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Individual Differences in the Evaluation of Ambiguous Visual and Auditory Threat-related Expressions

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ABSTRACT

This study investigated the neural correlates of the judgement of auditory and visual ambiguous threat-related information, and the influence of state anxiety on this process. Healthy subjects were scanned using a fast, high-resolution functional magnetic resonance imaging (fMRI) multiband sequence while they performed a two-alternative forced-choice emotion judgement task on faces and vocal utterances conveying explicit anger or fear, as well as ambiguous ones. Critically, the latter was specific to each subject, obtained through a morphing procedure and selected prior to scanning following a perceptual decision-making task. Behavioural results confirmed a greater task-difficulty for subject-specific ambiguous stimuli and also revealed a judgement bias for visual fear, and, to a lesser extent, for auditory anger. Imaging results showed increased activity in regions of the salience and frontoparietal control networks (FPCNs) and deactivation in areas of the default mode network for ambiguous, relative to explicit, expressions. In contrast, the right amygdala (AMG) responded more strongly to explicit stimuli. Interestingly, its response to the same ambiguous stimulus depended on the subjective judgement of the expression. Finally, we found that behavioural and neural differences between ambiguous and explicit expressions decreased as a function of state anxiety scores. Taken together, our results show that behavioural and brain responses to emotional expressions are determined not only by emotional clarity but also modality and the subjects' subjective perception of the emotion expressed, and that some of these responses are modulated by state anxiety levels.

1. INTRODUCTION

Neural systems involved in processing explicit emotions have been well-researched over the past several decades, highlighting the consistent recruitment of key regions such as the prefrontal cortex (PFC), anterior cingulate cortex (ACC), anterior insula (AI) and the amygdala (AMG, Lindquist et al., 2012; Phan et al., 2002; Phillips et al., 2003). Much of our understanding today has progressed from early days of investigating the neural response to fearful facial expressions, predominantly of the AMG (Aubé et al., 2015; Breiter et al., 1996; Morris et al., 1996; Van der Zwaag et al., 2012; Vuilleumier et al., 2001). There now exists a more comprehensive understanding of how emotions are processed, including, for example, the co-recruitment of distributed neural regions (Lindquist et al., 2012; Wager et al., 2015; Whitehead & Armony, 2018), recruitment of the AMG in processing both positive and negative affect (Fitzgerald et al., 2006) as well as processing emotional expressions in varying domains, such as bodies (de Gelder et al., 2004; Grèzes et al., 2007; Hadjikhani & de Gelder, 2003; Peelen et al., 2007; Pichon et al., 2009) and voices (Whitehead & Armony, 2019; Aubé et al., 2015; Fecteau et al., 2007; Herrmann et al., 2016; Phillips et al., 1998). Nonetheless, as most previous studies have employed explicit, prototypical expressions, little is currently known as to how these regions are involved in processing ambiguous emotional signals. Such findings are of relevance given that more of our day-to-day emotional interactions lack clarity and require greater attentional demands, as compared to the perception of explicit emotions within a laboratory setting, often perceived, at least by healthy individuals, with perfect or near-to-perfect accuracy.

In one of the few studies to investigate the neural response to emotional ambiguity, Neta et al. (2013) presented facial expressions of surprise (as well as emotionally ambiguous scenes) interpreted as either positive or negative, in a decision-making task of perceived valence. Their functional magnetic resonance imaging (fMRI) findings demonstrated an increased signal change in both the cingulo–opercular network (or salience network; SN), a region involved in perceptual decision-making (Chand & Dhamala, 2016, 2017; Keuken et al., 2014), and the ventral AMG, when judging the valence of ambiguous stimuli (these stimuli were not divided in the analysis as a function of how they were subjectively perceived). Interestingly, recruitment of the AMG here seems to contradict its reported negative association with increased task-difficulty (Critchley et al., 2000; Hariri et al., 2000; Lange et al., 2003). That is, meta-analysis findings have

demonstrated AMG inhibition in the context of emotional perception during task-based versus passive designs, whereby the former elicits greater demand for cognitive resources (Costafreda et al., 2008). These findings could be explained by Wyble et al.'s (2008) neural network model, which posits that a tradeoff must be made between the cognitive demands of a task and the emotional salience of the stimulus, given the limited attentional resources available. That is, with the increasing challenge of a task, attention may be redirected towards the cognitive aspect and away from the emotional salience of the stimulus. Consistent with this model, Thielscher and Pessoa (2007), who also investigated perceptual decision-making of emotionally ambiguous faces using morphs of fear through neutral to disgust expressions, observed a linear decrease in AMG activation as a function of increased neutral contribution to the morph (and increased task difficulty). Moreover, they reported enhanced activity in regions of the SN, such as bilateral insula/inferior frontal gyrus, and ACC, as well as the left middle frontal gyrus (part of the frontoparietal control network, FPCN), in response to perceptual decision-making during the more challenging task of judging neutral expressions. One caveat is that in these studies the classification of stimuli as ambiguous was based on an a priori selection (surprised or neutral expressions). That is, the degree of perceived emotional ambiguity (and task difficulty) was not equated, or controlled, across participants.

In addition to task demands, the perceptual judgement of an ambiguous emotion has shown to be influenced by individual differences in state (Qiao-Tasserit et al., 2017) and/or trait anxiety (Park et al., 2016; Qiao-Tasserit et al., 2017). Specifically, anxious individuals show a greater tendency to perceive ambiguous faces (e.g. surprise and happy–fear morph) as negative. The neural correlates of this relation remain to be determined, although the AMG is likely to play a role, as previous studies have shown that high anxiety is associated with increased AMG activity in response to viewing explicit emotional faces (Bishop et al., 2004; Dickie & Armony, 2008; Stein et al., 2007), as well as with altered attention–emotion interactions (e.g. greater distractibility by task-irrelevant stimuli) and the associated underlying functional processes (see, for review, Dolcos et al., 2020).

As these studies of emotional ambiguity focussed on facial expressions, it remains unclear whether similar effects would be observed in other modalities, such as audition. In one of the few studies to employ ambiguous auditory stimuli, Bestelmeyer et al. (2014) used a two-alternative forced-choice (2AFC) paradigm, in which subjects were required to select either fear or anger when presented with fear–anger morphed vocal expressions. Consistent with previous studies, activity in a distributed network, including regions within the SN, FPCN and default mode network (DMN), as well as occipital and temporal areas, was related to the process of emotional judgement (i.e. averaged participant's behavioural response), whereas the activity of the AMG and auditory cortices was instead associated with changes of emotional clarity or salience (i.e. morph step). However, as they did not specifically examine responses to ambiguous expressions, the question posed earlier remains unanswered.

Thus, we conducted an fMRI study to directly investigate behavioural and neural responses to ambiguous visual and auditory emotional expressions, hypothesising a comparable recruitment of regions historically associated with attention and salience detection, such as those in the SN, FPCN and DMN. To do so, we presented subjects with morphed (fear to anger) expressions of facial and vocal expressions in a 2AFC paradigm. Critically, before scanning, we calculated each subject's *point of subjective equality* (PSE), that is, the morph level that is perceived as maximally ambiguous (i.e. corresponding to the morph that would elicit fear or anger responses 50% of the trials, see Section 2). We then created the visual and auditory stimuli corresponding to that morph level, which were then used in the fMRI experiment for that subject, together with explicit expressions of fear and anger. We also investigated whether, and how, individual differences in anxiety modulated behavioural judgements and neural responses to these subject-specific ambiguous stimuli.

