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Mixed emotions to social situations: An fMRI investigation

Ryan J. Murray[a,b], Sylvia D. Kreibig[c], Corinna Pehrs[d], Patrik Vuilleumier[b,e], James J. Gross[c], Andrea C. Samson[b,f,g,*]

[a] Department of Psychiatry, Faculty of Medicine, University of Geneva, Geneva, Switzerland
[b] Swiss Center for Affective Sciences, University of Geneva, Campus Biotech, Geneva, Switzerland
[c] Department of Psychology, Stanford University, Stanford, CA 94305 USA
[d] Bernstein Center for Computational Neuroscience Berlin, BCCN, Berlin, Germany
[e] Neuroscience Department, Laboratory for Behavioral Neurology and Imaging of Cognition, Medical school, University of Geneva, Campus Biotech, Geneva, Switzerland
[f] Faculty of Psychology, UniDistance Suisse, Brig, Switzerland
[g] Institute of Special Education, University of Fribourg, Fribourg, Switzerland

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ABSTRACT

Background: Neuroscience research has generally studied emotions each taken in isolation. However, mixed emotional states (e.g., the co-occurrence of amusement and disgust, or sadness and pleasure) are common in everyday life. Psychophysiological and behavioral evidence suggests that mixed emotions may have response profiles that are distinguishable from their constituent emotions. Yet, the brain bases of mixed emotions remain unresolved.

Methods: We recruited 38 healthy adults who viewed short, validated film clips, eliciting either positive (amusing), negative (disgusting), neutral, or mixed (a mix of amusement and disgust) emotional states, while brain activity was assessed by functional magnetic resonance imaging (fMRI). We assessed mixed emotions in two ways: first by comparing neural reactivity to ambiguous (mixed) with that to unambiguous (positive and negative) film clips and second by conducting parametric analyses to measure neural reactivity with respect to individual emotional states. We thus obtained self-reports of amusement and disgust after each clip and computed a minimum feeling score (shared minimum of amusement and disgust) to quantify mixed emotional feelings.

Results: Both analyses revealed a network of the posterior cingulate (PCC), medial superior parietal lobe (SPL)/precuneus, and parieto-occipital sulcus to be involved in ambiguous contexts eliciting mixed emotions.

Conclusion: Our results are the first to shed light on the dedicated neural processes involved in dynamic social ambiguity processing. They suggest both higher-order (SPL) and lower-order (PCC) processes may be needed to process emotionally complex social scenes.

1. Introduction

Mixed emotional states are common in everyday life. However, research to date has typically sought to examine relatively pure emotional states. This leaves it unclear as to how we should conceptualize mixed emotional states. Particularly, ambiguous social behaviors can elicit conflictual social emotional responses in ourselves. For instance, the classic slapstick situation of someone slipping on a banana peel can simultaneously elicit repulsion for the pain the person might be experiencing when hitting the ground but also amusement in their helpless attempt at staying upright. Despite this, however, emotion processing in affective sciences is often studied from a categorical theoretical approach (Bertini et al., 2020; Vytal and Hamann, 2010) while more complex emotions, such as mixed emotional states, remain unaddressed. This study attempts to fill this gap. Still, we take into account competing emotion theories that propose different accounts of mixed emotions.

1.1. Mixed emotions: theoretical expectations

According to the classic Circumplex Model of Affect (Russell, 1980), emotions arise according to two bipolar and orthogonal dimensions of valence (ranging from negative to positive) and arousal (low to high). Thus, positive and negative emotional states are, theoretically, mutually exclusive (Schimmack, 2001). From this, the *differentiation account* proposes that a mixed emotion (i.e., experiencing opposing emotions simultaneously) reflects (and thus does not differ from) the patterns of one of its pure constituent emotions (Kreibig et al., 2013). On the other

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[*] Corresponding author at: Faculty of Psychology, UniDistance Suisse, Schinerstr. 18, 3900 Brig, Switzerland & Institute of Special Education, University of Fribourg, Rue St. Pierre Canisius 21, 1700 Fribourg, Switzerland.

E-mail addresses: andrea.samson@unifr.ch, andrea.samson@unidistance.ch (A.C. Samson).

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hand, according to certain appraisal theorists, a mixed emotional state develops from its pure constitutive components, although inappropriate tendencies are ultimately extinguished and dominant responses attenuated (Lerner and Keltner, 2000). This *additive account* would thus predict intensity differences in the mixed emotional state, relative to its pure constituent emotions (Kreibig et al., 2013). Still, other appraisal theories propose that mixed emotional states reflect a distinct emotional process (Scherer, 1984). In this *emergence account*, the patterns of a mixed emotional state would dissociate from their pure constituent emotions, resulting in a distinct emotional profile (Kreibig et al., 2013).

1.2. Mixed emotions: empirical findings

Initial psychophysiological evidence of mixed emotional states supports the *emergence account* (Kreibig et al., 2013), findings which were later replicated in a subsequent independent study (Kreibig et al., 2015). Using standardized film clips, Kreibig et al. (2013, 2015) elicited amusement, disgust, and mixed emotions (i.e., both amusement and disgust) while collecting 15 different physiological parameters, including facial electromyography, heart rate variability, blood pressure, skin temperature, and respiration. Analyses of facial expressions demonstrated coactivation of smile (zygomaticus major) and frown (corrugator supercilii) muscles during the mixed emotional state, which differed from simple smile activation during amusement and simple frown activation during disgust. Analysis of autonomic reactivity demonstrated that response profiles during mixed emotional states differed both in intensity and pattern from those of the pure constituent emotional states. Taken together, this suggests a distinct physiological response of the mixed emotional state. To date, however, such analyses have not yet been conducted in the brain, which may reveal neural patterns specific to the processing of ambiguity resulting from conflicting emotions. That is, no study to date has investigated neural responses to the simultaneous experience of mixed emotions which are diametrically opposed in terms of their valence. Minimum feeling would be an optimal measure to operationalize a mixed emotional state. The question that is asked is whether the sharing of two emotions is qualitatively different or overlapping with their basic emotional states.

Ambiguity indeed possesses elements of conflicting features as well as incongruence, both of which require several cognitive-affective processes, not the least of which include executive functions linked to response inhibition (Nomura et al., 2003), emotion regulation (Ochsner et al., 2012), and mental flexibility (Mayr, 2001; Sussman et al., 2014) to eventually disambiguate such conflictual information. Extant neuroimaging literature shows disambiguation of visual cues, both social and non-social, elicits activity in specific neural regions attributed to executive control. For instance, identifying the expression of emotionally ambiguous faces recruits lateral frontal regions linked to response inhibition (Nomura et al., 2003), whereas task-switching during non-social perceptual ambiguity elicits bilateral medial posterior parietal (i.e., precuneus) activity (Tsumura et al., 2021), a region associated with self-reflective memory (Piekema et al., 2010) and cognitive flexibility (Leber et al., 2008). Together, disambiguation of visual cues, both social and non-social, likely associates with an increase of affective and executive processing and memory demands.

Social neuroscience has begun to examine the neural systems that underlie the processing of emotionally ambiguous social situations via combinations of conflictual affective elements, i.e., the co-occurrence of two contextual elements that would otherwise be inappropriate or unexpected (Pehrs et al., 2014; Rohr et al., 2016). This includes instances where the social context is conflictual (e.g., positive romantic scene with sad music) (Pehrs et al., 2014) or the emotions communicated are conflictual (e.g., other inflicting pain while talking in a friendly voice) (Rohr et al., 2016). Such stimuli may give rise to mixed emotions. Rohr et al. (2016) presented emotionally conflicting social scenes and measured blood oxygen-level-dependent (BOLD) responding in relation to subjectively rated scores of emotional conflict. Participants thus indicated the degree to which the scenes were emotionally conflicting for them. The authors found greater neural activity in the precuneus, superior temporal sulcus, and superior frontal sulcus with increased perceived conflict (Rohr et al., 2016). Still, no study to date has investigated the main effect of mixed emotions on neural responding to a stimulus, regardless of the degree of mixed social co-occurring conflictual cues. Furthermore, emotional conflict presents a relatively complex affective state that may be difficult to qualify when probed directly (cf. Kreibig and Gross 2017). Thus, directly identifying one's own experience of mixed emotions may be prone to subjective bias. Calculating a minimum score, however, would reflect the lowest shared values of two basic emotions (e.g., amusement and disgust) that are perceived simultaneously. Thus, asking participants to rate their perception of amusement and disgust, thereby less complex than asking for their perception of a mix of the two, for instance, would provide a more objective measure of the intensity of mixed emotional processing without requiring the individual to focus on a potentially more elusive emotional experience. Finally, no study has hitherto investigated the specificity of neural processing to emotionally mixed social situations.

