Perceiving emotional expressions in others: activation likelihood estimation meta-analyses of explicit evaluation, passive perception and incidental perception of emotions

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Abstract

We conducted a series of activation likelihood estimation (ALE) meta-analyses to determine the commonalities and distinctions between separate levels of emotion perception, namely incidental processing, passive observation, and explicit evaluation of emotional expressions. Pooling together more than 180 neuroimaging experiments using facial, vocal or body expressions, our results are threefold. First, explicitly evaluating the emotions of others recruits brain regions associated with the sensory processing of expressions, such as the inferior occipital gyrus, middle fusiform gyrus and the superior temporal gyrus, and brain regions involved in low-level and high-level mindreading, namely the posterior superior temporal sulcus, the inferior frontal cortex and dorsomedial frontal cortex. Second, we show that only the sensory regions were also consistently active during the passive perception of emotional expressions. Third, we show that the brain regions involved in mindreading were active during the explicit evaluation of both facial and vocal expressions. We discuss these results in light of the existing literature and conclude by proposing a cognitive model for perceiving and evaluating the emotions of others.

Keywords: emotion; decision-making; theory of mind; amygdala; meta-analysis

1. Introduction

We can think of emotion perception as a spectrum that runs from subliminal perception (i.e. without conscious awareness) and incidental processing (i.e. perceiving the emotion despite focusing on another attribute of the individual, such as gender) to passive perception and the explicit identification of a person's emotion. It is at this end of the spectrum that emotion perception requires a conscious deliberative decision about the likelihood of a particular emotional state (Adolphs, 2002). This is especially true in the case of noisy or ambiguous cues (Bajaj et al., 2013; Donhauser et al., 2013; Fröhholz et al., 2009b; Scocchia et al., 2014). Furthermore, explicit emotion identification can be achieved by way of two mechanisms which differ on several accounts, such as the type of input that they use (Sabbagh et al., 2004; Tager-Flusberg and Sullivan, 2000), cognitive processes (Samson, 2009), and brain networks recruited (Spunt and Lieberman, 2012). Specifically, *emotion evaluation* is accomplished based on immediately observable perceptual cues (e.g. tone of voice, facial expressions), whereas *emotion attribution* relies on situational information in the absence of observable expressions. As such, emotion evaluation depends on domain-general cognitive processes (Beer and Ochsner, 2006), including discrimination (i.e. a smile from a frown) and categorization, and relies on brain regions such as the posterior superior temporal sulcus (Allison et al., 2000). Emotion attribution, on the other hand, depends on extended conceptual knowledge (Ong et al., 2015) in the form of person knowledge (e.g. someone's idiosyncrasies) and social knowledge (i.e. a lay theory on the relations between situations, emotions and behaviors; e.g. "not having what you want causes sadness"), and is subserved by brain regions such as the medial frontal cortex and inferior frontal cortex (Herbet et al., 2013).

While *emotion attribution*, as described above, has been associated with mindreading or theory of mind abilities (Addington et al., 2006; Bora et al., 2006; Sabbagh et al., 2004), much debate revolves around the computational nature of *emotion evaluation*. For example, some

researchers favor a simulation-based approach (i.e. people use their own minds and body to simulate and understand others' emotions; see (Goldman, 2008)), while others argue for the use of a lay theory (i.e. people use abstract causal principles about the world to understand and explain others' emotions; see (Skerry and Saxe, 2014; Tager-Flusberg and Sullivan, 2000)). Yet other authors suggest that emotion perception may equally induce affective reactions in the observer and trigger inferential processes about the perceived person's state of mind and intentions (Van Kleef, 2009; Van Kleef et al., 2010), especially when the perceived emotion is directed towards the observer (Van Kleef, 2010). In the broadest sense, emotions are cases of mental states which can be reliably decoded from observable features such as facial expressions and vocal expressions (Sabbagh et al., 2004; Tager-Flusberg and Sullivan, 2000). At the very least, emotions serve as proxy for beliefs and desires (Reisenzein, 2009; Wellman and Woolley, 1990). For instance, a happy expression reveals that a person's desire has been fulfilled, whereas a surprised expression reveals that the person held a false belief.

To date, there have been no systematic reviews of the evaluations that people make about the emotions they perceive in others, either at a behavioral or at a neural level. While several meta-analyses on emotion processing already exist from aggregated neuroimaging data, we argue that they suffer from conceptual and methodological shortcomings. Specifically, meta-analyses on emotions have grouped together distinct levels of emotion perception (i.e. incidental perception, passive perception, and explicit evaluation; see (Fusar-Poli et al., 2009; Phan et al., 2002; Wager et al., 2003)), emotion perception with emotion experience (Kober et al., 2008; Vytal and Hamann, 2010), and emotion perception with memory for emotional stimuli (Murphy et al., 2003). However, empirical studies across different perceptual modalities (Cunningham et al., 2004; Fröhholz et al., 2011; Habel et al., 2007; Lane, 2008; Taylor et al., 2003) strongly suggest that passive perception, incidental perception, and explicit emotion evaluation represent different forms of emotion perception with distinct brain mechanisms. Consequently, aggregating different levels of emotion processing will likely lead to misinterpretations.