2. MATERIALS AND METHODS

2.1 Participants

Thirty right-handed, healthy volunteers (age: M = 25 years old, SD = 3.2; 16 female) with no self-reported history of neurological or psychiatric illness, and normal audition and normal or corrected-to-normal vision, participated in the fMRI study. The sample size was determined based on previous studies, using comparable paradigms and/or analysis approaches, conducted by our group (Whitehead & Armony, 2018, 2019, 2022) and others (Bestelmeyer et al., 2014;

Duggirala et al., 2022; Thielscher & Pessoa, 2007). The study was approved by the McGill University Faculty of Medicine Research Ethics Office, in accordance with the Declaration of Helsinki.

2.2 Measures of State Anxiety

Subjects completed the state anxiety subscale (transitory mood; 10-item) of the Spielberger State–Trait Personality Inventory (STPI; Spielberger et al., 1995) before starting the experiment. The STPI, derived from the unidimensional State–Trait Anxiety Inventory (Spielberger, 1983), requires subjects to score the intensity of described feelings (e.g. 'I feel nervous') using a 4-point Likert scale ($1 = Not \ at \ All$; 2 = Somewhat; $3 = Moderately \ So$; $4 = Very \ Much \ So$). The state subscale requires subjects to respond based on feelings experienced *right now, at this very moment*. Results were used to relate subject-specific anxiety levels to behavioural and neuroimaging findings of the current study. The reliability and validity of the STPI have been confirmed (see, for review, Boyle et al., 2015; Spielberger & Reheiser, 2009) and have been previously used as a measure of anxiety in healthy subjects (e.g. Loebach Wetherell et al., 2002; Matthews et al., 2011; Smith et al., 2007).

2.3 Stimuli

Vocal stimuli consisted of brief emotional interjections (Duration: M = .68 s; SD = .22 s) using the French vowel ah (/a/) produced by one male and one female actor (Belin et al., 2008). Vocal expressions, hereafter referred to as vocalisations, of fear and anger were used as the prototypical emotions from which 99 intermediate steps on a fear–anger continuum were obtained through morphing. Morph stimuli were created using STRAIGHT software (Kawahara et al., 1999), where intermediate morphing steps were obtained through re-synthesis determined by the linear interpolation of time–frequency landmark templates (F0, frequency and amplitude; Figure 1). Stimuli were monaural, but presented binaurally, and resampled to 32 bits, at a sample rate of 44,100 Hz. Furthermore, stimuli were adjusted for loudness by normalising to the short-term loudness (STL) maximum using the Moore and Glasberg Loudness model (Glasberg & Moore, 2002), as implemented in the Loudness Toolbox in MATLAB ver. R2015b.

Faces of two individuals (one female) expressing fear and anger were selected from the KDEF

database (Lundqvist et al., 1998). Hair around the exterior of the face was removed from the images, which were further altered using Adobe Photoshop CS5.1 (Adobe Systems, San Jose CA) to attain uniform face size, resolution and contrast (Sergerie et al., 2006, 2007). Similar to auditory stimuli (Figure 1), 99 equally spaced intermediate morph steps along a fear–anger continuum were created using FantaMorph 5 (Abrosoft http://www.fantamorph.com/). Visual stimuli were presented for 1 s (determined during pilot testing to yield >95% mean accuracy in classifying the emotion expressed by the original, 100% prototypical emotions).

2.4 Procedure

2.4.1 Pre-scan Session: Subject-specific Stimulus Selection

Subjects initially completed a two-alternative forced-choice task outside of the scanner to determine the morph level corresponding to their own subjective perception of emotionally ambiguous stimuli, which would be then used during the *Scan* session that followed (see below). Participants were presented with voices (auditory run) or faces (visual run) of one identity, using Psychtoolbox-3 implemented in MATLAB (Brainard, 1997; Pelli, 1997), and asked to judge the emotion that they perceived to be expressed by the actor. The words '*Fear*' and '*Anger*' were presented on either side of the screen (locations pseudo-randomised across trials), and subjects made a response by pressing the mouse (left or right button) in accordance with the emotion they chose, after which the subsequent stimulus was presented. The task consisted of two auditory and visual runs, with an additional practice run prior to testing. An option to repeat the practice run was given. The order of runs, in terms of modality and stimulus identity (two identities per modality: one male and one female), was counterbalanced across subjects. Subjects received verbal and written instructions for the task through Psychtoolbox-3.

Morph steps were presented on a scale of percent-anger from 0% anger (i.e. 100% fear) to 100% anger (i.e. 0% fear). In each unimodal run, 17-morph steps (0%, 10%, 20%; 25%; 30%; 35%; 40%; 45%; 50%; 55%; 60%; 65%; 70%; 75%; 80%; 90%; 100% anger) were presented 15 times each, except for the continuum extremes (0% and 100% anger: 7 times; 10% and 90% anger: 8 times). Differences of presentation numbers for these morphs were based on pilot studies, which showed that their classification was highly consistent within and between subjects. Stimulus presentation was fully balanced with equal number of first-order transitions between different

morph steps (Brooks, 2012). Each run lasted on average 14 min, with no significant differences in duration between modalities.

After the task, a psychometric function was fitted to the data of each modality with a logistic curve, using the Palamedes toolbox (Prins & Kingdom, 2018) implemented in MATLAB, from which the PSE, corresponding to the morph that would elicit equal proportion of anger and fear responses, was calculated. Then, the three subject- and modality-specific stimuli from the 101-morph continuum closest to 45%, 50% and 55% anger responses derived from the psychometric curves were identified and used in the *Scan* session as emotionally *ambiguous* exemplars. The extreme morphs (80%, 90% and 100%) representing prototypical expressions of fear and angerwere used as emotionally *explicit* stimuli during the scan session (see Figure 1).

[FIGURE 1]

2.4.2 Scan Session Behavioral Task

The same two-alternative forced-choice task as in the *pre-scan* session was used during scanning, with the exception that auditory and visual stimuli were presented intermixed and that the inter-stimulus interval was 4 s. Each of the four runs consisted of six presentations of nine morph steps of each modality (see Figure 1), grouped as *explicit fear* (0%, 10% and 20% anger morph), *ambiguous* (subject-specific pre-scan 45%, 50% and 55% anger responses; see above) and *explicit anger* (80%, 90% and 100% anger morph). Stimuli were pseudo-randomised with equal probability transitions across morph steps and modalities. The participants responded to the stimuli using an MRI-compatible two-button mouse. Prior to the scan session, auditory and visual tests were conducted to ensure subjects could comfortably hear and see the stimuli and press the buttons.

fMRI Acquisition and Preprocessing

Functional images were acquired in a 3T Siemens Magnetom Prisma-Fit scanner with a 32channel head coil using a continuous multi-band accelerated pulse sequence with a factor of 12 (Setsompop et al., 2012). Multiband sequences have been shown to yield increased statistical power, at the expense of reduced signal-to-noise-ratio (SNR) (e.g. Bhandari et al., 2020; Chen et al., 2015; but see Demetriou et al., 2018). The experiment was divided into four similar runs, each consisting of 1000 volumes (72 slices per volume, interleaved acquisition; $FOV = 208 \times 208 \text{ mm}^2$, matrix = 104 × 104, voxel size = 2 × 2 × 2 mm^3; TR = 529 ms; TE = 35 ms) and lasting approximately 8 min. The first 10 scans of each run were discarded from the analyses. A high-resolution T1-weighted image (voxel size = 1 × 1 × 1 mm³) was acquired using a magnetisation-prepared rapid acquisition gradient echo (MPRAGE) sequence (192 slices, TR = 2.3 s; TE = 3 ms) for anatomical co-registration.