1.3. Present study

The main goal of the current study was to test the neural specificity of mixed emotions, as they relate to their pure emotional constituents. A second aim tested the degree to which increasing mixed feelings modulates BOLD variation when viewing social scenes. For the first aim, we examined BOLD activity via fMRI whilst participants viewed short dynamic film clips depicting social situations with varying degrees of both amusing and disgusting elements (i.e., ambiguous social emotional scenes) that have previously been shown to elicit mixed emotions (Kreibig and Gross, 2017; Kreibig et al., 2013, 2015; Samson et al., 2016). We measured three principal effects: (i) Emotion; (ii) Mixed Emotion; and (iii) Valence. For Emotion, we compared BOLD activation during social emotional film clips eliciting one main emotion (e.g., amusement, disgust) to social film clips with no prominent emotion (i.e., neutral). For Mixed Emotion, we compared BOLD activation to mixed film clips relative to unambiguous (one principal emotion) and when viewing neutral film clips. Finally, for Valence, we compared BOLD variation when viewing amusing film clips relative to disgusting film clips. For the second aim, we obtained self-report measures of amusement and disgust for each film clip. Mixed feelings were characterized by calculating a minimum feeling score (MinFeel), i.e. the shared minimum self-reported value between the amusement and disgust scores (Schimmack, 2001). That is, for each participant and film clip, we computed an index of mixed feelings that reflects coactivation of self-reported amusement and disgust. This index is based on the intensity of the weaker of the two feelings, i.e., $I[MF] = \mathrm{minimum}(I[AMU], I[DIS])$, with $I[MF]$: intensity of mixed feelings, $I[AMU]$: intensity of experienced amusement, and $I[DIS]$: intensity of experienced disgust (Schimmack, 2001). Values greater than zero signify presence of mixed feelings. We then regressed BOLD activation with this MinFeel score.

For the first aim, concerning mixed emotions, we predicted differential activity to mixed social scenes (i.e., when contrasted against pure emotion [i.e., positive or negative] scenes) (Kreibig et al., 2013, 2015), within neural regions associated with attention, working-memory and cognitive flexibility, particularly the lateral frontal areas and medial posterior parietal region (e.g., Rohr et al., 2016; Tsumura et al., 2021), as was demonstrated during the processing of conflict between emotional scenes and their background music (Rohr et al., 2016) and during the disambiguation of ambiguous perceptual stimuli (Tsumura et al., 2021). For the second aim, we hypothesized that social scenes of increasing emotional ambiguity (i.e., increasing mix of amusement and disgust, as indexed by the MinFeel measure) would yield a positive parametric modulation of neural activity within these frontal and parietal regions.

It is important to mention that the present study forms part of a larger study examining the effect of emotion regulation when experiencing mixed feelings. The principal goal of the current study was to conduct an assessment of neural processing of mixed feelings, without explicit engagement of regulatory mechanisms. Analyses of emotion regulation of mixed emotions will thus be separately reported.

2. Materials & methods

2.1. Participants

Forty-eight healthy participants were initially recruited with flyers at the campus of Stanford University. Inclusion criteria were that the participants were free of (self-reported) psychiatric or neurological disorders. Exclusion criteria for all participants were prior head trauma and any contraindication for MRI safety prerequisites (e.g., metal objects in body). All participants had normal or corrected-to-normal vision. All participants provided informed consent via a signed consent form. This study was approved by the University's Institutional Review Board. Written informed consent was obtained from all participants.

Eight participants were ultimately removed because of excessive movement artefacts (i.e., abrupt head movement greater than 3 voxels) and two were removed for missing/invalid MRI data due to technical errors. This resulted in a final sample of 38 participants (20 females, mean age 21.61 years, standard deviation +/- 2.61 years, range 18–31 years).

2.2. Experimental task

The stimuli for this study were drawn from the film clip library by Samson et al. (2016) which contains short film clips lasting 20–30 s inducing primarily Positive (amusing), primarily Negative (disgust), Mixed (mix of amusement and disgust), and Neutral emotions. Examples of the films include toddlers acting funny (Positive), teenagers experiencing accidents on skateboards (Negative), people explaining their leisure activities (Neutral), or in the Mixed condition, accidents that look funny but are not painful or in which people suffer negative consequences (thus inducing amusement and disgust). The valence category of these films (amusing, disgusting, mixed, neutral) was validated in a prior study with an independent sample of participant raters (Samson et al., 2016). That is, this prior study helped to determine which stimuli are good examples of purely amusing, purely disgusting, and mixed amusement-disgust using affective ratings from an independent sample.

As mentioned previously, this current study forms part of a larger empirical endeavor whose objective is also to identify the neural correlates of regulated viewing of social situations eliciting mixed emotions. In this current study, however, we first wished to establish a baseline understanding of the neural responses to mixed emotions, irrespective of emotional regulation. Therefore, we will focus on the analysis of the natural viewing instructions of Positive, Negative, Mixed, and Neutral film clips, but not on the additional conditions of mixed film clips paired with two different emotion regulation instructions: (i) Focus on positive elements and (ii) Focus on negative elements. Overall, the design of the study was an incompletely crossed 4 (film type: Positive, Negative, Mixed, Neutral) x 3 (instruction type: natural, focus on positive elements, focus on negative elements) within-subjects design. While the 12 Positive, 12 Negative, and 12 Neutral films clips were presented only with natural viewing instructions, the 36 Mixed films were presented with all three instruction types (12 mixed film clips with natural viewing instructions, 12 with the instruction to focus on positive elements, and 12 with the instruction to focus on negative elements). Although we will focus here on the analysis of the natural viewing condition, we included all trials (natural and regulated) at the first-level of fMRI analysis and employed the regulated trials (i.e., 2 conditions, 24 film clips) as covariates of no interest, in order to control for any variance possibly explained by emotion regulation (see also supplementary material).

The experiment consisted of 6 runs of maximally 11.6 min each. In total, participants were presented 72 20–30 s long film clips in 6 runs, in which 2 film clips were randomly drawn from 6 conditions and presented in random order. Each of the 72 trials consists of a 5 s fixation cross, 8 s presentation of the instruction, 20–30 s film, and 15 s self-report assessment of amusement, disgust, and effectiveness of applying the viewing instruction (which will be reported elsewhere). Five seconds were allowed for each rating.

2.3. Behavioral measures

After each film, participants were asked to rate the degree to which they found the prior film clip amusing (*amusement*) and disgusting (*disgust*). Scores ranged on a 5-point Likert scale from 1 (very low) to 5 (very high) for each rating. A *minimum feeling* (MinFeel) score was calculated to determine the degree of mixed feelings experienced in each film clip. This was achieved by taking the minimum shared score between *amusement* and *disgust* scores (Schimmack, 2001). For instance, if a participant reported a 3 for amusement and 5 for disgust relative to a specific film clip, the MinFeel score would thus be 3, as it is the minimum shared score between amusement (3) and disgust (5). Thus, the higher the MinFeel score, the greater the intensity of the mixed feeling of *amusement* and *disgust*. The MinFeel score addresses our current empirical focus, i.e., investigating the degree to which participants subjectively experienced a mixed emotion, and has been validated in previous studies (Kreibig et al., 2013, 2015; Schimmack, 2001).

To determine any significant variation within the different conditions according to perceived amusement and disgust, we conducted a repeated measures ANOVA with within-subjects factor Film Clip (Positive, Mixed, Negative, Neutral) and Emotion (separate mean emotional ratings of amusement and disgust for each film clip type). As a manipulation check, we then ran a repeated measures ANOVA on MinFeel scores, investigating a main effect of Film Type to determine if Mixed film clips elicited significantly greater feelings of mixed feelings (i.e., higher scores on the MinFeel measure) relative to the pure emotions film clips. Analyses were conducted using Statistical Package for the Social Sciences (SPSS, version 17).

2.4. fMRI

Functional brain images were acquired with a 3-T scanner (GE Discovery MR750) and a 32-channel Nova Medical head coil with a T2* sensitive gradient echo planar imaging (EPI) sequence to acquire 390 functional volumes across six functional runs from 41 oblique slices (TR=2000 ms, TE=30 ms, voxel size 2.9 mm^3, 77° flip angle, FOV=24.9 cm^2, 86×86 acquisition matrix, 2.9 mm slice thickness with no gaps). We minimized head-movement with foam padding. To acquire high-resolution T1-weighted images for anatomical normalization we used a 3D-fast spoiled gradient-recalled with inversion recovery (IR-Prep) sequence (TR=6.96, TE=2.61, inversion time= 450 ms, voxel size 1mm^3, 12° flip angle, FOV=24.0 cm^2, 240×240 acquisition matrix, 160 axial slices, 1 mm slice thickness). Image processing and statistical analyses were conducted using high performance computing at University of Geneva on the "Baobab" cluster, a dedicated resource for advanced scientific computing.

Preprocessing of the fMRI data was effectuated using the standard procedures implemented in SPM12 (www.fil.ion.ucl.ac.uk/spm) (see Supplementary Materials). At the first level, two principal general linear models were designed for the fMRI data of each participant. The first model was designed to investigate the main effect of Film Clip (Positive, Mixed, Negative, Neutral). The second model was designed to measure the parametric modulation (PMOD) of elicited subjective feelings (amusement, disgust, MinFeel). For the Film Clip analysis, a first-level model was designed using the six conditions with film clips of varying durations. Four film clip types were paired with natural viewing instructions: (i) Positive; (ii) Mixed; (iii) Negative; and (iv) Neutral. As this study is nested in a larger ongoing research project on emotion regulation, the two additional conditions were paired with emotion regulation instructions. Given that emotion regulation remains outside the purview of the present study, these two conditions were not modeled at the second-level. Rather, they served as regressors of non-interest and thus improved the precision of the models for this study (see also Supplementary Materials for a detailed explanation).

