedent-focused regulation strategy (REAP), leading to increased cognitive load and subjective threat. This accords with the view that avoidantly attached persons might display better control and inhibition of attachment relevant information under normal circumstances, but that such mechanisms may fail when they are confronted with cues evoking experiences of insecurity (Gillath et al., 2009), forced

to exert suppression too long (Sutin & Gillath, 2009), or taxed with additional cognitive load (Edelstein & Gillath, 2008). This could also account for the fMRI results of Gillath et al. (2005), who found that high AV was associated with less deactivation in cingulate and lateral prefrontal cortex in a think/no-think task, suggesting less efficient suppression and greater effort or conflict when dealing with attachment-related scenarios.

Anxious attachment style and social emotions

AX is associated with hyperactivating strategies that maintain and even intensify negative affect, especially concerning attachment-related scenarios (Mikulincer & Shaver, 2007). Thus, AX is characterized by increased vigilance to signs of social rejection or support and related emotions, with eased access to memories and ruminations about potential threats (Mikulincer & Shaver, 2007). We therefore expected that anxiously attached participants should display increased activations in limbic regions to unpleasant social scenes during explicit emotional judgments, with or without difficulties in down-regulating negative emotions in the reappraisal or suppression regulation conditions (Fraley & Shaver, 1997).

Our fMRI data revealed differential effects of AX during the NAT condition only, involving both social pleasant and unpleasant scenes (see Figure 5). On the one hand, AX scores correlated with selective increases to social pleasant scenarios in the parahippocampal gyrus. This area is crucially involved in novelty detection and perceptual aspects of memory (Burgess, Maguire, & O'Keefe, 2002). It is plausible that it was more activated in anxiously attached participants because they generally tend to show eased access to emotional memories through hyperactivating strategies (Mikulincer & Shaver, 2007) and could more often recall emotionally relevant situations reminiscent of those seen during scanning. The predominance of this effect for pleasant scenes might reflect the greater concern and need for supportive interactions, with richer memory representations for contexts associated with pleasant social experiences.

On the other hand, AX was also correlated with a differential increase to social unpleasant scenes in the right amygdala, and this selectively during the NAT condition. More precisely, this pattern reflected the fact that for high anxiously attached participants, amygdala activation was stronger to social than nonsocial unpleasant scenes, whereas no such differential activation was found in low anxiously

attached participants. Social specificity of amygdala responses thus increased as a function of AX. This finding dovetails with recent imaging studies showing enhanced amygdala activation in anxiously attached individuals to socially unpleasant or threatening cues, such as words with rejection meaning (Lemche et al., 2006) and faces with angry expressions (Vrtička et al., 2008). Furthermore, in the latter study, amygdala activation was specifically related to the social value of angry expression because it arose only when these faces were presented as negative feedback from virtual partners, not in a different feedback context. Because the amygdala is known to be critically implicated in processing threatening and self-relevant affective information (Hsu & Pessoa, 2007; Sander et al., 2003), and has strong projections to autonomic and attentional systems (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005), these imaging results support the notion that a key aspect of AX involves hypervigilance toward socially significant cues, and provide a plausible neural substrate for increased arousal responses to socially and emotionally significant stimuli in our study. Moreover, the current correlation with AX was specific to the right amygdala, which has been particularly linked to arousal and relatively automatic detection of emotional stimuli (Sergerie, Lepage, & Armony, 2006; Vrtička et al., 2011), unlike the increase during REAP that was associated with AV and involved the left amygdala to a stronger degree instead.