Image pre-processing was conducted using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm), as in our previous studies (Whitehead & Armony, 2018, 2019). Briefly, images were realigned to the first volume of the first run, normalised to the Montreal Neurological Institute (MNI) 152 template and for the univariate analysis, and smoothed using a 6 mm full width at half maximum (FWHM) isotropic Gaussian kernel.

2.5 Data Analysis

2.5.1 Behavior

Responses to explicit anger and fear expressions from the *Pre-scan* and *Scan* sessions were entered in a generalised linear mixed-effects model with a logit link function, with session (Pre-scan/Scan), modality (Visual/Auditory) and emotion (Anger/Fear) as within-subject factors, using the *lme4* library (Bates et al., 2015) implemented in *R*. Subjects' state anxiety score was included as a covariate. For the specification of random effects, we used a maximal structure including by-subject random intercepts and slopes of within-subjects fixed factors to maximise the modelling generalisability (Barr et al., 2013). When significant interaction effects were found, we conducted post hoc tests using the *emmeans* R library (Lenth, 2020). Correction for multiple tests was applied to *p*-values when appropriate, using the Holm–Bonferroni method (Holm, 1979) and reported as *p*_{HB}.

A similar analysis was conducted for the subject-specific ambiguous stimuli. However, as these stimuli were derived from a fitted psychometric curve and thus not necessarily presented during the pre-scan session, we did not include session as a factor and, instead, only analysed the responses during the scan session and compared them to the expected value of .5 (that is, the

subjects' PSE).

Response times (RTs) during scanning were used as an indirect measure of task difficulty, and thus as a marker for cognitive load (Deupree & Simon, 1963). They were log-transformed and entered in a linear mixed-effects model. Only 'correct' responses were included in the case of explicit expressions (i.e. anger responses to Anger and fear responses to Fear). Thus, the model included modality (visual/auditory), emotional clarity (explicit/ambiguous) and response (fear/anger) as within-subject factors.

2.5.2 Univariate FMRI Data Analysis

Univariate General Linear Model

Subject-specific statistical analysis was performed in SPM12 using a univariate general linear model (GLM) with four categories of interest for each modality, as function of the a priori emotion category (Anger, Fear and Ambiguous) and subject's response (Anger or Fear): Anger/Anger, Fear/Fear, Ambiguous/Anger and Ambiguous/Fear. That is, in the case of explicit emotions, only correct responses were included (any incorrect or no-response trials were included as additional covariates of no interest). Each stimulus was represented as a boxcar of a length equal to its duration and convolved with the canonical haemodynamic response function. Subject-specific conditions were averaged across the four runs and, taken to a second level, repeated-measures GLM. Regions responding significantly differently to ambiguous and explicit expressions were obtained by computing the corresponding contrasts. As previous studies have shown that task difficulty modulates both so-called *task-positive* (i.e. positive responses relative to baseline) and *task-negative* (i.e. negative responses relative to baseline) regions (Chand & Dhamala, 2016), we used the overall main > 0 and main < 0 contrasts to distinguish activations from deactivations, respectively. That is, we used both [(Ambiguous > Explicit) \cap Main > 0] and [(Ambiguous \leq Explicit) \cap Main \leq 0)] contrasts to identify voxels responding significantly more to ambiguous than explicit expressions (and vice versa). Statistical significance was determined using a voxel threshold of p = .05, corrected for multiple comparisons with a family-wise error rate (FWE) computed through Gaussian random field theory.

Post-hoc Linear Mixed Models

Post-hoc linear mixed models (LMMs) were conducted using the mean absolute value of parameter estimates for each contrast, with modality (Auditory vs. Visual), emotion judgement (Fear vs. Anger) and emotional clarity (Ambiguous vs. Explicit), and Network as within-subject factors. The within-subject factor 'Network' was defined by assigning significant voxels to one of the seven functional cortical networks (visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal and default) defined in Yeo et al. (2011) from resting-state connectivity analyses. Additionally, subjects' state anxiety score was included as a covariate in the LMMs. The random structure of the models, and the procedure for unpacking interactions through post-hoc tests, was similar to that described for RTs.

2.5.3 Multivariate fMRI Pattern Analysis

We conducted a complementary whole-brain multivariate pattern analysis to assess whether explicit versus ambiguous emotional stimuli could be accurately distinguished based on the overall brain activation patterns they elicited (Whitehead & Armony, 2019). Specifically, preprocessing and first level analysis was performed as for the univariate analysis, with the exception that volumes were only moderately smoothed using a 2-mm FWHM isotropic Gaussian kernel (Gardumi et al., 2016). Condition- and subject-specific parameter estimates (betas) obtained from the univariate GLM were averaged across the four runs and used in a multivariate pattern analysis conducted in PRoNTo (Schrouff et al., 2013). A mask of the cerebrum formed by 90 regions (excluding cerebellum and vermis) of the Automated Anatomical Labelling (AAL; Tzourio-Mazoyer et al., 2002) atlas was used. A binary support vector machine classifier with a Gaussian kernel was trained to identify activity patterns across voxels, as extracted from mean beta images (SVM; Burges, 1998), using the LIBSVM implementation (Chang & Lin, 2011). A leave-one-subject-out (LOSO) cross-validation was conducted, and classification accuracy was obtained (Schrouff et al., 2018). Model performance was evaluated with a p = .05 threshold, calculated using 1000 permutations of the training labels. Weights per voxel were computed a posteriori (Schrouff et al., 2013) and identification of regions contributing greatest to classifications performed by identifying the top 1% positive and negative weights, with a minimum size of 10 neighbouring voxels. The associated *p*-value for each voxel weight was calculated through permutation testing, where the condition labels were randomised (N=1000) and weight maps acquired from each classification (Whitehead & Armony, 2019).

Model performance was evaluated based on classification accuracy, area under the receiver operating characteristic (ROC) curve (AUC), and the sensitivity and specificity of the classification. Although the experimental design used here may not be optimal for multivariate analysis (in turn, a design optimal for mulvariate analysis will likely not be so for univariate analysis), this approach enables directly testing whether the processing of ambiguous expressions is indeed carried out by a distributed set of regions.