For the PMOD analysis, first-level models were designed for each of the three subjective feeling scores, along with one regressor of interest (amusement, disgust, or MinFeel). These models included all four film clip types (Positive, Mixed, Negative, Neutral) for a main effect of the PMOD regressor (PMOD-Main) or one PMOD of interest only (e.g., amusement) for one film type only (e.g., Mixed) (PMOD-Film Type).

The second (group) level proceeded according to the specific analysis of interest (Film Clip, PMOD). For the Film Clip analysis, we wished to investigate the effect of Film Clip type (four dynamic natural viewing film clip types: Positive, Mixed, Negative, Neutral), looking in particular at the effect of Emotion (Positive+Negative <> Neutral, Positive>Neutral, Negative>Neutral, Mixed>Neutral), Mixed Emotions (Mixed <> Positive+Negative) and Valence (Positive <> Negative). A flexible factorial design was thus created, testing for Film Clip type with Subject as a random-effects factor (cf. Gläscher and Gitelman 2008).

For the PMOD analysis, we wished to discern the effect of the subjectively perceived emotion (amusement, disgust, MinFeel). We aimed to investigate this across all four film clip types (PMOD-Main) as an overall main effect of the PMOD. We also wished to investigate this separately for the three valenced film clip types (Positive, Mixed, Negative) (PMOD-Film Clip) as this analysis would allow a direct comparison between conditions. For instance, the contrast Mixed-MinFeel vs. Positive/Negative-MinFeel should discern the BOLD activation specific to increased mixed feelings during mixed films relative to both the Positive and Negative film clips.

More specifically, for the PMOD-Main analysis, we conducted a one-sample *t*-test correlating BOLD variation during all four film clip types with the average of each participant's PMOD score. For these one-sample *t*-tests, we measured BOLD variation, averaged across all four film clip types, as a function of each participant's score from one specific PMOD (amusement, disgust, or MinFeel). In order to conduct the PMOD-Film Clip analysis, we conducted separate one-sample *t*-tests, measuring BOLD variation during either one film clip type (e.g., Positive) or as an average across a combination of film clip types (e.g., Positive, Negative), depending on the analysis of interest. This combination included Positive only, Mixed only, Negative only, and Positive+Negative only. For two-sample *t*-tests, we used the latter individual valenced film clips to compare neural specificity for certain film clips with regards to subjectively experienced emotion. That is, we contrasted two of these one-sample *t*-tests (e.g., Mixed and Pure [positive+negative]) for one PMOD regressor (e.g., MinFeel). These analyses would thus provide insight into the unique variance of BOLD activity attributed specifically to the PMOD regressor within the condition of interest (e.g., Mixed MinFeel vs. Pure MinFeel).

Second-level analyses and multiple comparison corrections were implemented using SPM12. Analyses were conducted using 2nd level weightings at the group-level using weighted contrasts, thus ensuring all contrast vectors are fully balanced. Effects from all analyzes (Condition and PMOD) were reported using a minimum of $p < .05$ cluster-level FWE-correction, with a cluster-forming threshold at voxel-level $p < .001$ (i.e., *p*-FWEc<0.05). When appropriate, in order to increase anatomical precision due to oversized cluster sizes, we implemented a stricter threshold of cluster-forming threshold at voxel-level *p*-FWE<0.05 (i.e., *p*-FWE<0.05). Peak cluster locations of all analyses are reported using the Montreal Neurological Institute (MNI) coordinates. Labels of neural regions were defined with the aid of the Harvard-Oxford Cortical-Subcortical Structural Atlas (Goldstein et al., 2007) and the probabilistic cerebellar atlas (Diedrichsen et al., 2009). Interpretations of results were informed using a data-driven approach facilitated by the Neurosynth neuroimaging data platform (Yarkoni et al., 2011).

3. Results

3.1. Behavioral measures

When examining the self-report emotion measures, we observed a main effect of Film Type (*F*(2, 79)=211.98, $p < .001$, partial η^2=0.862, sphericity not assumed), whereby Neutral film clips were rated as significantly less disgusting than Positive ($t = 5.395$, $p < .001$), Mixed ($t = 10.097$, $p < .001$) and Negative film clips ($t = 20.425$, $p < .001$). We observed no main effect of Emotion (*F*(1, 34)=0.81, *p*=.374), whereby participants did not perceive the film clips as significantly more amusing or disgusting overall. We did, however observe a Film Type × Emotion interaction effect (*F*(2, 71)=211.93, $p < .001$, partial η^2=0.862), whereby Positive (i.e., amusing) film clips were rated as significantly more amusing and less disgusting than Negative (i.e., disgusting) film clips, which were, in turn, rated as significantly less amusing and more disgusting than Positive film clips (Fig. 1A). These data thus validate the effect of our Positive and Negative conditions.

Next, we ran a repeated measures ANOVA on MinFeel scores, investigating a main effect of Film Type. We observed a significant effect (*F*(2, 63)=35.58, *p*<.001, partial η^2=0.511), where Mixed film clips elicited significantly higher MinFeel (mean 1.93 +/- 0.51) than Positive (1.31 +/ - 0.23), Negative (1.46 +/- 0.53) and Neutral (1.05 +/- 0.09) film clips (Fig. 1B). This latter finding confirms Mixed film clips' success in eliciting greater mixed feelings (i.e., ambiguity).

3.2. fMRI

3.2.1. Condition

In our fMRI data analysis, we first tested any main effects of Film Type (Positive, Mixed, Negative, Neutral). Specifically, we computed the effects of *Emotion* (Positive+Negative vs. Neutral), *Mixed Emotion* (i.e., Mixed vs. Positive+Negative) and *Valence* (Positive vs. Negative). Given the scope of the current study, the effects of *Emotion* are reported visually in the Supplementary Materials.

Emotion. We observed a widespread effect of Emotion, whereby emotional film clips (Positive and Negative), compared to Neutral film clips, elicited significantly greater neural activity in the superior frontal gyrus (SFG), dorsomedial prefrontal cortex (dMPFC), orbitofrontal cortex (OFC), mid frontal gyrus (MFG), amygdala, brain stem extending into the thalamus, temporoparietal junction (TPJ), fusiform gyrus, superior parietal lobe (SPL), precuneus, and cerebellum (*p*-FWE<0.05, Supplementary Materials, Table S1A). Looking more specifically at each film clip type, Positive, relative to Neutral, film clips elicited greater activity in the striatum (putamen), precentral gyrus, amygdala, mid temporal gyrus (MTG), brain stem, and fusiform gyrus (*p*-FWE<0.05, Table S2A). Negative, relative to Neutral, yielded elevated activity in the frontal pole, dorsomedial prefrontal cortex (dMPFC), SFG, OFC, superior temporal gyrus (STG), brain stem, TPJ, and cerebellum (*p*-FWE<0.05, Table S2B).

Mixed emotions. Mixed, relative to Neutral, film clips, elicited greater activity within the inferior frontal gyrus (IFG), temporal pole, SFG, brain stem, MTG, TPJ, cerebellum, fusiform, and lingual gyrus (*p*-FWE<0.05, Table S2C). When directly comparing (Mixed) and Pure (Positive + Negative) film clips, however, we observed significantly greater neural activity in the SFG, precuneus and posterior cingulate cortex (PCC) (Fig. 2A, Table 1A) (*p*-FWE<0.05). Conversely, compared to Mixed film clips, Pure (Positive + Negative) film clips elicited greater neural activity in the superior and mid temporal gyri (STG and MTG) (Fig. 2B, Table 1B) (*p*-FWEc<0.05).