We found no effect of AX during the REAP condition. AX is usually related to hyperactivating strategies that lead to enhancing or up-regulating emotions (particularly if social unpleasant) through cognitive reappraisal mechanisms and ruminations (Mikulincer & Shaver, 2007), but there is no clear evidence for a systematic strategy to down-regulate affect. Thus, our results imply that anxiously attached individuals were able to follow regulation instructions during REAP and ESUP, and thereby successfully reduce the emotional impact of social unpleasant stimuli. These data may partly differ from those of Gillath et al. (2005), who found that AX correlated with increased activation in temporal pole during the inhibition of thoughts related to negative relationship scenarios and sadness. However, the paradigm used in their study was very different from ours. Therefore, the effect of AX on reappraisal and control of unpleasant social emotions still remains to be more fully investigated, as some behavioral evidence suggests that anxiously attached individuals might have difficulty with suppressing negative emotions, even when asked to do so (Fraley & Shaver, 1997).

CONCLUSION

This fMRI study investigated how AAS modulates the perception and regulation of social emotions. Our new data reveal that when asked to make explicit “spontaneous” judgments of social scenes, high avoidantly attached participants recruited several prefrontal brain areas implicated in emotion regulation (DLPFC), evaluation of decision outcomes (mOFC), and detection of cognitive as well as emotional conflicts (ACC). Avoidant attachment style was also correlated with differential activation patterns when participants were asked to employ emotion regulation strategies. These individuals exhibited sustained increases in DLPFC and left amygdala to unpleasant social stimuli during REAP, suggesting a relative failure to down-regulate unpleasant affect through cognitive re-evaluation. In addition, they showed increased activity to pleasant social stimuli in SMA and ventral caudate predominantly during ESUP, in accordance with stronger inhibition of emotion expression and behavior in response to such social stimuli. Conversely, AX was associated with a modulation of brain responses to both pleasant and unpleasant social scenes, during spontaneous emotional judgments (NAT). Higher AX scores correlated with greater activation of the left parahippocampal cortex to pleasant stimuli, compatible with a facilitation of memories for attachment-related situations; whereas unpleasant stimuli revealed greater right amygdala differentiation between social and nonsocial responses, suggestive of increased emotional arousal and vigilance to social threats.

Taken together, these findings accord with but also extend current knowledge on AAS. We provide for the first time direct evidence that individual differences in avoidant and anxious dimensions of attachment in adults are associated with distinct brain activity patterns during the regulation of social emotions. Further research is needed to verify these results in larger samples and male participants, as well as with personally relevant attachment-related material. It would also be important to provide more direct comparisons between regulation processes specifically associated with individual attachment styles and those subserving particular aspects of reappraisal or suppression in secure individuals. A better understanding of emotion regulation mechanisms and individual differences may ultimately help us to clarify clinical disorders in social behaviors, as well as design more effective approaches for therapeutic intervention in social dysfunction.

REFERENCES

Aiken, L. S., & West, S. G. (1991). *Multiple regression: Testing and interpreting interactions*. Newbury Park, CA: Sage.

Ainsworth, M. D. S. (1978). Bowlby-Ainsworth attachment theory. *Behavioral and Brain Sciences*, 1(3), 436–438.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7(4), 268–277.

Balderston, N. L., Schultz, D. H., & Helmstetter, F. J. (2011). The human amygdala plays a stimulus specific role in the detection of novelty. *NeuroImage*, 55(4), 1889–1898.

Bartholomew, K., & Horowitz, L. M. (1991). Attachment styles among young adults – a test of a 4-category model. *Journal of Personality and Social Psychology*, 61(2), 226–244.

Bowlby, J. (1969). *Attachment and loss*. New York, NY: Basic Books.

Bowlby, J. (1982). *Attachment and loss* (2nd ed.). New York, NY: Basic Books.

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *J. Behav. Ther. Exp. Psychiatry*, 25(1), 49–59.

Brennan, K. A., Clark, C. L., & Shaver, P. R. (1998). Self-report measurement of adult attachment: An integrative overview. In J. A. Simpson & W. S. Rholes (Eds.), *Attachment theory and close relationships* (pp. 46–76). New York, NY: Guilford Press.

Britton, J. C., Phan, K. L., Taylor, S. F., Welsh, R. C., Berridge, K. C., & Liberzon, I. (2006). Neural correlates of social and nonsocial emotions: An fMRI study. *NeuroImage*, 31(1), 397–409.