3. RESULTS

One male subject was removed because of poor behavioural performance, whereas three subjects (two female) were removed as they scored above normative values for their corresponding age group in measures of state anxiety (Spielberger, 1995). Thus, data from 26 subjects (14 female) were entered in the analyses.

3.1 Behaviour

Subjects' mean state anxiety score was 18 (SD = 3.6, range 12–25). Group-averaged responses (% anger) to explicit anger and fear expressions from the *pre-scan* and *scan* sessions, as well as stimuli perceived as ambiguous during *scan* sessions are reported in Table 1. The group-averaged PSEs for visual and auditory stimuli in the pre-scan session were 60.8% (SD = 6.8%) and 47.5% (SD = 6.3%) anger morph, respectively (Figure 2a; t[25] = 6.62, p < .001, d = 1.63), with no significant correlation between modalities (r = -.22, p = .24). As expected, the RTs exhibited an inverted U-shape pattern centred on the subjects' PSE (Figure 2b). This was confirmed statistically by a significant correlation between the individual subjects' PSE and their morph step with largest RT (Visual: r = .57, p = .002; Auditory: r = .79, p < .001). There were no significant differences in response times (logRT) as a function of the response (Anger/Fear) for the morph step closest to each subject's PSE (Visual: t(25) = .38, p = .71; Auditory: t(25) = .25, p = .80).

[TABLE 1]

Responses to explicit expressions of fear and anger were entered in a generalised LMM with session (Pre-scan/Scan), emotion (Anger/Fear) and stimulus modality (Visual/Auditory) as

within-subject factors, and subjects' state anxiety score was included as a continuous betweensubject factors. There was an expected main effect of emotion (more anger responses to angry than fearful expressions, $\chi^2 = 763.89$, p < .0001), as well as emotion-by-session ($\chi^2 = 7.56$, p = .006), emotion-by-session-by-anxiety ($\chi^2 = 4.86$, p = .027) and emotion-bymodality-by-session-by-anxiety ($\chi^2 = 6.10$, p = .014) interactions. Post-hoc tests revealed that these effects were because of an increase in 'errors' when judging facial expressions (i.e. fear responses to explicit anger and vice versa) during scanning, compared to the pre-scan session, as a function of state anxiety scores ($p_{BH} = .004$; see Figure 2a).

Analysis of responses to subject-specific ambiguous expressions during the scanning session revealed a main effect of modality ($\chi^2 = 6.17$, p = .01). Post-hoc tests showed that this effect was because of the fact that, whereas responses to ambiguous voices remained at chance level (M = .48, SE = .02, p = .36), there was a significant increase in fear responses to ambiguous faces (M = .68, SE = .02, p < .0001).

A LMM for logRTs during scanning, with modality, emotional clarity (explicit/ambiguous) and response (anger/fear) as within-subject factors, and state anxiety scores as a parametric betweensubjects factor, revealed a main effect of modality [$\chi^2 = 70.82$, p < .0001: faster responses for visual than auditory stimuli]; emotional clarity [$\chi^2 = 152.48$, p < .0001: faster for explicit than ambiguous stimuli] and state anxiety [$\chi^2 = 6.85$, p = .009: faster for higher anxiety scores]. There were also significant modality-by-response [$\chi^2 = 25.29$, p < .0001: faster fear responses for faces (p < .02) and the opposite for voices (p = .04)], modality-by-emotional clarity $[\chi^2 = 6.$ 00, p = .014; larger difference for voices than faces], response-by-emotional clarity $[\chi^2 = 28.57, p < .0001;$ larger difference for anger than fear responses] and emotional clarity-byanxiety [$\chi^2 = 9.83$, p = .002: decreasing difference in RT between ambiguous and explicit expressions as a function of anxiety] interactions. Interestingly, further three-way interactions revealed that the anxiety modulation of RTs was particularly evident in the case of visual stimuli (modality-by-emotional clarity-by-anxiety interaction, $\chi^2 = 5$. 85, p = .016) and for those perceived as fearful (response-by-emotional clarity-by-anxiety interaction, $\chi^2 = 6.83$, p = .009), although the four-way interaction was not statistically significant, suggesting an additive effect. Consistent with this, a significant negative correlation between ambiguous minus explicit logRT

and anxiety was observed only in the case of ambiguous faces perceived as fearful, when correcting for multiple comparisons ($p_{BH} = .009$; Figure 2c).

In summary, during the scan session, subjects tended to judge ambiguous and angry faces as expressing fear more often and faster, especially those experiencing higher levels of anxiety. Subjects also responded more quickly to faces perceived as fearful, while in contrast, voices were more quickly perceived as angry.

[FIGURE 2]

4. FMRI DATA ANALYSIS

4.1 Univariate Analysis

Significant clusters of activity for the contrasts Ambiguous versus Explicit expressions are reported with their coordinates, *z*-scores, and cluster extents in Table 2. Greater *activation* in response to Ambiguous than Explicit emotional expressions was observed bilaterally in several frontal regions—including the bilateral supplementary motor area (SMA), superior frontal gyrus (SFG), ACC, the dorsolateral PFC (dlPFC) and AI, as well as the inferior parietal lobe (IPL) and occipital activity. The majority (81.4%) of the significant voxels were located within three of the seven-network cortical parcellation derived by Yeo et al. (2011) from resting-state data: the FPCN (43.1%), ventral attention (26.5%; also known, and referred henceforward, as salience, SN; Seeley et al., 2007) and visual (VN; 11.9%) networks (Figure 3a and Table 2).

[TABLE 2]

Greater *deactivation* observed in response to Ambiguous as compared to Explicit Emotion was located within the bilateral ventromedial PFC (vmPFC), angular gyrus, precuneus and posterior cingulate cortex (PCC), as well as in the bilateral middle temporal gyrus and fusiform gyrus (FG; Figure 3a). Most of these voxels (74.6%) were located within the DMN.

Clusters exhibiting significantly greater *activation* in response to Explicit than Ambiguous Emotion conditions included the right AMG and bilateral superior temporal sulcus (STS; Figure 3a).

For completeness, and to identify any modality-specific regions involved in the evaluation of ambiguous expressions, we conducted supplementary analyses for each modality separately. The only additional region observed was in the right auditory cortex (superior temporal gyrus: [x,y,x] = 52-4 0, z = 5.38, $K_E = 28$) which responded more to explicit vocal expressions. Post-hoc analysis revealed an interaction with emotion, as the difference, although significant for both, was larger for anger than fear (F[1,72]-4.95, p = .03).

[FIGURE 3]

4.2 Linear Mixed Models

The voxels where the (absolute) magnitude of the response to the ambiguous expressions was significantly larger than to explicit ones were assigned to one of the four resting-state networks (SN, FPCN, DMN and VN; see Section 2 for details), and the network- and session-averaged parameter estimates entered in a LMM with modality, emotion judgement, emotional clarity and network as within-subject factors, and state anxiety as a covariate. In addition to the expected significant effect of emotional clarity (F[1672] = 409.31, p < .001), there was a network-by-modality interaction (F[1, 672] = 96.89, p < .001) with greater activity for visual than auditory stimuli in the VN and the opposite for the other three networks. There were also interactions between emotion judgement and both modality (F[1, 672] = 5.07, p = .025) and emotional clarity (F[1, 672] = 6.72, p = .010), because of stronger responses to expressions judged as angry, compared to fearful, for visual (p = .009) and ambiguous (p = .004) stimuli, respectively. Finally, a triple modality-by-emotional clarity-by-anxiety interaction (F[1, 672] = 6.82, p = .009) was mainly driven by a decreasing difference between emotion intensities (ambiguous minus explicit) in the visual modality as anxiety scores increased (Figure 4b).