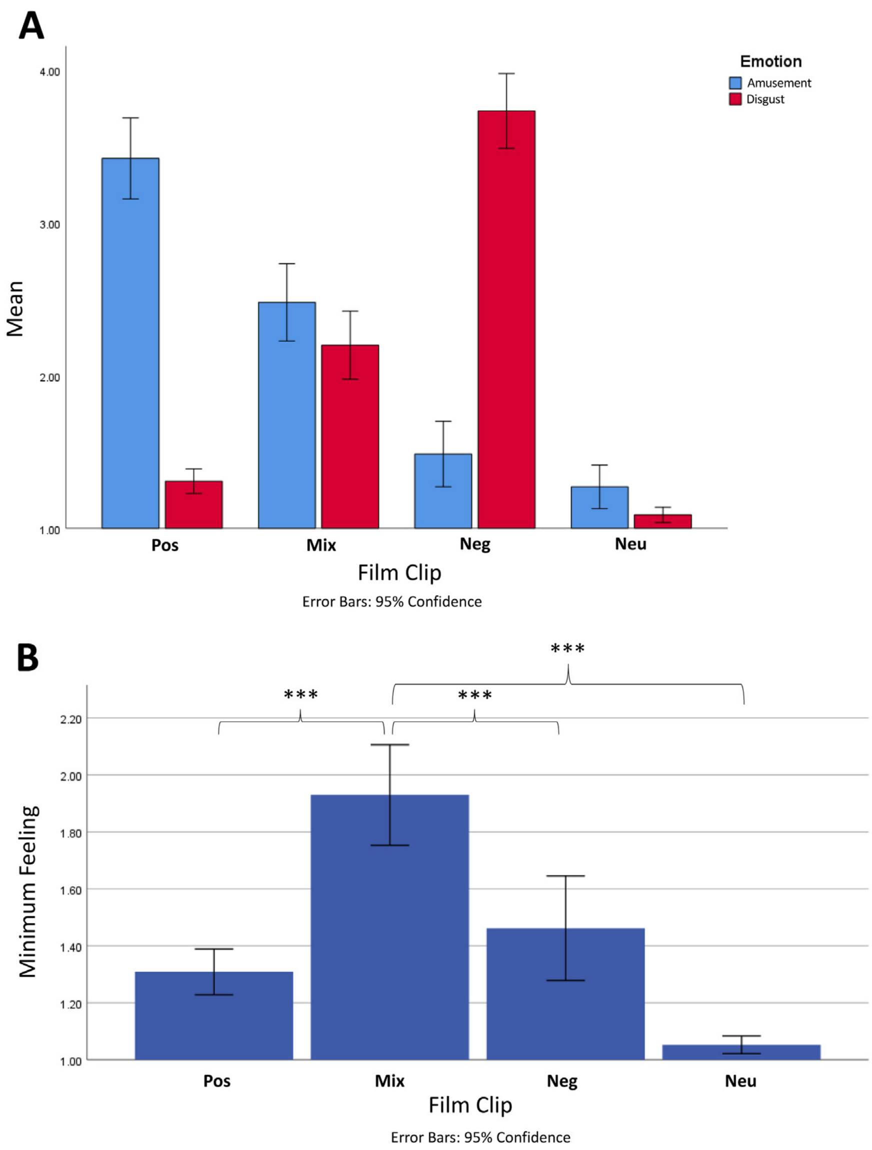

Fig. 1. Mean ratings of amusement, disgust, and minimum feeling for four film clip type conditions (Positive, Mixed, Negative, and Neutral). Scores ranged on a 5-point Likert scale from 1 (very low) to 5 (very high). (A) Mean ratings for amusement and disgust across four film clips. (B) Mean ratings for minimum feeling across four film clip type conditions. Findings show the Mixed condition to elicit significantly greater minimum feeling than all other film clip type conditions. Error bars are presented at 95% confidence levels. *** $p < .001$. Abbreviations. Mix: Mixed emotions film clip type, Pos: Positive film clip type, Neg: Negative film clip type, Neu: Neutral film clip type.

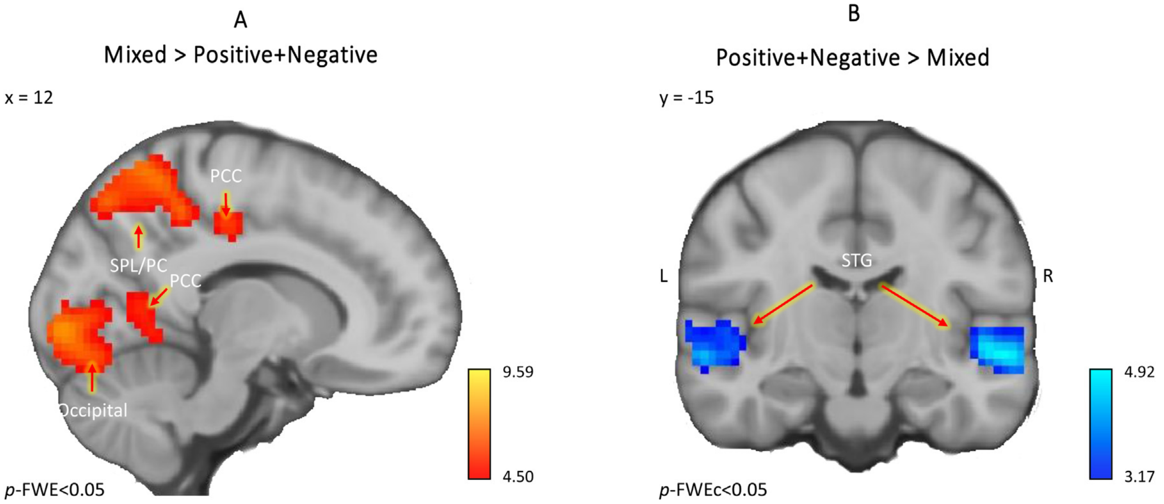

Fig. 2. Main effect of *Mixed Emotions*. (A) Significantly elevated blood oxygen-level-dependent (BOLD) activity when comparing Mixed to Positive and Negative film clips (p-FWE<0.05, $k = 00$ voxels). (B) Significantly elevated BOLD activity when comparing Positive and Negative to Mixed film clips (p-FWEc<0.05, $k = 293$ voxels). Color bars represent t-values. Abbreviations. FWE: family-wise error correction, k: cluster-level extent threshold (voxels), PC: precuneus, PCC: posterior cingulate cortex, p-FWE: cluster-forming family-wise error corrected threshold at voxel-level $p<.05$, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p<.05$, with a cluster-forming uncorrected threshold at voxel-level $p<.001$, SPL: superior parietal lobe, STG: superior temporal gyrus.

Table 1
Main effect Mixed Emotions. Table illustrates blood oxygen-level-dependent response to main effect of Mixed relative to Positive and Negative film clips (A) Mixed film clips contrasted against pure emotional film clips (p-FWE<0.05, k = 05). (B) Pure emotional (Positive and Negative) contrasted against Mixed film clips (p-FWEc<0.05, k = 293). Abbreviations. FWE: family-wise error correction, hem: hemisphere, k: cluster-level extent threshold (voxels), L: left, p-FWE: cluster-forming family-wise error corrected threshold at voxel-level $p < .05$, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$, R: right.

				MNI Coordinates		
Region/Sub-Region	Hem	k	T	x	y	z
(A) Mixed > Positive+Negative						
Fusiform Gyrus	L	3406	9.59	-27	-45	-15
Lateral Occipital Cortex	L		8.19	-12	-63	57
Fusiform Gyrus	R		8.05	27	-42	-18
Superior Frontal Gyrus	L	115	6.68	-21	-3	57
Superior Frontal Gyrus	R	85	5.96	27	0	57
Posterior Cingulate Cortex	R	46	5.66	12	-24	42
Precuneus	L	15	5.07	-21	-60	12
(B) Positive+Negative > Mixed						
Superior Temporal Gyrus	L	397	4.92	-57	-15	-6
Mid Temporal Gyrus	L		4.38	-60	-39	0
Superior Temporal Gyrus	L		4.14	-54	3	-12
Mid Temporal Gyrus	R	293	4.48	54	-27	-3
Superior Temporal Gyrus	R		4.44	60	-15	-6
Planum Polare	R		4.11	51	-6	-6

In alignment with our first aim, we then examined whether there were differences in activation specificity as a function of mixed vs. pure emotions. We thus conducted two-sample t-tests separately comparing Mixed to Positive film clips and Mixed to Negative film clips. When comparing Mixed to Positive film clips, we observed significant and robust neural activity within the SFG and MFG, PCC, precuneus, SPL and brainstem (p-FWE<0.05) (Fig. 3Ai, Table 2A). When compared to Negative film clips, Mixed film clips elicited significantly greater neural activity within the occipital lobe only (p-FWE<0.05) (Fig. 3Bi, Table 2C). Inversely, when contrasted against Mixed film clips, Positive film clips elicited more neural activity within the MTG, amygdala, posterior insula, and lateral orbitofrontal cortex (p-FWE<0.05) (Fig. S2A, Table S3A), whereas Negative, relative to Mixed, film clips yielded no significant results. These data thus show robust neural differences between mixed and positive clips whereas differences between mixed and negative clip appear limited.

Finally, we observed an effect of valence, whereby Negative, relative to Positive, film clips elicited significantly greater neural activity within the MFG, dorsal lateral prefrontal cortex (dLPFC), precentral gyrus, SFG brain stem, inferior temporal gyrus, cerebellum, and parieto-occipital sulcus extending into the SPL precuneus, PCC and lingual gyrus (PCC) (p-FWE<0.05, Fig. 3Bi, Table 2C). Inversely, Positive, relative to Negative, film clips elicited significantly more neural activity within the temporal pole, parahippocampal gyrus, hippocampus extending into the amygdala, precentral gyrus, posterior insula, and MTG and STG (p-FWEc<0.05, Fig. 3Bii, Table 2D).

3.2.2. Parametric modulation (PMOD)

In alignment with our second aim, we next investigated the BOLD variation related to subjective feeling (amusement, disgust, MinFeel). We thus first tested any linear modulation of our three feeling scores on all four film conditions (Positive, Mixed, Negative, Neutral), as a main effect of the parametric modulator (PMOD) using one-sample t-tests. We then contrasted the effect of each PMOD across film type conditions using two-sample t-tests.