In this study, we conducted a series of meta-analyses that address these shortcomings by separately compiling neuroimaging studies on (explicit) emotion evaluation, passive perception, and incidental perception of emotions. The main goal was to reveal the brain structures associated with evaluating and deliberating over the emotional expressions of others. In line with the literature, we hypothesized that emotion evaluation stands at the interface between perceptual processing and mental states inference. Accordingly, we expected to reveal brain regions associated with processing the perceptual cues from observable stimuli depending on stimulus modality (e.g. fusiform gyri for perceiving faces; superior temporal gyrus for perceiving voices), as well as brain regions associated with mentalizing about others (e.g. medial frontal cortex, inferior frontal cortex).

2. Materials and methods

2.1. Literature selection and inclusion criteria

We identified eligible studies by conducting a search on PubMed for studies published between January 1990 and December 2015, using the following combination of keywords: (fMRI OR PET), (emotion* OR affective), (face* OR facial), (body or posture*) and (voice* OR vocal). The selection process of the articles took place in two stages. First, we assessed the titles and abstracts, and the articles were retrieved based on relevance. Second, we assessed the full text of relevant articles to determine whether any inclusion criteria were not met. Study inclusion was restricted to whole-brain fMRI studies or PET studies written in English. We further applied a series of inclusion and exclusion criteria at the level of participants, stimuli, task instructions, imaging data, and imaging contrasts reported.

2.1.1. Participants

Only healthy adults with a median or average age between 18 and 59 years old were included in the analyses. Studies with less than eight participants were excluded, as they would mostly introduce noise in the data (Eickhoff et al., 2012; Eickhoff et al., 2016). Clinical and pharmaceutical studies were included if they reported separate, within-group analyses for the controls or the placebo condition. Studies on imaging genetics were included as long as they randomly selected the sample out of the general population and allowed the allele quotas to fall out naturally.

2.1.2. Stimuli

We included studies that used emotional expressions conveyed in the face, voice or body postures according to either a basic emotions model (i.e. anger, fear, joy, sadness, disgust, surprise) or a valence-arousal model (e.g. mildly/highly pleasant/unpleasant). Emotional expressions were either prototypical or morphed/filtered; unimodal (e.g. faces only, voices only) or multimodal (e.g. faces and voices together) presented in a static or dynamic form. Furthermore, the emotional stimuli must have been previously validated as pertaining to an emotional construct (e.g. Ekman faces) or must have been validated in a pilot study specific for the paradigm in question. For the sake of material uniformity, we excluded one study using point-light stimuli to depict emotional facial and body expressions (Atkinson et al., 2012). Painful expressions were not included since they more readily and automatically trigger an empathic response when observed in others (e.g. facial expression of pain following a needle in a hand (Goldman, 2008)). Studies assessing mental states (e.g. Mind in the Eye Task) and sexual or erotic stimuli were also excluded. Likewise, studies that required emotional expressions to be imagined, remembered, anticipated or generated were excluded.

2.1.3. Task instructions

Studies must have used one of the following paradigms: active deliberation over perceived emotional expressions (e.g. identify; categorize; discriminate), passive perception (i.e. no motor response or judgment required), or gender discrimination of the perceived individual (i.e. incidental processing). Based on the task instructions, experiments were indexed separately into three categories: explicit evaluation, passive perception and incidental processing of emotional expressions. We chose gender discrimination as the representative class of incidental processing of emotions for two reasons. First, it is by far the most frequently used paradigm of incidental processing in affective neuroscience either as a stand-alone task or as a baseline contrast for explicit tasks. Second, we believe that alternative tasks of incidental processing of emotions such as age discrimination or social appraisal come with several confounding factors (Carvajal et al., 2013; Ebner et al., 2013). We specifically excluded studies that prompted the participants to feel the emotion perceived or to react to it, as well as studies looking into learning (e.g. fear conditioning), memory for emotional stimuli (e.g. recall of happy versus neutral faces) or the effects of emotion on cognition. Studies on backward masking of emotions (i.e. an emotional face presented at a near-threshold detection rate e.g. 67ms) and binocular rivalry (e.g. emotional faces superimposed on houses) were included so long as the participants were consciously aware of the stimuli.