[FIGURE 4]

A similar analysis for the cluster in the right AMG obtained in the contrast Explicit minus Ambiguous expressions yielded, in addition to the main effect of emotional clarity (F[1144] = 65.04, p < .001), interactions between modality and emotion judgement (F[1, 144] = 5.31, p = .022), as well as a triple interaction among emotion clarity level, emotion judgement and modality (F[1, 144] = 7.89, p = .006). The latter was because of a larger AMG response to ambiguous auditory expressions when these were judged as angry compared to fearful (p = .004), with the opposite pattern for visual stimuli (p = .04), as shown in Figure 5a. Additionally, subjects' state anxiety scores interacted with emotional clarity (reduced difference between explicit and ambiguous expressions for higher scores; F[1, 144] = 10.53, p = .001) and emotion judgement (overall larger response to expressions perceived as angry; F[1144] = 10.53, p = .001; see Figure 5b).

The cluster located in the STS revealed significant effects of emotional clarity (F[1, 144] = 76.28, p < .001) and modality (F[1,24] = 31.30, p < .001), as well as an interaction between these factors (F[1, 144] = 11.35, p = .001). The latter was because of a larger difference between visual explicit and ambiguous expressions than their auditory counterparts (Figure 5a).

[FIGURE 5]

4.3 Multivariate Analysis

The model performance of Ambiguous versus Explicit emotion perception yielded an above chance classification accuracy of 85.1% (p < .001), with an AUC of 0.90, true positives for ambiguous stimuli of 74.0%, and true positives for explicit expressions of 96.1%, and kappa = .7. There was no significant difference in accuracy for visual and auditory stimuli (82% and 88%, respectively, p = .2). The clusters corresponding to the top 1% of voxels that contributed the greatest weight to the classification included frontal regions (e.g. SMA, dlPFC and insula), superior parietal lobe, thalamus, lingual and parahippocampal gyri. As observed in the univariate analysis, the majority of these clusters were located within the frontoparietal control (46.3%), salience (10.9%) and visual (9.0%) networks. In contrast, voxels in the DMN seem to play a lesser role in the accurate classification of ambiguous expressions, as only 5.7% of the top 1% contributing (negative) weights were located in regions associated with that network. Other top negative weights came primarily from the AMG, extending into the parahippocampal gyrus, and fusiform gyrus, with contributions from voxels located in the cuneus, putamen and caudate, as

well as lingual, posterior superior and mid-temporal gyri (Figure 3b and Table 3).

[TABLE 3]

5. DISCUSSION

The aim of the study was to use high spatial- and temporal-resolution fMRI to explore the behavioural and neural processing of ambiguous versus explicit threat-related expressions across auditory and visual modalities. We observed a recruitment of regions within task positive and default mode networks when judging the emotion displayed by ambiguous facial and vocal expressions. The task positive network encompassed frontal regions, such as the bilateral SMA, SFG, ACC, the dlPFC and AI, as well as the IPL and occipital activity, whereas recruitment of regions in the default mode network included the bilateral vmPFC, angular gyrus, precuneus and PCC, as well as in the bilateral middle temporal gyrus and fusiform gyrus. Activity in these regions was modulated not only by emotional clarity (ambiguous vs. explicit expressions) but also modality (auditory vs. visual) and the subjects' subjective perception of the emotion expressed (fear vs. anger). The AMG, in contrast, responded more strongly to explicit expressions of emotion but was also modulated by the subjects' subjective judgement of ambiguous expressions. Finally, we showed that state anxiety dynamically interacts with the two opposing systems: higher scores were associated with greater recruitment of regions within networks involved in salience detection, visual processing, attention, decision-making, faster response times, and an increasingly similar magnitude of the AMG's response to explicit and ambiguous expressions. In the succeeding texts, we describe these results in more detail and discuss their possible implications.

5.1 Processing of Ambiguous and Explicit Emotional Expressions

Behavioural data confirmed that during scanning, subjects were more uncertain about the emotion expressed by visual and auditory ambiguous stimuli, as evidenced by less consistent and slower responses, compared to the explicit ones. The increased response time to ambiguous expressions agrees with previous studies (Bestelmeyer et al., 2014; Ito et al., 2017; Wang et al., 2017) and likely reflects the increased difficulty in disambiguating subtle emotional expressions (Deupree & Simon, 1963).

Results from univariate and multivariate analyses of the fMRI data were consistent with this interpretation. Indeed, most of the cortical areas engaged during emotional evaluation of ambiguous expressions, some of which were also reported to respond to ambiguous affect in previous studies (Bestelmeyer et al., 2014; Thielscher & Pessoa, 2007), belonged to taskpositive (Salience, Frontoparietal and Visual Networks) and task-negative networks (Default Mode Network) (Fox et al., 2005) typically associated with problem solving, decision-making and other cognitively demanding tasks (Boyatzis et al., 2014; Keuken et al., 2014). The salience network, responding to level of subjective salience elicited by a stimulus or task (Menon, 2015; Menon & Uddin, 2010; Peters et al., 2016), is actively involved in perceptually judging ambiguity and uncertainty (Lamichhane et al., 2016a, 2016b; Lamichhane & Dhamala, 2015; Neta et al., 2013). The FPCN, recruited during problem-solving and decision-making tasks (Sridharan et al., 2008), functions by modifying and sustaining relevant information in working memory (see, for review, Menon, 2011). These two networks present opposing activity to the default mode network, which is often active at rest, and involved in self-reference, mentalising and theory of mind (Mars et al., 2012). Suppression of this network is commonly observed in situations requiring greater cognitive or attentional demands (Binder et al., 1999; Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997), a potentially relevant process for perceptual decision-making tasks of increasing difficulty (Chand & Dhamala, 2016; McKiernan et al., 2003; Ruff et al., 2010).

The pattern of involvement of the visual network in the perceptual judgement of ambiguity was distinct from above-mentioned networks, as it was mainly active during judgement of visual stimuli. This may be a product of late-stage processing of attention-directed eye movements during decision-making (see, for review, Orquin & Loose, 2013). It may also reflect a sustained response of the visual cortex during visual working memory and/or visual attention (see, for review, Sreenivasan et al., 2014; faces specifically, Nelissen et al., 2013), or from using strategies of visual imagery (Keogh & Pearson, 2011). In contrast, the magnitude of responses in regions of the SN, FPCN and DMN networks was significantly higher for auditory than visual expressions, which may indicate that deciding the emotion expressed by auditory expressions may have been more challenging than their visual counterparts, a hypothesis also supported by

the slower response times to voices than faces.