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, 35(4), 625–641.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4(6), 215–222.

Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: An update of theory and data. *Cognitive, Affective, & Behavioral Neuroscience*, 7(4), 367–379.

Cojan, Y., Waber, L., Schwartz, S., Rossier, L., Forster, A., & Vuilleumier, P. (2009). The brain under self-control: Modulation of inhibitory and monitoring cortical networks during hypnotic paralysis. *Neuron*, 62(6), 862–875.

Dozier, M., & Kobak, R. R. (1992). Psychophysiology in attachment interviews – converging evidence for deactivating strategies. *Child Development*, 63(6), 1473–1480.

Edelstein, R. S., & Gillath, O. (2008). Avoiding interference: Adult attachment and emotional processing biases. *Personality and Social Psychology Bulletin*, 34(2), 171–181.

Egner, T., Etkin, A., Gale, S., & Hirsch, J. (2008). Dissociable neural systems resolve conflict from emotional versus nonemotional distractors. *Cerebral Cortex*, 18(6), 1475–1484.

Fisher, H. E., Aron, A., & Brown, L. L. (2006). Romantic love: A mammalian brain system for mate choice. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 361(1476), 2173–2186.

Fraley, R. C., Niedenthal, P. M., Marks, M., Brumbaugh, C., & Vicary, A. (2006). Adult attachment and the perception of emotional expressions: Probing the hyperactivating strategies underlying anxious attachment. *Journal of Personality*, 74(4), 1163–1190.

Fraley, R. C., & Shaver, P. R. (1997). Adult attachment and the suppression of unwanted thoughts. *Journal of Personality and Social Psychology*, 73(5), 1080–1091.

Fujita, F., Diener, E., & Sandvik, E. (1991). Gender differences in negative affect and well-being – the case for emotional intensity. *Journal of Personality and Social Psychology*, 61(3), 427–434.

Gillath, O., Bunge, S. A., Shaver, P. R., Wendelken, C., & Mikulincer, M. (2005). Attachment-style differences in the ability to suppress negative thoughts: Exploring the neural correlates. *NeuroImage*, 28(4), 835–847.

Gillath, O., Giesbrecht, B., & Shaver, P. R. (2009). Attachment, attention, and cognitive control: Attachment style and performance on general attention tasks. *Journal of Experimental Social Psychology*, 45(4), 647–654.

Goldin, P. R., McRae, K., Ramel, W., & Gross, J. J. (2008). The neural bases of emotion regulation: Reappraisal and suppression of negative emotion. *Biological Psychiatry*, 63(6), 577–586.

Goossens, L., Kukolja, J., Onur, O. A., Fink, G. R., Maier, W., Griez, E., et al. (2009). Selective processing of social stimuli in the superficial amygdala. *Human Brain Mapping*, 30(10), 3332–3338.

Griffin, D., & Bartholomew, K. (1994). Models of the self and Other – fundamental dimensions underlying measures of adult attachment. *Journal of Personality and Social Psychology*, 67(3), 430–445.

Gross, J. J. (2002). Emotion regulation: Affective, cognitive, and social consequences. *Psychophysiology*, 39(3), 281–291.

Gross, J. J., & John, O. P. (2003). Individual differences in two emotion regulation processes: Implications for affect, relationships, and well-being. *Journal of Personality and Social Psychology*, 85(2), 348–362.

Guédéne, N., Fermanian, J., & Bifulco, A. (2010). Construct validation study of the Relationship Scales Questionnaire (RSQ) in an adult sample. *Encephale*, 36(1), 69–76.

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *NeuroImage*, 50(3), 1313–1319.

Hare, T. A., Tottenham, N., Davidson, M. C., Glover, G. H., & Casey, B. J. (2005). Contributions of amygdala and striatal activity in emotion regulation. *Biological Psychiatry*, 57(6), 624–632.