2.1.4. Imaging data

Only activation data reported either in MNI or Talairach space were included. Similarly, only studies on changes in regional activation (i.e. as revealed by task comparison or by image subtraction method) were included. Deactivation data were excluded, as well as data on changes in functional or effective connectivity, and data reporting an interaction between stimulus and time, or task and time.

2.1.5. Imaging contrasts

We were particularly interested in an “emotion versus neutral” contrast within each level of emotion perception (e.g. explicit evaluation, passive observation, gender discrimination). Therefore, we primarily included studies reporting either a main effect of emotion (irrespective of the type of emotion, e.g. all emotions versus neutral; irrespective of modality, e.g. emotional faces and voices versus neutral faces and voices) or simple effects of emotion (e.g. discriminate happy versus discriminate neutral, when other emotions were also reported). Studies were also included if they reported a main effect of task (e.g. discriminate emotional faces versus discriminate geometrical shapes). We specifically excluded contrasts using resting state or fixation cross as baseline for comparison or contrasts comparing various emotions against each other. Finally, we excluded imaging contrasts correlating with other attributes (e.g. anxiety, personality traits).

2.2. The Activation Likelihood Estimation algorithm

2.2.1. Individual meta-analyses

The main focus of the present meta-analysis was to determine which brain regions are most consistently active when participants have to explicitly identify and evaluate the emotions perceived in others. To this end, we opted for the coordinate-based activation likelihood estimation (ALE) meta-analysis, which identifies converging areas of activity across different experiments, empirically determining whether this clustering is greater than expected by chance. The ALE algorithm, as implemented in GingerALE 2.3.6 (<http://brainmap.org/ale>), captures the spatial uncertainty associated with reported coordinates, treating them as the centers for 3D Gaussian probability distributions (Turkeltaub et al., 2002) with widths based on empirical between-subject and between-template comparisons (Eickhoff et al., 2009). One modeled activation (MA) map is then created for each experiment by merging the probability distributions of all activation foci (Turkeltaub et al., 2012). If more than one focus from a single experiment is

jointly influencing the modeled activation map, then the maximum probability associated with any one focus reported by the given experiment is used. Voxel-wise ALE scores (union across these MA maps) then quantify the convergence across experiments at each location in the brain. As functional activations occur predominantly in grey matter areas, ALE scores are computed only for voxels with more than 10% probability of containing grey matter (Evans et al., 1992). The resulting random-effects inference focuses on the above-chance convergence across studies rather than the clustering within a particular study (Eickhoff et al., 2009). To distinguish “true” from random convergence, ALE scores are compared to an empirical null distribution reflecting a random spatial association among all MA maps. This null hypothesis is derived by computing the distribution that would be obtained when sampling a voxel at random from each of the MA maps and taking the union of these values in the same manner as for the (spatially contingent) voxels in the original analysis (Eickhoff et al., 2012). The p value of a “true” ALE score is then given by the proportion of equal or higher values obtained under the null distribution.

2.2.2. Conjunction and contrast analyses

In addition to individual meta-analyses, the GingerALE algorithm can perform conjunction and contrast analyses. The conjunction is computed using the conservative minimum statistic inference (Nichols et al., 2005), which calculates a simple overlap between regions that were found statistically significant in the individual meta-analyses. This implies that only regions significant on a corrected level in both individual meta-analyses are considered. Contrast analyses are performed by computing the voxel-wise difference between two ensuing ALE maps (Eickhoff et al., 2011). All experiments contributing to either analysis are then pooled and randomly divided into two groups of the same size similar to the two original sets of experiments reflecting the contrasted ALE analyses. ALE scores for these two randomly assembled groups are calculated and the difference between these ALE scores is recorded for each voxel in the brain. Repeating this process several thousand times yields an expected distribution of ALE-score

differences under the assumption of exchangeability. The “true” difference in ALE scores is tested against this null-distribution yielding a posterior probability that the true difference was not due to random noise in an exchangeable set of labels, based on the proportion of lower differences in the random exchange. The resulting probability values are then thresholded and inclusively masked them by the respective main effects, i.e. the significant effects of the ALE analysis for the particular condition. A correction for multiple comparisons is not applied to the contrasts analyses because GingerALE restricts the search space to voxels that have survived the threshold in the main effect for the minuend (Eickhoff et al., 2011).