On the other hand, both univariate and multivariate analyses confirmed the involvement of the AMG in processing explicit emotional expression. This structure has been consistently shown to play a key role in detecting and valuating salient emotional information (see, for review, Phelps & LeDoux, 2005; Armony, 2012) and, in particular, to respond to different forms of (explicit) threat-related emotional expressions, such as faces, body postures, vocalisations and music (Lin et al., 2020; Aubé et al., 2015; Whitehead & Armony, 2019). Moreover, a modulation of AMG response to increasing levels of emotional salience was directly confirmed for facial (Thielscher & Pessoa, 2007; Wang et al., 2017) and vocal (Bestelmeyer et al., 2014) stimuli. A similar decrease in AMG response to facial expressions as a function of their ambiguity was observed in single cell recordings in neurosurgical patients (Wang et al., 2017).

Consistent with previous findings (Bestelmeyer et al., 2014), we also observed that the STS—a region involved in processing speech, faces, biological motion and audiovisual integration (Allison et al., 2000; Hein & Knight, 2008; Beauchamp, Argall, et al., 2004; Beauchamp, Lee, et al., 2004; Beauchamp et al., 2008)—was sensitive to emotional clarity and modality. This region is recognised as the hub for distributed neural processing of social perception (Lahnakoski et al., 2012), dependent upon co-activation of connecting regions and sub-systems to integrate the 'what' and 'where' of others' actions (Allison et al., 2000; Hein & Knight, 2008). The observed interaction of clarity and modality, driven by a greater difference between ambiguous expressions for faces than voices, may in part result from the sensitivity of the posterior STS to facial expressions in general (Schobert et al., 2018) or to the 'implied' biological motion associated with static emotional facial expressions (Engell & Haxby, 2007), although this remains to be further explored (for example, by manipulating eye gaze in faces and location in voices).

Behavioural and neural responses to ambiguous expressions were modulated by state anxiety scores. Specifically, anxious subjects exhibited greater engagement of the AMG when perceiving ambiguous stimuli. There is considerable evidence that activity of this structure in response to threat-related information is modulated as a function of state (Bishop et al., 2004; Somerville et al., 2004) anxiety, which has often been interpreted as reflecting an increased sensitivity to these

stimuli in anxious individuals. Consistent with this, the difference between ambiguous and explicit facial expressions decreased as a function of anxiety in cortical regions that tracked ambiguity. Thus, these findings, together with the negative correlation between response times to ambiguous stimuli and anxiety scores, support the notion of an enhanced emotional salience of ambiguous stimuli in anxious individuals.

5.2 Modality-specific Perceptual Bias in Emotional Judgments

Behavioural and imaging results suggested differences between modalities in the processing of emotionally ambiguous expressions during the scanning session, which in most cases was modulated by individual differences in state anxiety scores.

There was a fear bias when judging expressions in the visual modality: faces that represented (subject-specific) maximal emotional ambiguity before scanning were later perceived, on average, more often as fearful than angry. Importantly, these stimuli were still significantly judged as fearful less often than explicit expressions, thus ruling out a change in strategy. This shift in response bias cannot be explained either by carry-over after effects (Skuk & Schweinberger, 2013) as stimulus presentation order was fully counter-balanced, in terms of first-order transition probabilities, across modalities and morph levels. Rather, this change in response could reflect a *re-calibration phenomenon* of an already present fear bias in the judgement of ambiguous faces. Indeed, whereas the pre-scan average PSE for auditory stimuli was close to a 50% anger-fear morph, in the case of faces, a higher contribution of fear (60%) was necessary to achieve maximal perceptual ambiguity. Interestingly, this bias appeared to be more pronounced in subjects with higher scores of state anxiety: they made decisions more quickly to ambiguous facial expressions when they perceived them as fearful. Additionally, they responded more often fear to explicit angry expressions, compared to their response to the exact same stimuli in the pre-scan session. This was unlikely because of a change in perception of those stimuli, as they were still judged, the vast majority of the time, as expressing the intended emotion. Instead, we believe that these responses were mistakes towards the prepotent choice (fear) associated with the faster motor responses (as reported in subjects with high non-clinical anxiety; Ciucurel, 2012; Shrooten et al., 2012) or a result of enhanced impulsivity as previously observed in both clinical (see for review, Jakuszkowiak-Wojten et al., 2015) and non-clinical

(Xia et al., 2017) high anxiety individuals. This evidence also supports findings from Brown et al. (2017), who propose that an automatic emotional response is prioritised over the intended decision when under acute stress, which may occur in anxious individuals in the context of an MRI scan (Munn & Jordan, 2011).

The fMRI results were also consistent with a hypothesised visual fear bias: regions of the SN, FPCN and DMN that were more active for ambiguous than explicit expressions, and likely reflecting increased difficulty in their emotional assessment (see discussions earlier), responded more strongly to faces judged as expressing anger. Similar findings, and interpretation (albeit with different emotions), can be found in Sreenivas et al. (2012): in a comparable fMRI study of facial emotion recognition, the authors attributed the observed greater deactivation of the DMN and longer response times when perceiving sad and angry, versus happy, faces to differences in the degree of automaticity when processing these different emotions. That is, they suggested that processing happy expressions is less effortful and thus does not require substantial reallocation of attentional resources.

Moreover, the AMG was engaged to a larger degree by ambiguous faces when they were perceived as fearful; that is, its response in these trials was more similar to those in which an explicit emotional expression was present. Naturally, this modulation of the AMG responses to ambiguous stimuli based on the subjects' trial-specific responses reflects differences in the subjective perception of these stimuli, as their physical attributes remained unchanged (i.e. they were the exact same stimuli). This suggests that activity of the AMG may not only be modulated in accordance with the emotional salience of the stimulus but also to the perceived emotion and/or the degree of ambiguity or uncertainty. That is, contrary to the conclusions drawn by Bestelmeyer et al. (2014), our findings suggest that AMG responses are not only determined by the salience of a stimulus but also by the subject's emotional judgement of that expression at that time. This finding is in agreement with a single-cell recording study (Wang et al., 2014) in which subjects were presented with degraded happy and fearful facial expressions. The authors found that the AMG neurons that distinguished these emotions followed subjects' subjective judgements, rather than the actual emotion expressed by the face. *Similar findings were obtained for emotional angry and fearful voices, employing similar stimuli and morphing procedures as*

we did here (Zhang et al., 2022).

An emotion bias was also present in the auditory modality, albeit in the opposite direction and weaker than the visual one. Specifically, subjects responded faster to voices when having judged them as expressing anger, and their AMG responded more strongly to ambiguous auditory expressions when they were perceived as angry. However, unlike faces, judgement of ambiguous voices remained at chance levels during the scanning session, and, consistent with this, activity in SN, FPCN, DM or VN was not dependent on which emotion the voices were perceived as expressing.