PMOD: main. We observed a main effect of amusement across all four conditions, with increasing amusement correlating significantly with increased neural activity within the temporal pole, precentral gyrus, amygdala/hippocampus, MTG and STG and angular gyrus, (p-FWE<0.05) (Fig. 4Ai, Table 3A). Inversely, decreasing amusement correlated with increasing activation in the cuneus, supracalcarine cortex, and lateral occipital cortex (p-FWEc<0.05) (Fig. 4Bi, Table 3B). Disgust correlated positively with the precentral gyrus, inferior frontal gyrus, SFG brain stem, fusiform gyrus, cerebellum, and parieto-occipital sulcus extending into the precuneus and PCC (p-FWE<0.05, Fig. 4Aii, Table 3C), while it correlated negatively with the precentral gyrus, central opercular cortex, and posterior insula (p-FWEc<0.05, Fig. 4Bii, Table S3D). Finally, MinFeel correlated positively with the SPL, precuneus, PCC, and premotor cortex (p-FWE<0.05) (Fig. 4Aiii, Table 3E). There were no significant negative correlations with MinFeel.

PMOD: condition. Finally, we contrasted the parametric modulation effects between film clip types Mixed > Positive + Negative as a function of the different feeling scores. This aims at testing mixed emotions by probing how one emotion rating varies in movies congruent or not with this emotion. When comparing Mixed against Pure (Positive+Negative) film clips, higher amusement ratings correlated with increased precuneus/SPL activity (p-FWE<0.05) (Fig. 5A, Table 4), with no significant findings for the inverse correlation. For disgust ratings, however, a floor effect was observed with the Amusement film clips, whereby several participants rated these films with the lowest disgust rating possible (i.e., 1), thus preventing us from comparing disgust in the Amusement conditions relative to other conditions (e.g., Mixed-Disgust > Positive-Disgust). Therefore, to measure neural specificity of mixed emotions as a function of disgust, relative to Negative film clips only, we contrasted parametric effects of the Mixed-Disgust against Negative-Disgust ratings, which resulted in no significant activations, with the inverse contrast also yielding no significant results. This suggests that the variance of BOLD response modulated by disgust was generally shared between Mixed and Negative (i.e., disgusting) film clips. We observed no significant results for any other contrast or PMOD.

4. Discussion

In this study, we sought to identify the neural specificity of mixed emotions relative to their pure constituent emotions, by comparing BOLD variation when viewing social film clips that elicit both amusement and disgust to those that elicit only amusement or disgust, respectively. Our findings show that when compared to unambiguous social scenes (i.e., mostly amusing or disgusting), ambiguous social emotional scenes (mix of amusing and disgusting) elicited consistent neural activity in the precuneus/SPL and PCC. We observed this not only through direct contrasts of ambiguous against unambiguous scenes, but also from a parametric modulation of the participants' self-reported perception of mixed emotions (i.e., MinFeel), irrespective of condition. Contrary to our hypotheses, however, we did not find differential activity within the lateral frontal region. Further contrary to our hypotheses, neural responses of mixed emotions resembled disgust processing rather than resembling patterns distinct from either two pure constituent emotions. To our knowledge, this is the first study to demonstrate differential neural correlates of mixed emotions in emotionally complex, dynamic, social situations by comparing ambiguous to unambiguous social scenes, as well as by including a parametric analysis across all film clips taking into account mixed emotional states. This, therefore, allowed for the measurement of mixed emotional perceptions/states.

4.1. Mixed emotions: theory and findings

Despite prior psychophysiological evidence demonstrating results supporting the *emergence account* of mixed emotions (Kreibig et al., 2013, 2015), which postulates a distinct response pattern uniquely engaged during mixed or conflicting emotional experience, our neuroimaging results show strong topographical neural overlap between mixed emotion and disgust in the parieto-occipital sulcus,

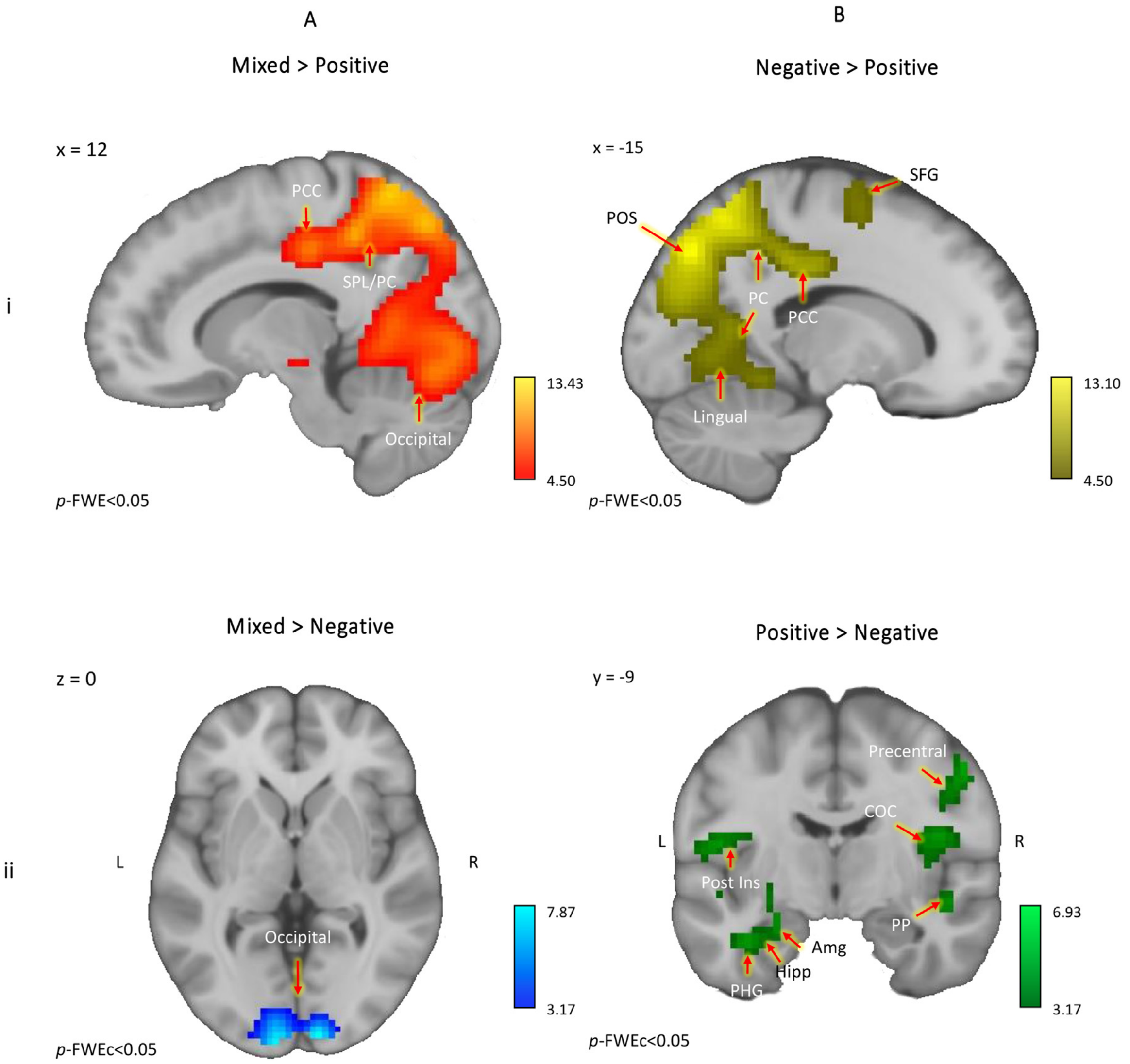

Fig. 3. Effect of Mixed Emotion and Valence. Figure illustrates blood oxygen-level-dependent activity occurring when (i) Mixed film clips are contrasted against Positive and Negative film clips, and (ii) Positive and Negative film clips are contrasted against each other. Color bars represent *t*-values. Abbreviations. Amg: amygdala, COC: central opercular cortex, FWE: family-wise error correction, Hipp: Hippocampus, PC: precuneus, PCC: posterior cingulate cortex, *p*-FWE: cluster-forming family-wise error corrected threshold at voxel-level $p < .05$, *p*-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$, PHG: parahippocampal gyrus, Post Ins: posterior insula, POS: parieto-occipital sulcus, PP: planum polare, SFG: superior frontal gyrus, SPL: superior parietal lobe, STG: superior temporal gyrus.

SPL/Precuneus, and PCC. These effects further boil down to only the precuneus when contrasting mixed emotions against pure emotions while accounting for increased amusement. Still, contrasting mixed emotions against amusement (i.e., in Positive film types) as a function of self-reports also highlights a similar activation in posterior parietal cortex, whereas no significant difference is observed when contrasting against disgust (in Negative film types). These findings may accord instead with the *differentiation account* of mixed emotions (Russell, 1980). Under this theoretical perspective, the neural pattern of mixed emotion would correspond to one of the pure constituent emotions more than a pattern reflective of a distinct emotion per se. They also support the *additive account*, where ambiguity processing is reflected as a variant of intensity in neural reactivity relative to its constituent emotion, disgust (Kreibig et al., 2013). The neural pattern does not seem to reflect a unique and distinct emotion pattern per se, however, as proposed by the *emergence account* of mixed emotions (Scherer, 1984). While this complicates the conclusions of earlier studies using psychophysiological and behavioral measures (Kreibig et al., 2013, 2015), it invites more integrative research incorporating physiological and behavioral recordings with fMRI acquisitions, which may provide insight into specific neural signatures linked to the distinctive physiological and behavioral patterns of mixed emotion as previously identified (Kreibig et al., 2013, 2015). Indeed, the generation and integration of emotional response patterns might vary across the different components of the various emotional response levels. This includes the emotional episode, particularly in terms of their peripheral physiology/autonomic effects, motor expressions, affective experience, expressive behavior, and feeling reports as opposed to their central, autonomic, endocrine reactivity (Evers et al., 2014; Mauss et al., 2005). To better understand its organizing principles thus requires a multi-level analysis approach (Cacioppo and Decety, 2011). Furthermore, future neuroimaging assessments might design novel neuropsychological testing paradigms to determine the degree to which these overlapping posterior regions are engaged by specific disgust and ambiguity features, or perhaps by more fundamental and shared processes associated with executive control functions (e.g., mental flexibility, switching, conflict monitoring).