2.3. *Data analysis*

We first conducted separate meta-analyses on explicit emotion evaluation, passive perception of emotions, and incidental perception of emotions. Because we pooled together studies across different perceptual modalities (and across different tasks in the case of explicit emotion evaluation), we opted for a more conservative threshold than the one suggested by (Eickhoff et al., 2012). Specifically, we used a cluster-forming threshold at voxel level of $p < 0.0001$, and a threshold of $p < 0.01$ at cluster-level (family-wise error rate-corrected for multiple comparisons). To determine null-distributions for the individual ALE maps, we conducted 5000 permutation tests. Whenever coordinates were reported in the Talairach and Tournoux stereotaxic space (Talairach and Tournoux, 1988), they were converted into Montreal Neurological Institute (MNI) space using the TAL- MNI tool provided in GingerALE.s

Since the ALE algorithm tests for significant areas of convergence compared to a null hypothesis of random spatial association between experiments, a much higher ratio of visual stimuli compared to auditory stimuli would result in a high likelihood that the overall activation is driven mainly by evaluating facial stimuli. Consequently, we further split the tasks of emotion evaluation based on modality, and we looked at the processing of facial expressions separately for emotion evaluation, passive perception and incidental perception. Unfortunately, due to the

low number of studies using passive perception and gender discrimination of emotional voices (5 and 9 experiments, respectively) and body expressions (4 experiments and none, respectively), we were not able to perform separate meta-analyses on these types of paradigms (Eickhoff et al., 2016). We did, however, look separately at the explicit evaluation of facial expressions (N=75) and vocal expressions (N=18) of emotions.

Because we only included studies that used contrasts between emotional stimuli and neutral stimuli or another appropriate control task, brain activity pertaining to certain task attributes such as basic attention, response selection, and motor preparation should have already been canceled out. The remaining brain activation should thus explain cognitive processes pertaining to the integration and evaluation of emotional cues. Additionally, we wanted to determine which areas, if any, were unique to the deliberation over emotional expressions as opposed to deliberation in general. In this regard, we performed contrast and conjunction analyses between the ALE map of explicit emotion evaluation and the ALE map of incidental perception of emotions. Because gender discrimination of emotional stimuli is also a deliberation process, we expected that the comparison with explicit emotion evaluation would isolate deliberation over emotional cues from deliberation over non-emotional cues. Moreover, we performed contrasts and conjunctions between the ALE map of explicit emotion evaluation and the ALE map of passive perception, with the intention to differentiate between brain regions involved in the perception and recognition of emotional expressions, and those involved in the evaluation process. All contrast analyses were thresholded at $p < 0.05$ (i.e. 5% probability that the differences observed between datasets are due to random noise).

3. Results

3.1. *Eligible studies*

Following our inclusion and exclusion criteria, we identified 2456 initial publications, of which 98 articles (102 experiments) fulfilled all inclusion criteria for explicit emotion evaluation, 32 articles (33 experiments) for passive observation and 46 articles (47 experiments) for incidental processing of emotions (i.e. gender discrimination). **Tab. 1** shows a breakdown of the studies included in the meta-analysis with descriptive statistics of the corresponding number of articles, experiments, participants and foci of each paradigm. Facial expressions constituted the vast majority of stimuli that these studies used (**Tab. 2**). **Supplementary Tab. 1** lists the articles included in our meta-analysis.

3.2. *Individual meta-analyses*

The meta-analysis of the pooled 102 experiments contrasting evaluation of emotional versus control stimuli revealed significant convergence in seven bilateral clusters: inferior frontal cortex (IFC), posterior superior temporal sulcus (pSTS), dorsal medial frontal cortex (dMFC), amygdala (Amy), middle fusiform gyrus (MFG), and the visual association areas (**Fig. 1, Supplementary Tab. 2**). Additionally, there was significant activation in the left thalamus (Thal) and the left insula.

Evaluating emotions from facial expressions alone showed remarkably similar activation (**Fig. 2, Supplementary Tab. 2**). Lowering the voxel-level threshold from $p < 0.0001$ to $p < 0.001$ revealed additional activation in bilateral intraparietal sulcus (**Supplementary Tab. 2**). Explicitly evaluating vocal expressions of emotions triggered activation in bilateral pars triangularis of the IFC, dMFC, the left frontal operculum (fOp) and the right superior temporal gyrus (STG) (**Fig. 3, Supplementary Tab. 2**). Lowering the voxel-level threshold to $p < 0.001$ revealed additional activation in the left STG (**Supplementary Tab. 2**).

Passively attending to emotional expressions triggered significant convergence in bilateral Amy, pSTS, inferior occipital gyri (IOG), pars orbitalis of the IFC, as well as the left MFG and the right precentral gyrus (**Fig. 4A, Supplementary Tab. 3**). Incidental processing of emotional expressions while judging the gender of the person activated bilateral Amy and the right MFG (**Fig. 4B, Supplementary Tab. 3**). Passive observation of facial expressions alone activated bilateral Amy, the right pSTS, the left MFG, the right IOG, and the right precentral gyrus (**Supplementary Tab. 3**), whereas the incidental perception of facial expressions alone recruited bilateral Amy, MFG and the left middle occipital gyrus (**Supplementary Tab. 3**).