Taken, together, these findings would suggest that greater resources were directed towards the more *challenging* modality-emotion pairs (visual anger and auditory fear). Previous studies investigating the judgement of morphed fear-anger facial expressions have consistently shown healthy subjects to rate ambiguous fear-anger expressions more often as fearful (Comfort et al., 2013; Graham et al., 2006; Wegrzvn et al., 2017). Findings from Comfort et al. (2013) demonstrated that coarse low- and medium-spatial frequency components are used to encode fear in facial expressions, components which are processed rapidly and possibly nonconsciously through the pulvinar, superior colliculi and AMG (Vuilleumier et al., 2003). Interestingly, Graham et al. (2006) reported that a patient bilateral AMG damage perceived ambiguous fearanger morphs as more often angry, compared to healthy controls, suggesting a potentially more innate processing of visual fear (Whalen et al., 1998). In contrast, these deficits in fear perception do not seem to extend to the auditory modality, as shown in individuals with comparable AMG lesions (Adolphs & Tranel, 1999; Bach et al., 2013). Instead, the AMG may be more sensitive to vocal expressions of anger (see for review, Frühholz et al., 2014), potentially because of its responsivity to angry prosody irrespective of attentional demands (Sander et al., 2005).

5.3 Limitations and Future Directions

Several issues need to be considered when interpreting our findings, including the limited set of stimuli used (one male and one female identity per modality), which prevented a generalisation to a variety of stimuli of both modalities. Indeed, it is possible that stimulus identity may bias

emotion perception, as evident in variability reported during emotion recognition (e.g. KDEF validation study; Goeleven et al., 2008). However, because of the technical challenges involved in morphing the available auditory expressions, it was not possible to generate vocal stimuli from several individuals to then test across subjects. Moreover, generating subject- and actor-specific ambiguous stimuli for the fMRI session required extensive testing before that session, in order to generate a reliable psychometric curve. Adding more identities would have substantially increased the duration of the experiment, leading, in turn, to a possible reduction of subjects' attention during the task. Importantly, our main objective was to explore the within-subject brain–behaviour relationship in response to ambiguous emotional information across modalities, which we believe was not substantially affected by the reduced number of stimuli. Nonetheless, future studies using a larger stimulus set (either as a between-subjects factor or across several sessions) could help confirm and extend the present findings. Additionally, the study did not investigate sex as a between-subject variable, given a larger sample size would be required to test the high-order interactions that are investigated. Obtaining a larger sample size to investigate sex differences, including interactions of subject sex with perceived gender of the actor, could provide novel insights into interactions of sex, anxiety, and emotion perception.

The assessment of state anxiety was limited to a single self-report measure, which was entered in the analyses as a between-subject variable. Multiple measures of state anxiety at different time points could reveal dynamic behavioural and neural patterns associated with possible changes in anxiety levels throughout the experiment. Moreover, as mentioned above, experimentally manipulating state anxiety as a within-subject factor would be needed to assess causality in the relation between anxiety level and brain activity and better address the important issue of reliability of individual differences in fMRI studies (Elliot et al., 2020). Future studies with clinical populations, such as those clinically diagnosed with generalised anxiety disorder (GAD), could shed light on how the observed brain-behaviour patterns may translate to those with greater symptom severity.

AUTHOR CONTRIBUTIONS

Funding acquisition was managed by Jorge L. Armony and Jocelyne C. Whitehead. Jorge L. Armony provisioned the resources, and Jocelyne C. Whitehead conducted the project

administrative tasks. The experimental design, including the conceptualisation and methodology, was developed collaboratively by Jocelyne C. Whitehead, Jorge L. Armony and Ignacio Spiousas. Scripts for behavioural data collection were written by Ignacio Spiousas, with the assistance from Jocelyne C. Whitehead and Jorge L. Armony. Data were acquired by Jocelyne C. Whitehead and Ignacio Spiousas, and curated and validated jointly by Jocelyne C. Whitehead, Jorge L. Armony and Ignacio Spiousas. Neuroimaging data were analysed by Jocelyne C. Whitehead, whereas behavioural data were analysed by Jocelyne C. Whitehead and Ignacio Spiousas, all with guidance and supervision from Jorge L. Armony. The first draft of the manuscript was written by Jocelyne C. Whitehead, whereas the subsequent drafts were reviewed and edited by Jorge L. Armony, Ignacio Spiousas and Jocelyne C. Whitehead. The final draft of the manuscript was approved by all authors.

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CONFLICTS OF INTEREST STATEMENT

The authors have no competing interests to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT

Data for the experiments reported here can be made available upon reasonable request.

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FIGURE 1: Schematic of the procedure to select subject-specific stimuli to use in the scanning session. For each modality, stimuli closest to 45%, 50% and 55% anger responses derived from the psychometric curves in the pre-scan session were obtained from a 101-step fear–anger morph continuum. Examples from visual data of two subjects are depicted to highlight the fact the ambiguous stimuli were specific to each participant. In contrast, the fear and anger explicit expressions corresponded to the objective morph steps of 0%, 10%, 20% and 80%, 90%, 100%, respectively, and thus were the same for all subjects (and between prescan and scan sessions). More details of the procedure are given in Section 2.



FIGURE 2: (a) Visual (left) and auditory (right) responses and psychometric curves of pre-scan (dotted line and diamonds) and scan (filled line and circles) responses averaged across all subjects. For illustration, subjects are median-split (blue: low; red: high) as a function of their state anxiety scores (actual analyses were conducted in a parametric fashion, with scores as a continuous variable; see Section 2). (b) Average pre-scan log response times for each morph step and the corresponding psychometric curve for auditory (blue) and visual (black) stimuli. (c) Correlation of state anxiety scores with the difference of ambiguous versus explicit log response times (logRTs) for stimuli perceived as fearful.



FIGURE 3: (a) Renderings of the clusters of significant activation (top) and deactivation (bottom) in response to contrasts ambiguous versus explicit emotion (p < .05 FWE). Numbers correspond to the clusters in Table 2. (b) Significant clusters in the right amygdala and STS obtained in the contrast explicit minus ambiguous expressions. (c) Weight map of positive (red) and negative (blue) weights presenting clusters corresponding to the classification of ambiguous versus explicit emotion conditions, expressed in arbitrary units (a.u.). FEW, family-wise error rate; STS, superior temporal sulcus.



FIGURE 4: (a) Box-whisker plots of the parameter estimates for the voxel-averaged clusters obtained in the contrast ambiguous versus explicit expressions, grouped as a function of Yeo et al. (2011)'s seven-network cortical parcellation (see methods for details). (b) Scatter plot showing the correlation between subjects' state anxiety scores and brain activation for the contrast ambiguous versus explicit expressions for voices (left) and faces (right). The latter are summarised as the contrast value averaged across the significant voxels which were located within the four networks shown in Figure 4a. The y-axes represent (linear combinations of) parameter estimates (β) plotted in arbitrary units (a.u.). DMN: default mode network; SN, salience network; VN, visual network.



FIGURE 5: Scatter plots showing the correlation between subjects' state anxiety scores and the difference in amygdala activity (a) between anger and fear responses for explicit (left) and ambiguous (right) expressions and (b) between explicit and ambiguous expressions for voices (left) and faces (right), as obtained in the corresponding LMM (see Section 3 for details). The y-axes represent (linear combinations of) parameter estimates (β) plotted in arbitrary units (a.u.). Error bars next to the ordinate axis represent the group mean and standard error of the mean for each condition depicted in that plot. (c) Box-whisker plots of the parameter estimates for the voxel-averaged STS clusters. LMM, linear mixed model; STS, superior temporal sulcus.