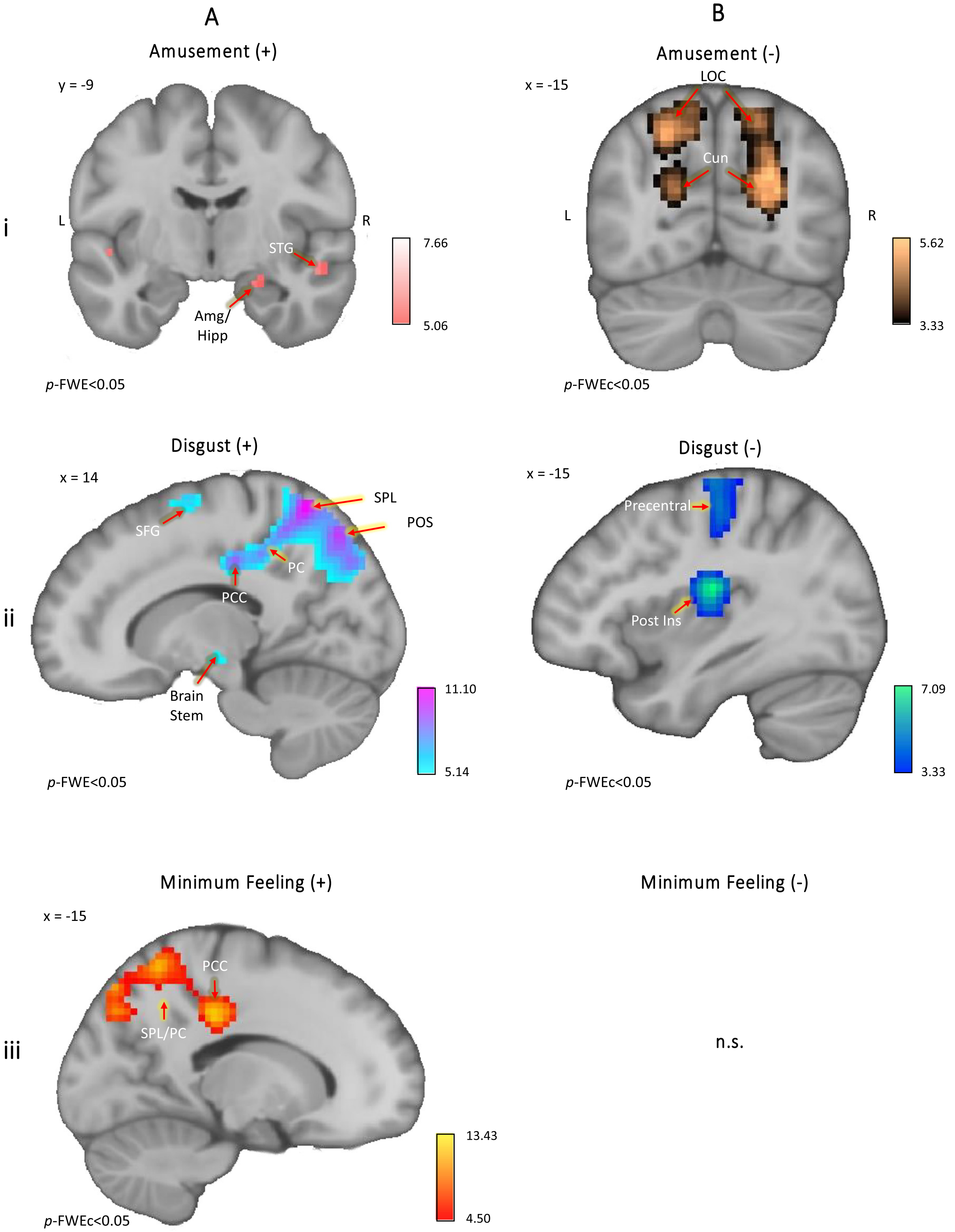

Fig. 4. Main effect of Parametric Modulators (PMODs). Figure illustrates blood oxygen-level-dependent activity correlating (A) positively and (B) negatively with PMODs (i) Amusement, (ii) Disgust and (iii) Minimum Feeling (i.e., MinFeel) across all four conditions (Positive, Mixed, Negative, Neutral). (Ai) Positive correlation with Amusement (*p*-FWE<0.05, k = 04 voxels); (Bi) Negative correlation with Amusement (*p*-FWEc<0.05, k = 408 voxels); (Aii) Positive correlation with Disgust (*p*-FWE<0.05, k = 03 voxels); (Bii) Negative correlation with Disgust (*p*-FWEc<0.05, k = 176 voxels); (Aiii) Positive correlation with Minimum Feeling (*p*-FWEc<0.05, k = 327 voxels, N = 37); and (Biii) Negative correlation with Minimum Feeling (not significant). Color bars represent t-values. Abbreviations. Amg: amygdala, Cun: cuneus; FWE: family-wise error correction, Hipp: Hippocampus, k: cluster-level extent threshold (voxels), L: left, LOC: lateral occipital cortex, n.s.: not significant, PC: precuneus, PCC: posterior cingulate cortex, *p*-FWE: cluster-forming family-wise error corrected threshold at voxel-level $p < .05$, *p*-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$, Post Ins: posterior insula, POS: parieto-occipital sulcus, R: right, SFG: superior frontal gyrus, SPL: superior parietal lobe, STG: superior temporal gyrus.

Table 2

Effect of Mixed Emotion and Valence. Table illustrates blood oxygen-level-dependent response to the effects of Mixed relative to either Positive or Negative film clips as well as to the effects of Positive versus Negative film clips. (A) Mixed contrasted against Positive film clips (p-FWE<0.05, k = 05 voxels), (B) Mixed contrasted against Positive film clips (p-FWEc<0.05, k = 391), (C) Negative contrasted against Positive film clips (p-FWE<0.05, k = 05 voxels), (D) Positive contrasted against Negative film clips (p-FWEc<0.05, k = 230 voxels). Abbreviations. FWE: family-wise error correction, hem: hemisphere, k: cluster-level extent threshold (voxels), Left, p-FWE: cluster-forming family-wise error corrected threshold at voxel-level $p < .05$, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$, R: right.

				MNI Coordinates		
Region/Sub-Region	Hem	k	T	x	y	z
(A) Mixed > Positive						
Temporal/fusiform	L	8306	13.43	-27	-48	-12
Precuneus	L		12.84	-12	-63	57
Parieto-Occipital sulcus	L		12.67	-15	-75	45
Superior frontal gyrus	L	328	10.53	-21	-3	60
Superior frontal gyrus	R	382	10.1	24	0	60
Brainstem	R	78	5.87	6	-24	-9
	R		5.1	3	-27	-18
Middle frontal gyrus	R	11	5.76	36	36	45
Brainstem	L/R	5	4.7	0	-33	-33
(B) Mixed > Negative						
Occipital pole	R	391	7.87	12	-96	0
Occipital pole	L		7.65	-9	-99	0
	R		5.9	12	-93	12
(C) Negative > Positive						
Parieto-occipital sulcus	L	7492	13.1	-15	-75	42
Lateral occipital cortex	L		12.75	-24	-78	24
	L		12.2	-15	-63	57
Precentral gyrus	R	366	10.2	27	-6	54
Superior frontal gyrus	L	268	9.67	-21	-6	60
Brain stem	R	99	6.17	3	-15	-12
Inferior temporal gyrus	R	48	5.97	48	-60	-15
Precentral gyrus	R	17	5.41	48	6	27
Mid frontal gyrus/dLPFC	R	19	5.3	36	36	45
Mid frontal gyrus/dLPFC	R		4.7	30	33	36
Cerebellum	L	7	5.14	-3	-72	-30
(D) Positive > Negative						
Precentral gyrus	R	779	6.93	15	-27	72
Precentral gyrus	L		5.8	-33	-18	69
	L		5.03	-18	-27	66
Heschl’s gyrus	R	526	6	39	-21	9
Superior temporal gyrus	R		5.1	45	-21	-3
Mid temporal gyrus	R		4.72	48	-36	-3
Central opercular cortex/posterior insula	L	585	5.77	-39	-15	18
Mid temporal gyrus	L		5.58	-63	-39	-3
Parahippocampal Gyrus	L	230	4.69	-36	-6	-27
Hippocampus	L		4.31	-24	-12	-21
Temporal pole	L		4.25	-39	6	-27

4.2. *Neural specificity: hypotheses and findings*

4.2.1. *Superior parietal lobe/precuneus*

When comparing Ambiguous to Unambiguous social scenes, we observed bilateral precuneus/SPL responding. Extant literature suggests the precuneus/SPL region mediates higher-order executive processing necessary to disambiguate complex social situations. The SPL is linked to volitional control of emotional responding (Krendl et al., 2012), attentional shifting to spatially predictive social cues (Corbetta et al., 2005), and task switching with emotional stimuli (Piguet et al., 2016). It is also sensitive to contextually complex social situations (Krendl et al., 2013) and to social features (e.g., facial versus verbal information) of emotional scenes (Hofstetter et al., 2012). The latter authors showed the precuneus/SPL responds to images of homeless individuals, particularly in contexts implying that their state is uncontrollable rather than controllable, and thus potentially eliciting empathy and positive reappraisal (Krendl et al., 2013). This is also likely to require a degree of executive control, including shifts of attention, perspective taking, and emotion regulation.