3.3. *Contrasts and conjunction analyses*

3.3.1. *Explicit evaluation of emotions from faces and voices*

Evaluating emotions from facial expressions compared to vocal expressions distinctly recruited regions in bilateral Amy, MFG and visual association areas (**Fig. 5, Supplementary Tab. 4**). The left dMFC, fOp, pars triangularis of the IFC and the right STG were uniquely recruited when evaluating emotions from voices compared to faces (**Fig. 5, Supplementary Tab. 4**). The conjunction analysis revealed that the right pars triangularis of the IFC, the right dMFC, pSTS and the left insula were jointly recruited during evaluation of emotions from the face and the voice (**Fig. 5, Supplementary Tab. 4**).

3.3.2. *Explicit evaluation and passive perception of emotions*

Compared to passive perception of emotional expressions, explicitly evaluating emotions regardless of sensory modality distinctly recruited bilateral IFC, dMFC, peri-amygdala, the right visual association areas, and the right middle fusiform gyrus (**Fig. 6, Supplementary Tab. 5**). In contrast, passively attending to emotional expressions in the face, voice or body distinctly recruited bilateral pars orbitalis of the IFC, IOG, pSTS, the right precentral gyrus, the right hippocampus, the left MFG, and the left posterior middle temporal gyrus (**Supplementary Tab.**

5). The conjunction analysis revealed that bilateral amygdala, pSTS, right IOG, left MFG, and the left pars orbitalis of the IFC were jointly recruited during explicit evaluation and passive perception of emotions (**Fig. 6, Supplementary Tab. 5**).

Evaluating emotions from the face compared to passively observing emotional faces distinctly recruited bilateral dMFC, peri-amygdala, the left IFC, the left IPS and the right occipital gyrus (**Supplementary Tab. 6**). The amygdala, the left MFG, the right IOG, and the right pSTS were jointly active when explicitly evaluating emotional faces and passively observing them (**Supplementary Tab. 6**).

3.3.3. Explicit evaluation and incidental perception of emotions

Deliberating over a perceived emotion versus deliberating over the gender of a person strongly recruited bilateral dMFC, pSTS, IFC, the right visual association areas, the right inferior occipital gyrus, the left peri-amygdala and the left insula (**Fig. 7, Supplemental Tab. 7**). Judging the gender of a person, in return, distinctly recruited subcortical regions in the right claustrum and the left hippocampus (**Supplemental Tab. 7**). The conjunction analysis revealed that bilateral amygdala and the right MFG were jointly recruited when evaluating the emotion and discriminating the gender of a person (**Supplemental Tab. 7**).

Evaluating emotions from the face alone compared to incidentally perceiving emotional faces activated bilateral pars triangularis of the IFC, pSTS, dMFC, occipital gyri, the right IOG, the right Amy and the left peri-amygdala (**Supplemental Tab. 6**). Bilateral Amy and MFG were jointly active during emotion evaluation in the face and incidentally perceiving emotional faces (**Supplemental Tab. 6**).

3.3.4. Explicit evaluation, passive perception and incidental perception of emotions

The conjunction analysis between all forms of emotion processing, namely explicit evaluation, passive perception and incidental perception, revealed bilateral clusters in the amygdala (**Fig. 8**).

4. Discussion

Our study is the first systematic attempt to reveal the commonalities and distinctions between different levels of emotion perception, namely incidental processing, passive observation, and explicit evaluation of emotional expressions. To this end, we pooled together neuroimaging studies spanning 26 years in order to reveal those brain areas with significant convergence across emotions and types of instructions underlying emotion evaluation.

Our main results are threefold. First, and in line with our hypotheses, we found that explicitly evaluating the emotional expressions of others recruits, on one hand, brain regions involved in the sensory processing of emotions, such as the IOG, MFG, and the right STG, and, on the other hand, brain regions involved in low-level and high-level mindreading, such as the pSTS, IFC and dMFC. Second, we show that sensory processing regions are also consistently active during passive perception of emotional expressions. Third, we show that the brain regions involved in mindreading are equally present during the explicit evaluation of emotional expressions from faces and from voices.

In the following sections, we discuss the significance of each of our main findings and we conclude by proposing a model for understanding and evaluating emotions perceived in others (summarized in **Fig. 9**). We argue that deliberating over which emotions we perceive in others significantly activates brain regions associated with mindreading - the process of accurately inferring the beliefs, desires and mental states of others.