Hariri, A. R., Tessitore, A., Mattay, V. S., Fera, F., & Weinberger, D. R. (2002). The amygdala response to emotional stimuli: A comparison of faces and scenes. *NeuroImage*, 17(1), 317–323.

Hsu, S. M., & Pessoa, L. (2007). Dissociable effects of bottom-up and top-down factors on the processing of unattended fearful faces. *Neuropsychologia*, 45(13), 3075–3086.

Iwase, M., Ouchi, Y., Okada, H., Yokoyama, C., Nobezawa, S., Yoshikawa, E., et al. (2002). Neural substrates of human facial expression of pleasant emotion induced by comic films: A PET study. *NeuroImage*, 17(2), 758–768.

Kim, S. H., & Hamann, S. (2007). Neural correlates of positive and negative emotion regulation. *Journal of Cognitive Neuroscience*, 19(5), 776–798.

Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, 72(5), 341–372.

Kurdek, L. A. (2002). On being insecure about the assessment of attachment styles. *Journal of Social and Personal Relationships*, 19(6), 811–834.

Lemche, E., Giampietro, V. P., Surguladze, S. A., Amaro, E. J., Andrew, C. M., Williams, S. C. R., et al. (2006). Human attachment security is mediated by the amygdala: Evidence from combined fMRI and psychophysiological measures. *Human Brain Mapping*, 27(8), 623–635.

Levesque, J., Eugene, F., Joannette, Y., Paquette, V., Mensour, B., Beaudoin, G., et al. (2003). Neural circuitry underlying voluntary suppression of sadness. *Biological Psychiatry*, 53(6), 502–510.

Lieberman, M. D., & Cunningham, W. A. (2009). Type I and type II error concerns in fMRI research: Re-balancing the scale. *Social Cognitive and Affective Neuroscience*, 4(4), 423–428.

Mikulincer, M., & Shaver, P. R. (2007). *Attachment in adulthood: Structure, dynamics, and change*. New York, NY: Guilford Press.

Minagawa-Kawai, Y., Matsuoka, S., Dan, I., Naoi, N., Nakamura, K., & Kojima, S. (2009). Prefrontal activation associated with social attachment: Facial-emotion recognition in mothers and infants. *Cerebral Cortex*, 19(2), 284–292.

Mohanty, A., Engels, A. S., Herrington, J. D., Heller, W., Ho, M. H. R., Banich, M. T., et al. (2007). Differential engagement of anterior cingulate cortex subdivisions for cognitive and emotional function. *Psychophysiology*, 44(3), 343–351.

Montague, P. R., & Berns, G. S. (2002). Neural economics and the biological substrates of valuation. *Neuron*, 36(2), 265–284.

Niedenthal, P. M., Brauer, M., Robin, L., & Innes-Ker, A. H. (2002). Adult attachment and the perception of facial expression of emotion. *Journal of Personality and Social Psychology*, 82(3), 419–433.

Nitschke, J. B., Nelson, E. E., Rusch, B. D., Fox, A. S., Oakes, T. R., & Davidson, R. J. (2004). Orbitofrontal cortex tracks positive mood in mothers viewing pictures of their newborn infants. *NeuroImage*, 21(2), 583–592.

Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. E. (2002). Rethinking feelings: An fMRI study of the cognitive regulation of emotion. *Journal of Cognitive Neuroscience*, 14(8), 1215–1229.

Ochsner, K. N., Ray, R. D., Cooper, J. C., Robertson, E. R., Chopra, S., Gabrieli, J. D. E., et al. (2004). For better or for worse: Neural systems supporting the cognitive down- and up-regulation of negative emotion. *NeuroImage*, 23(2), 483–499.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, 41(2), 147–155.

Pezawas, L., Meyer-Lindenberg, A., Drabant, E. M., Verchinski, B. A., Munoz, K. E., Kolachana, B. S., et al. (2005). 5-HTTLPR polymorphism impacts human cingulate-amygdala interactions: A genetic susceptibility mechanism for depression. *Nature Neuroscience*, 8(6), 828–834.