In fact, the medial portion of SPL is commonly implicated in attention and spatial context processing (Walter and Dassonville, 2008), including mental imagery tasks (Andersson et al., 2019). Specifically, it is engaged by endogenous (voluntary) attentional shifting to motivationally relevant events and objects after predictive cues (Mayer et al., 2009; Mohanty et al., 2009; Stoppel et al., 2013), including social cues (Corbetta et al., 2005). As stated earlier, ambiguity possesses elements of conflicting features as well as incongruence, which demands mental flexibility (Mayr, 2001; Sussman et al., 2014) and perspective taking (Habel et al., 2007). Thus, the precuneus/SPL may facilitate the processing of emotionally ambiguous contexts via volitional emotion regulation and attentional shifting to contextually- or socially-relevant information. Together, such cognitive flexibility subtended by precuneus/SPL activation (Leber et al., 2008; Tsumura et al., 2021) could allow disambiguating complex situational contexts, via volitional attentional selec-

Table 3
Main effect of Parametric Modulator (PMOD). Table illustrates blood oxygen-level-dependent activity correlating positively and negatively with PMODs Amusement, Disgust and Minimum Feeling (i.e., MinFeel). (A) Positive correlation with Amusement (p-FWE<0.05, k = 04 voxels); (B) Negative correlation with Amusement (p-FWEc<0.05, k = 408 voxels); (C) Positive correlation with Disgust (p-FWE<0.05, k = 03 voxels); (D) Negative correlation with Disgust (p-FWEc<0.05, k = 176 voxels); (E) Positive correlation with Minimum Feeling (p-FWEc<0.05, k = 327 voxels, N = 37); and (F) Negative correlation with Minimum Feeling (not significant). Abbreviations. FWE: family-wise error correction, hem: hemisphere, k: cluster-level extent threshold (voxels), L: left, p-FWE: cluster-forming family-wise error corrected threshold at voxel-level p<.05, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level p<.05, with a cluster-forming uncorrected threshold at voxel-level p<.001, R: right.

				MNI Coordinates		
Region/Sub-Region	Hem	k	T	x	y	z
(A) Amusement (+)						
Mid Temporal Gyrus	R	331	7.66	48	-18	-12
Mid Temporal Gyrus	R		6.53	51	-33	-3
	R		6.43	60	-27	-6
Angular gyrus	L	100	6.86	-63	-54	12
Mid temporal gyrus	L		5.99	-60	-42	0
Superior Temporal Gyrus	L	102	6.39	-48	-18	-3
	L		6.18	-57	-18	-6
Supplementary Motor Cortex	R	21	6.16	6	6	66
Temporal Pole	L	25	6	-45	15	-27
Temporal pole	L		5.4	-48	12	-18
Precentral Gyrus	R	5	5.69	51	0	48
Amygdala/Hippocampus	R	4	5.43	21	-9	-18
Heschl's Gyrus	L	7	5.3	-39	-30	3
(B) Amusement (-)						
Supracalcarine Cortex	L	721	5.62	-21	-66	15
Lateral occipital cortex	L		5.61	-24	-69	27
Cuneus	L		5.34	-21	-63	51
Parieto-occipital sulcus	R	408	5.51	18	-75	48
Cuneus	R		4.66	18	-69	21
Lateral occipital cortex/Parieto-occipital	R		4.4	12	-69	57
(C) Disgust (+)						
Lateral Occipital Cortex/Superior parietal lobe	R	3146	11.1	12	-57	66
Parieto-occipital sulcus	L		10.52	-15	-78	42
Superior parietal lobe	L		10.21	-15	-57	66
Brain Stem	R	277	8.83	3	-24	-6
	L/R		7.93	0	-18	-12
	L		7.49	-12	-18	-9
Superior Frontal Gyrus	R	180	8.4	27	0	57
Superior Frontal Gyrus	L	100	7.5	-21	-6	63
Precentral Gyrus	L		7.13	-15	-6	72
Cerebellum	L	7	6.95	-33	-45	-36
Temporoparietal Junction	L	100	6.67	-54	-36	27
Precentral Gyrus/Inferior Frontal Gyrus	R	26	6.57	48	9	30
Fusiform Gyrus	L	50	6.52	-27	-51	-12
Cerebellum	L	35	5.97	-3	-72	-9
	R		5.69	6	-72	-12
Fusiform Gyrus	R	19	5.87	24	-66	-15
Fusiform Gyrus	R	3	5.4	27	-57	-9
(D) Disgust (-)						
Posterior Insula	L	176	7.09	-36	-18	18
Precentral Gyrus	R	1145	6.25	18	-27	66
Central Opercular Cortex	R		5.46	45	-12	18
Precentral Gyrus	R		5.26	54	-9	45
(E) Minimum Feeling (+)						
Precuneus/Superior Parietal Lobule	R	635	4.97	12	-75	54
Lateral occipital	R		4.56	24	-72	30
	R		4.5	33	-75	21
Posterior cingulate	L	327	4.59	-15	-30	39
Superior parietal lobe	L		4.47	-15	-57	60
Lateral occipital	L		4.33	-15	-78	51
(F) Minimum Feeling (-)						
Not significant						

tion of relevant elements encountered in ambiguous scenes that elicit mixed emotions.

In addition, processing and regulating one's response to emotionally ambiguous social scenarios may induce a degree of emotional interference, thus requiring inhibition of predominant emotional responses (e.g., disgust). The precuneus/SPL is indeed linked to cognitive-affective conflict processing, shifting attention away from (i.e., ignoring) irrelevant emotional stimuli (Vetter et al., 2015) or between task-relevant emotionally stimuli (Piguet et al., 2016). While this was shown in adolescents, activation in precuneus/SPL is also observed during similar

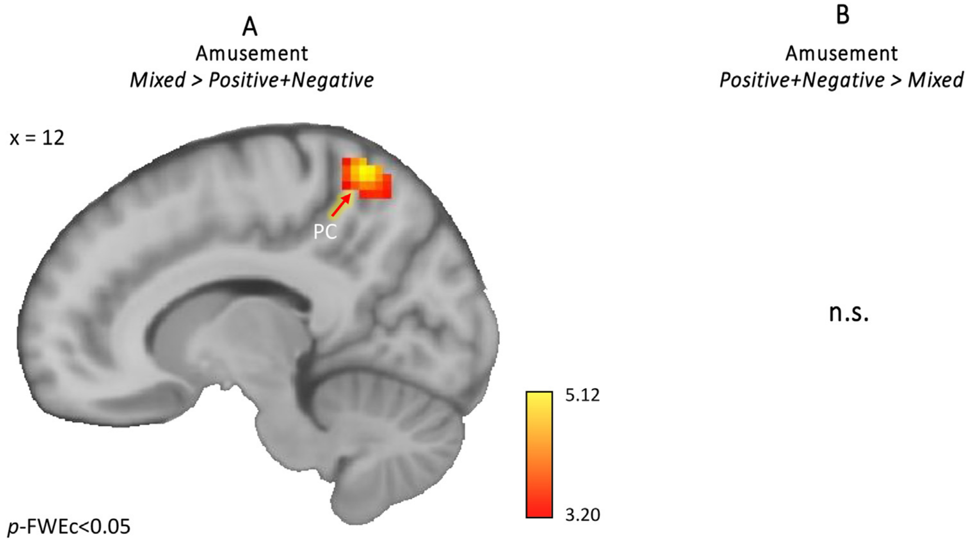

Fig. 5. Effect of Condition in *Amusement*. Figure illustrates contrasts between two regressions: blood oxygen-level-dependent (BOLD) activity during Mixed film clips as a function of increasing Amusement and BOLD activity during Pure (i.e., Positive + Negative) film clips as a function of increasing Amusement. (A) BOLD activation during Mixed versus Pure film clips, as a function of increasing amusement (p-FWEc<0.05, k = 366 voxels). (B) BOLD activation during Pure versus Mixed film clips, as a function of increasing amusement (not significant). Color bars represent t-values. Abbreviations. FWE: family-wise error correction, k: cluster-level extent threshold (voxels), n.s.: not significant, PC: precuneus, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$.