4.1. *Sensory-processing regions*

4.1.1. *Perceiving emotional faces*

Processing emotional expressions from the face recruited bilateral activation in the visual association cortices, IOG, MFG, pSTS, the intraparietal sulci, the amygdalae, the left insula and the left thalamus. Unsurprisingly, the seminal model of processing human faces proposed by

Haxby involves these regions (Haxby et al., 2000, 2002). In the model, face perception involves the coordinated participation of multiple regions broadly termed the 'core system' and the 'extended system'. The core system consists of two processing streams, one leading from the IOG to the MFG, in which invariant aspects of faces such as identity and gender are represented, and another stream leading from the IOG to the STS, in which changeable aspects of faces such as emotional expression and gaze orientation are represented. These core regions are supported by other brain areas located throughout the brain, which constitute the 'extended face system'. They contribute to specific demands of face processing in a task-dependent manner. For example, the intraparietal sulcus is involved in spatially directed attention (Corbetta et al., 2008) which can be used to attend and to switch between several facial features. Similarly, the amygdala and the insula are recruited when processing emotional expressions (Haxby et al., 2000; Hoffman and Haxby, 2000). The insula projects to both the amygdala and the prefrontal cortex (Aggleton et al., 1980; Cloutman et al., 2012) and is a crucial part of the neural system specialized to decode emotions from facial expressions, as lesion studies (Dal Monte et al., 2013) and neuroimaging studies have shown (Duerden et al., 2013; Quarto et al., 2016).

Although the Haxby model assumes bilateral interactions between modules and brain regions, it remains, for the most part, a hierarchical model of processing faces. Recent studies from lesion patients, transcranial magnetic stimulation and neuroimaging have argued against a strict feed-forward hierarchical model of face perception, in which the IOG is the main source of input (Atkinson and Adolphs, 2011; Rossion, 2008). Instead, these findings refine the 'core network' proposed by Haxby by allowing a much more interactive processing of faces. Specifically, while the IOG and MFG may be recruited at different time points and for different computational purposes, both structures are involved in processing invariant and changeable features of the face, such as judging facial identity and emotional expressions (Atkinson and Adolphs, 2011; Wegrzyn et al., 2015). Following early visual analysis in the association cortices, the IOG is first recruited to process individual parts of the face (e.g. the mouth, the eyes) as early

as 60ms (Pitcher, 2014; Pitcher et al., 2008), whereas the MFG is recruited later on to generate a holistic representation of the face, defined as a single global representation of multiple elements of the face (Arcurio et al., 2012; Pitcher et al., 2011; Rossion, 2008; Yovel, 2016). This has prompted researchers to theorize a two-stage model of processing faces – an initial stage during which the IOG segregates the core face network from the rest of the brain upon the detection of face parts, and a second stage when the MFG integrates facial information from multiple face-selective regions to holistically process faces (Liu et al., 2002; Wang et al., 2016). This global but coarse representation of faces is continuously refined through reentrant interactions between the MFG and the IOG (Atkinson and Adolphs, 2011; Rossion, 2008), and between the MFG and other structures such as the amygdala (Sabatinelli et al., 2005) until a complete facial percept has been extracted (Rossion, 2015).

In our results, we additionally found differences between the levels of emotion processing in terms of hemispheric lateralization and specific coordinates in the visual association areas, the fusiform gyri and inferior occipital gyri. This is in line with recent findings of several face-sensitive clusters in the brain beyond the ones included in the Haxby model (Rossion, 2015).

4.1.2. Perceiving emotional voices

When pooling together studies on evaluating emotional voices, the only sensory processing region that survived statistical testing was the right middle STG. This result is in line with the literature on several accounts (Ceravolo et al., 2016a; Ceravolo et al., 2016b; Ethofer et al., 2011; Frühholz and Grandjean, 2013a; Frühholz et al., 2016; Schirmer and Kotz, 2006). For example, Belin called the right middle STG the “auditory face” region because it responds maximally to human voices as opposed to non-human vocal and non-vocal sounds (Belin et al., 2004; Belin et al., 2000). Similar to facial expressions, emotional voices are more dynamic and richer in acoustic

features than neutral voices (Rao et al., 2013), thus recruiting a sensory processing region (i.e. the right STG) to a larger extent.

4.2. Mindreading regions

4.2.1. Posterior superior temporal sulcus

We found that the pSTS was active during both passive perception and explicit evaluation of emotional versus neutral stimuli. Extensive research has shown that this major sulcal landmark in the temporal lobe is sensitive to gaze orientation (Hooker et al., 2003) and the movement of the human body (Kourtzi and Kanwisher, 2000; Saxe et al., 2004b), hands (Gallagher and Frith, 2004; Holle et al., 2010) and face (Lee et al., 2010), either through direct perception (Allison et al., 2000) or implied movement (David and Senior, 2000). However, the pSTS is not sensitive to just any kind of movement as significantly more activation occurs when people view others perform complex versus simple actions (Castelli et al., 2000), physically possible movements compared to impossible movements (Stevens et al., 2000), meaningful versus meaningless movements (Decety et al., 1997; Schultz et al., 2004), and when people observe the transition between meaningful actions within a larger goal-directed activity such as cleaning the kitchen (Zacks et al., 2001). The overwhelming evidence suggests that the human pSTS is involved in decoding and understanding meaningful social actions conveyed by gaze direction, body movement and other types of goal-directed meaningful motion (see Frith and Frith, 1999).