Phan, K. L., Fitzgerald, D. A., Nathan, P. J., Moore, G. J., Uhde, T. W., & Tancer, M. E. (2005). Neural substrates for voluntary suppression of negative affect: A functional magnetic resonance imaging study. *Biological Psychiatry*, 57(3), 210–219.

Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C., & Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: A trial-related fMRI study. *NeuroImage*, 21(2), 768–780.

Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F. O., & Vuilleumier, P. (2005). View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: An event-related fMRI study. *NeuroImage*, 24(4), 1214–1224.

Rushworth, M. F. S., Behrens, T. E. J., Rudebeck, P. H., & Walton, M. E. (2007). Contrasting roles for cingulate and orbitofrontal cortex in decisions and social behaviour. *Trends in Cognitive Sciences*, 11(4), 168–176.

Sagaspe, P., Schwartz, S., & Vuilleumier, P. (2011). Fear and stop: A role for the amygdala in motor inhibition by emotional signals. *NeuroImage*, 55(4), 1825–1835.

Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: An evolved system for relevance detection. *Reviews in the Neurosciences*, 14(4), 303–316.

Sergerie, K., Lepage, M., & Armony, J. L. (2006). A process-specific functional dissociation of the amygdala in emotional memory. *Journal of Cognitive Neuroscience*, 18(8), 1359–1367.

Simpson, J. A., Rholes, W. S., & Nelligan, J. S. (1992). Support seeking and support giving within couples in an anxiety-provoking situation – the role of attachment styles. *Journal of Personality and Social Psychology*, 62(3), 434–446.

Somerville, L. H., Heatherton, T. F., & Kelley, W. M. (2006). Anterior cingulate cortex responds differentially to expectancy violation and social rejection. *Nature Neuroscience*, 9(8), 1007–1008.

Spielberger, C. D. (1983). *Manual for the State-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.

Spielberger, C. D., Sydeman, S. J., Owen, A. E., & Marsh, B. J. (1999). Measuring anxiety and anger with the State-Trait Anxiety Inventory (STAII) and the State-Trait Anger Expression Inventory (STAXI). In M. D. Maruish (Ed.), *The use of psychological testing for treatment planning and outcomes assessment* (2nd ed.) (pp. 993–1021). Mahwah, NJ: Laurence Erlbaum Associates, Inc.

Strathearn, L., Fonagy, P., Amico, J., & Montague, P. R. (2009). Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology*, 34(13), 2655–2666.

Sutin, A. R., & Gillath, O. (2009). Autobiographical memory phenomenology and content mediate attachment style and psychological distress. *Journal of Counseling Psychology*, 56(3), 351–364.

Voon, V., Brezing, C., Gallea, C., Ameli, R., Roelofs, K., LaFrance, W. C., et al. (2010). Emotional stimuli and motor conversion disorder. *Brain*, 133, 1526–1536.

Vrtička, P., Andersson, F., Grandjean, D., Sander, D., & Vuilleumier, P. (2008). Individual attachment style modulates human amygdala and striatum activation during social appraisal. *PLoS ONE*, 3(8), e2868.

Vrtička, P., Andersson, F., Sander, D., & Vuilleumier, P. (2009). Memory for friends or foes: The social context of past encounters with faces modulates their subsequent neural traces in the brain. *Social Neuroscience*, 4(5), 384–401.

Vrtička, P., Sander, D., & Vuilleumier, P. (2011). Effects of emotion regulation strategy on brain responses to the valence and social content of visual scenes. *Neuropsychologia*, 49(5), 1067–1082.

Vrtička, P., Sander, D., & Vuilleumier, P. (in press). The influence of adult attachment style on the perception of social and nonsocial emotional scenes. *Journal of Social and Personal Relationships*.

Vuilleumier, P., & Sander, D. (2008). Trust and valence processing in the amygdala. *Social Cognitive and Affective Neuroscience*, 3(4), 299–302.

Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, 4(1), 58–73.