Table 4

Effect of Condition in *Amusement.* Table illustrates contrasts between two regressions: blood oxygen-level-dependent (BOLD) activity during Mixed film clips as a function of increasing Amusement and BOLD activity during Pure (i.e., Positive + Negative) film clips as a function of increasing Amusement. (A) BOLD activation during Mixed versus Pure film clips, as a function of increasing amusement (p-FWEc<0.05, k = 366 voxels). Abbreviations. FWE: family-wise error correction, hem: hemisphere, k: cluster-level extent threshold (voxels), L: left, p-FWEc: cluster-forming family-wise error corrected threshold at cluster-level $p < .05$, with a cluster-forming uncorrected threshold at voxel-level $p < .001$, R: right.

				MNI Coordinates		
Region/Sub-Region	Hem	k	T	x	y	z
(A) Amusement: Mixed > Positive+Negative						
Superior parietal/precuneus	R	366	5.12	12	-54	66
Parieto-occipital sulcus/precuneus	R		3.96	18	-72	48
Lateral occipital/superior parietal	R		3.73	24	-57	42
(B) Amusement: Positive+Negative > Mixed						
Not significant						

conflict processing in adults, although not specific to emotional stimuli (Chechko et al., 2013), and appears exaggerated in patients with mood disorders due to impaired emotion regulation abilities (Piguet et al., 2016). Accordingly, increased precuneus/SPL activity is also linked to multi-tasking (Deprez et al., 2013), rule reversal learning (Votinov et al., 2015), and error monitoring (Wright et al., 2013), suggesting a general role in mental flexibility demands for mental schema manipulations from conflicting socio-affective information (Habel et al., 2007). Adjusting initial interpretations to accommodate new and potentially conflictual information is a critical component of disambiguation (cf. Beer 2012), and may thus critically engage the precuneus/SPL during mixed emotions.

Taken together, these data converge to indicate that the capacity to disambiguate complex social situations may require an acute ability to perceive and maintain divergent affective cues while evaluating various visuo-spatial contextual indices in the effort to adequately interpret the social situation and thus guide one's own social behavior. In keeping with this, we witness the involvement of medial posterior regions consistently implicated in top-down cognitive processes linked to perspective taking, attentional orienting, and cognitive flexibility during disambiguation of affectively complex, dynamic, social situations.

4.2.2. *Lateral frontal*

Our hypothesis of prefrontal regions being implicated in the processing of ambiguity was not supported by our data. Such activations were expected based on prior studies showing the lateral frontal area to respond to conflicting emotional expressions (Ross et al., 2013) and ambiguous faces (Nomura et al., 2003), although these studies presented static stimuli only. The lack of lateral frontal sensitivity to social ambiguity in our study may be due to the recruitment of these regions when our participants observed disgusting or amusing film clips in non-ambiguous scenes (see Fig. S2). The demands of attentional control and emotion regulation, known to elicit lateral frontal regions (Ochsner et al., 2012), may be strong enough in these conditions to annul any additional effect of ambiguity when the same type of emotion (i.e., disgust) is also present to a certain degree.

4.2.3. *Posterior cingulate*

We also observed increased bilateral PCC to respond consistently during social ambiguous video clips, relative to clips with unambiguous social situations. Extant literature suggests this region is implicated in both social (Knutson et al., 2008; Turella et al., 2009) and affective (Morawetz et al., 2017) processing. The PCC may be particularly sensitive to contextual features (e.g., position, association) of emotional stimuli (Mattson et al., 2014), which may act to facilitate orientation toward specific elements within social scenes (Zhang et al., 2012). It also appears to be particularly responsive to observed social behaviors (Turella et al., 2009) as well as expressed emotions (Britton et al., 2006; Immordino-Yang et al., 2014). For instance, the PCC was reported to activate to social emotion when comparing both positive and negative versus neutral social events in short film clips (Britton et al., 2006).

Further, evidence suggests activity within PCC dissociates from higher-order executive processing. First, the PCC is an established hub in the default mode network (Fox et al., 2005; Vincent et al., 2006), suggesting a contribution to low-level affective processing of internal mental schema. In contrast, in task-based paradigms, it is inhibited during higher-order planning (Boghi et al., 2006), unfamiliar (>familiar) viewing angles (Schendan and Stern, 2008), error (>correct) monitoring (King et al., 2010), and working-memory demands (Habeck et al., 2005; Woodward et al., 2013). Taken together, we surmise this PCC region may subserve basic affective responding necessary to process familiar social schema in the attempt to disambiguate emotionally complex social scenes.

4.3. Clinical implications

The capacity to adequately interpret ambiguous social situations implies adaptive social behavior critical for social bonding and affiliation. Such capacity is impaired in socially anxious individuals (Stopa and Clark, 2000), where the processing of social ambiguity often results in subjective feelings of threat (Gerrans and Murray, 2020). This ultimately results in symptomatic behavior, such as safety behaviors and withdrawal (Zimmer-Gembeck and Nesdale, 2013). Our understanding of social anxiety symptoms and the neural underpinnings of social disambiguation would therefore greatly benefit from future research employing similar designs in socially anxious individuals through the presentation of dynamic social scenes of varying socio-affective ambiguity.

4.4. Limitations and future directions

The current study successfully distinguished neural regions likely modulated by varying intensity of mixed emotions. However, its methods are not without limitations. While our mixed feeling scores (MinFeel) measure the presence and intensity of mixed emotion, it cannot measure the degree of ambiguity. As it is a minimum score, it may be the case that one perceived emotion significantly differed from the other. For instance, a participant may have a MinFeel score of three. This would hide the fact that, in this example, the degree of disgust is five while amusement is three. The degree of ambiguity would thus be less in this instance than if both scores (amusement, disgust) were actually three. There is thus greater dominance of one emotion relative to the other in the first instance, which the MinFeel score cannot ascertain. We chose to calculate a MinFeel score, nonetheless, as it allowed us to measure the shared intensity of both amusement and disgust. This validated method (Kreibig et al., 2013, 2015; Schimmack, 2001) allowed us to address our second aim to investigate the degree to which mixed emotions modulate BOLD response during the viewing of social film clips.

An additional limitation is the small number of participants showing variation of disgust during the Amusement condition. This, fortunately, illustrates that Positive film clips successfully elicited one pure emotion of amusement, relative to disgust. However, given most participants rated several Positive film clips with a disgust rating of 1, we could not model BOLD responses in this condition with our participants. This also prohibited us from conducting analyses where Positive film clips were included individually in a contrast, as a function of disgust. Nonetheless, our analyses being focused on mixed emotions, we were able to achieve our second aim of comparing Ambiguous to Unambiguous film clips, as a function of either amusement or disgust.

It is worth noting that the two emotional states, amusement and disgust, which we used in the current study, reflect affective states with opposite valence, i.e., they are located at opposite ends of a bipolar valence dimension. We chose these emotions for optimal juxtaposition between them in the mixed emotional condition (cf. Hemenover and Schimmack 2007). The fact that amusement and disgust are of opposite valence, may, however, have favored (Russell's, 1980) Circumplex Model. Complementary studies should test the predictions advanced in the present study with emotions matched not only on arousal but also on valence (e.g., fear and anger for negative emotions).

4.5. Conclusions

Our results reveal mixed emotions (i.e., both amusement and disgust) in social settings produce significant activation in the precuneus/SPL and PCC compared to their pure constituent emotions (i.e., principally amusement or principally disgust). This is supported by results showing that the BOLD response in this region increases as a function of experienced mixed emotions (simultaneous amusement and disgust). Despite this specificity, the pattern of neural responding to ambiguity also partly overlaps with disgust processing, and may thus suggest that the neural representation of mixed emotions reflects one of the pure constituent emotions rather than a distinct emotion per se. Still, future testing should consider the likely increase of executive demands when processing either disgust or ambiguity. Activity within the neural regions specific to mixed emotions suggests increased demands for perspective taking, cognitive flexibility, contextual integration, as well as social-emotional processing likely involved in disambiguating relatively complex social situations. The precuneus/SPL may be key to facilitating executive and attention processes linked to domain-general disambiguation of emotional social cues. Besides, the PCC may also be required to facilitate the disambiguation of dynamic situations in which complex social and affective contextual cues are present. Taken together, these findings may help future clinical research in untangling the neural mechanisms underlying impairments in social ambiguity processing, often witnessed in disorders such as social anxiety. To our knowledge, our results are the first to shed light on the dedicated neural processes involved in dynamic social ambiguity processing. They suggest both higher- and lower-order processes may be needed to process emotionally complex social scenes.

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Data and code availability statement

Our data are currently not openly available, as they are being analysed for a different study. The Matlab scripts and codes used to conduct our analyses are available here: https://osf.io/j5a4u/. These were elaborated using Matlab 2011.

Ethical standards

The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional committees on human experimentation and with the Helsinki Declaration of 1975, as revised in 2008.

Declaration of Competing Interest

None.

Credit authorship contribution statement

Ryan J. Murray: Formal analysis, Writing – original draft. **Sylvia D. Kreibig:** Conceptualization, Data curation, Writing – review & editing. **Corinna Pehrs:** Formal analysis. **Patrik Vuilleumier:** Formal analysis, Writing – review & editing. **James J. Gross:** Conceptualization, Writing

– review & editing. **Andrea C. Samson:** Conceptualization, Data curation, Formal analysis, Writing – review & editing.

Data Availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119973.

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