Tables

Table 1

Group-averaged Response (% Anger) to Explicit and Ambiguous Expressions of Voice and Face During Pre-scan and Scan Sessions

% Anger	Explici	t Fear	Ambig	uous	Explicit Anger			
	Voice	Face	Voice	Face	Voice	Face		
Pre-scan	1.3	1.3			98.1	97.4		
Scan	3.0	1.2	48.3	31.6	97.1	94.0		

Table 2

Significant Activations Associated with Contrasts of Interest at the Group Level

Ambiguous vs. Explicit Emotion											
Anatomical Location		L			R		Z-score	KE			
	x	у	z	x	у	z	(peak voxel)				
Ambiguous > Emotion – Activation											
L/R Supplementary Motor Area	-2	22	44				10.35	1393			
L/R sup. Frontal gyrus	-4	10	56				8.45				
L ant. Cingulate cortex	-10	26	30				6.10				
L mid. Cingulate cortex											
L anterior insula	-30	22	2				9.23	1390			
L dorsolateral Prefrontal cortex	-46	18	26				8.11				
L Precentral gyrus	-36	8	30				6.17				
L dorsolateral Prefrontal cortex	-42	38	8				5.43	20			
R anterior insula				34	24	-2	9.03	1890			
R dorsolateral Prefrontal cortex				44	24	22	8.11				
R mid. Frontal gyrus				42	18	-4	7.88				
L inf. Parietal lobe	-32	-48	42				5.90	51			
R inf. Parietal lobe	38	-48	46				5.57	33			
L inf. Occipital gyrus	-18	-100	2				6.90	520			
L mid. Occipital gyrus	-18	-104	-6				6.36				
	-36	-90	-2				5.74				
R inf. Occipital cortex				22	-96	4	6.43	258			
R mid. Occipital cortex				18	-104	8	5.85				
R sup. Occipital cortex				30	-90	-6	5.05				
R Calcarine gyrus											

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L Cerebellum	-8	-80	-28				5.14	7				
L Cerebellum	-32	-58	-30				5.08	1				
Ambiguous > Emotion – Deactivation												
L Angular gyrus	-44	-68	30				8.25	1538				
L sup. Temporal gyrus	-38	-78	40				7.31					
L mid. Temporal gyrus	-52	-54	38				7.13					
L mid. Occipital gyrus												
R Angular gyrus				48	-68	30	7.19	673				
R sup. Temporal gyrus				40	-78	38	6.46					
R mid. Temporal gyrus				56	-58	22	6.14					
R mid. Occipital gyrus												
R Supramarginal gyrus				52	-30	28	5.29	32				
				58	-26	22	5.07					
L sup. Frontal gyrus	-6	52	-6				7.54	3295				
L ventromedial Prefrontal cortex	-16	42	48				7.27					
L mid. Frontal gyrus	-16	48	38				7.21					
L ant. Cingulate cortex												
L ventromedial Prefrontal cortex	0	44	-24				5.78	39				
L mid. Cingulate gyrus	0	-10	34				4.94	1				
R sup. Frontal gyrus				28	32	44	6.97	223				
R mid. Frontal gyrus												
R Ventromedial Prefrontal												
cortex												
R sup. Frontal gyrus				24	20	58	5.69	51				
R mid. Frontal gyrus												
R ant. Cingulate cortex				4	28	12	5.38	9				
R sup. Frontal gyrus				14	50	36	4.98	4				
L/R precuneus	-6	-52	34				6.98	1060				
L/R Calcarine gyrus	-4	-44	36				6.88					
L/R mid. Cingulate cortex				0	-40	46	6.93					
L/R post. Cingulate cortex												
L mid. Temporal gyrus	-60	-22	-12				6.92	569				
L inf. Temporal gyrus	-60	-6	-22				6.76					
	-56	4	-24				6.24					
L mid. Temporal gyrus	-60	-56	-2				5.88	23				
L inf. Temporal gyrus												
L Temporal pole	-40	16	-34		_		5.12	4				
R mid. Temporal gyrus				64	-8	-14	6.02	157				
				62	-24	-16	5.48					
				64	0	-16	5.20					
R Temporal pole				46	18	-32	5.83	56				
R mid. Temporal gyrus				52	0	-26	5.21	13				
L Fusiform gyrus	-30	-42	-10				6.40	87				
R Fusiform gyrus				32	-32	-16	6.28	65				
R parahippocampus												

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Explicit > Ambiguous – Activation											
R Amygdala				26	0	-22	5.22	11			
L sup. Temporal sulcus	-62	-22	-8				6.08	44			
	-62	-8	-10				5.33				
L mid. Temporal gyrus	-50	-62	18				5.63	6			
L mid. Temporal gyrus	-60	-42	0				4.98	2			
R sup. Temporal sulcus				62	-6	-12	5.92	74			
				64	-20	-6	5.52				
R Parietal Operculum				46	-30	20	4.90	1			

Table 3

Ranking of Anatomically Defined Clusters (Having a Cluster Size >10 Voxels) that Contributed to the Top 1% of the Weight Contribution in the Above-chance Classification Accuracy of Ambiguous Versus Explicit Emotion Conditions. The Peak Coordinates of Cluster, Cluster Sizes and Percent Occurrence in 1,000 Permutations are Reported for Each Anatomical Location.

Anatomical location	Positive Weights						Anatomical Location	Negative Weights						
	L/R	x	у	z	K _E	%		L/R	x	у	z	K _E	%	
Supplementary Motor Area Mid. Cingulate cortex	L/R	-4	10	58	294	99.6	Amygdala Parahippocampal gyrus	R	18	0	-12	43	95.2	
Dorsolateral Prefrontal	L	L -46 16 32 95 99.4		-	R	24	4	-22	19	97.6				
cortex	L	-46	34	18	11	99.6		L	-18	-2	-14	30	94.6	
Precentral gyrus	L	-46	26	20	10	99.9	Fusiform gyrus	R	26	-44	-14	33	96.0	
	R	54	20	34	49	99.5	Cuneus	R	4	-78	28	19	98.4	
	R	46	12	30	30	99.9	Sup. Temporal gyrus (posterior)	L	-56	-30	18	18	99.1	
Insula	L	-32	24	4	45	99.0	Mid. Temporal	R	62	-32	4	13	99.4	
	R	32	24	6	21	99.5	gyrus (posterior)	L	-62	-38	-4	10	99.4	
Sup. parietal lobe	L	-32	-66	54	15	99.8	Putamen	L	-32	0	-6	12	96.1	
Thalamus	L	-16	-18	0	15	96.1	Lingual gyrus	R	20	-46	-6	12	95.6	
	L	-12	-24	14	11	94.3		R	14	-32	-10	11	93.1	
	R	8	-16	12	11	91.9	Caudate	R	10	10	-8	10	97.5	
	R	4	-8	12	10	95.3								
Caudate	R	10	6	12	13	94.4								
Lingual gyrus	R	12	-56	4	11	96.1								
Parahippocampal gyrus	L	-24	-38	-6	10	96.1								
	L	-16	-34	-8	10	85.3								

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