A recent extensive meta-analysis showed that tasks of theory of mind, which heavily rely on imagining or understanding movement in order to infer intentions, strongly recruit bilateral pSTS (Schurz et al., 2014). This form of inference has been called teleological reasoning (Gergely and Csibra, 2003; Perner and Roessler, 2012) and is also present in primates (Myowa-Yamakoshi et al., 2012) and very young children (Perner and Esken, 2015; Wellman and Brandone, 2009). Such low-level mindreading (Frith and Frith, 1999; Perner and Esken, 2015; Wellman and

Brandone, 2009) posits that, if an individual performs an action, then he or she must do so with the purpose of achieving a goal (i.e. means-end reasoning). Together, the evidence presented above strongly suggest that the pSTS may support a basic representation of intentionality extracted from perceived motion that is neither tied to specific perceptual parameters (Peelen et al., 2010) nor fully conceptual (Skerry and Saxe, 2014).

Facial expressions are considered a special form of highly meaningful motion where a complex of facial muscles evolve and vary in a sequence (Hoffman and Haxby, 2000; Ishai et al., 2005; Said et al., 2010). Unsurprisingly, perceiving emotional expressions in the face, either from still images or from video clips, recruits the pSTS (Frühholz et al., 2009a; Hasselmo et al., 1989; Haxby et al., 2002; Ojemann et al., 1992; Rapcsak et al., 1989; Winston et al., 2004). Auditory stimuli such as voices (Hein and Knight, 2008) or the sound of footsteps (Bidet-Caulet et al., 2005) equally recruit the pSTS. In fact, the pSTS is a multimodal integration region (Peelen et al., 2010) where visual and auditory information is combined into meaningful percepts about objects, especially when these percepts consist of naturally occurring, highly correlated features such as an animal's shape and its motion (Beauchamp et al., 2004) or a person's emotional expression and their actions (Vander Wyk et al., 2009). This body of research therefore reinforces the link between goals, actions, and emotional expressions.

The pSTS was present in our results on evaluations of emotional faces but it was not immediately evident for evaluations of emotional voices. However, the conjunction analysis between evaluations of faces and voices revealed common activation in the right pSTS. This is in line with the findings of a supra-additive response to facial and vocal emotions in the right pSTS (Hagan et al., 2009). A considerably larger activation in the right pSTS was also present in our pooled meta-analysis of emotion evaluation, which is consistent with the literature (Allison et al., 2000; Pelphey and Morris, 2006; Posamentier and Abdi, 2003). The extensive role of the pSTS in recognizing and understanding emotional versus neutral expressions was further reinforced by the lack of pSTS activation during incidental processing of emotions (see also (Gazzola et al.,

2012) and (LaBar et al., 2003)). Although we could not test it formally, our meta-analyses suggest that it could be the interaction between the attentional focus and the emotional features of faces and voices that recruits the pSTS, in addition to the perceived congruency between emotion expressions and actions (Vander Wyk et al., 2009).

The common activation of pSTS in our results during both passive perception and explicit evaluation of emotional versus neutral expressions is in line with the literature on two accounts. First, emotional faces - whether movie clips or still images - are inherently dynamic whereas facial muscles at rest define neutral faces. Similarly, neutral voices have plain auditory features compared to emotional voices which are more aroused (Scherer, 1995; Tao et al., 2006). Therefore, emotional stimuli might activate the pSTS in a bottom-up fashion more so than neutral stimuli. Second, both perceiving and deliberating about an emotion presuppose a common requirement, namely that the expression has to be recognized and understood. We argue that, following the sensory processing of stimuli, a basic form of intentionality is represented in the pSTS which is necessary for the understanding and recognition of emotions but not sufficient for mentalizing about them (see also Yang et al., 2015).

4.2.2. Dorsomedial frontal cortex

The activation of the dmFC (Brodmann area [BA] 8) was specific to the explicit evaluations of emotional expressions, a finding that was supported by the standalone meta-analyses and by the direct comparisons against incidental processing and passive perception of emotions. Although the medial frontal cortex spans several structurally distinct regions (Öngür et al., 2003) that might subserve different functions in social cognition (Amodio and Frith, 2006), the same portion of the dmFC as found by us (BA 8) is consistently reported in verbal and nonverbal tasks that require thinking about the mental states of both human and nonhuman agents (Döhnell et al., 2012; Gallagher et al., 2000; Kim et al., 2005; Schlaffke et al., 2015; Schurz et al., 2014; Völlm et al., 2006). In addition to reasoning about other people's transient mental states such as beliefs and

desires, medial BA 8 is equally involved in inferring more stable characteristics such as personality traits and dispositions (Iidaka et al., 2010; Mitchell et al., 2004, 2005b), intelligence (Hall et al., 2010) and approachability (Hall et al., 2012; Toki et al., 2013).

Several studies have pointed to a functional distinction within the medial frontal cortex along the self-other spectrum, possibly due to the diverse cytoarchitecture and connectivity of this structure (Öngür et al., 2003; Öngür and Price, 2000). Specifically, the ventromedial parts of the frontal cortex have been associated with accurate attribution of mental states to self (Schulte-Rüther et al., 2007) and to similar others (Mitchell et al., 2005a; Schurz et al., 2014), whereas dorsomedial parts of the frontal cortex have been associated with accurate inference about dissimilar others (Frith and Frith, 2006; Mitchell et al., 2006; Tamir and Mitchell, 2010). Interestingly, (Takahashi et al., 2009) elicited short episodes of envy and found that activity in dmFC (BA 8) correlated with the degree of self-reported envy. In addition, the bigger the difference between the respondent and the target individual on the comparison domain, the higher the activity displayed in medial BA 8 (Takahashi et al., 2009). Medial BA 8 also correlates with dispositional envy (Xiang et al., 2016), defined as an increased sensitivity and need to compare to those that possess a greater amount of self-relevant attributes (Smith et al., 1999). In the domain of emotions, (Williams et al., 2007) found that acute tryptophan depletion reduced the functional activity in medial BA 8 and left pSTS when judging emotional faces. The dmFC (BA 8) is highly active when judging the appropriateness of specific facial emotions in a given context (Kim et al., 2005) or inferring whether someone is genuinely sad/happy or is simply posing for the camera (McLellan et al., 2012). Finally, medial BA 8 is also recruited when participants have to reason about the most likely scenario that caused a facial expression emotion (Prochnow et al., 2014).

The interpretations above constitute 'reverse inferences' in which a cognitive process – mentalizing about other people's inner states – is inferred from neuroimaging data (Poldrack, 2011). Lesion studies and transcranial magnetic stimulation (TMS) could provide stronger forms

of evidence (Schuwerk et al., 2014a). Although focal lesion studies to the medial BA 8 are rare (Bird et al., 2004), widespread lesions to medial frontal cortex that incorporate BA 8 significantly impair the ability to infer whether someone is trying to deceive them (Stuss et al., 2001), the capacity to reflect upon others' intentions (Herbet et al., 2013), and the ability to recognize emotions from facial expressions (Heberlein et al., 2008). Furthermore, dementia affecting medial frontal cortex impairs performance on a series of false belief and mentalizing tasks (Modinos et al., 2009). Inhibiting the medial BA 8 by applying low-frequency repetitive TMS significantly impairs participants' ability to distinguish between one's perspective and another's perspective in a false belief task (Schuwerk et al., 2014b). (Krause et al., 2012) also delivered low-frequency deep repetitive TMS to bilateral medial BA 8 and investigated performance on a task in which mental states are inferred based on eye gaze and facial expression. The authors found a double dissociation, where the TMS disrupted task performance in participants with high self-reported empathy but it improved performance in those with low self-reported empathy. TMS over medial BA 8 also impairs participants' inferences about others' social traits (Ferrari et al., 2014). In the domain of emotions, TMS over medial BA 8 equally impairs the discrimination of facial expressions (Balconi and Bortolotti, 2013; Harmer et al., 2001).

In light of the evidence above, the presence of the dMFC in our meta-analyses on emotion evaluation can be explained in terms of mentalizing about others' internal states. At face value, the dMFC could reflect the degree of dissimilarity between the participants, which are placed inside the scanner in an emotionally neutral state, and the people that they perceive in different states of emotionality. A stronger form of generalization would be that the deliberation process itself regarding which emotion is been perceived requires elements of mindreading. Put in other words, when we evaluate the emotions of others we do not merely perceive and associate an emotional expression with a particular emotional construct (e.g. a happy face; an angry voice), but we also make spontaneous assumptions about the perceived other's corresponding mental state (e.g. something made you happy; someone made him angry).

4.2.3. *Inferior frontal cortex*

Our meta-analysis also shows that the IFC plays a crucial role in evaluating emotions. We found several patches of activation in bilateral mid and posterior IFC when comparing explicit evaluation against passive perception and implicit perception. Although active emotion evaluation is a de facto decision-making process, we did not find additional activations in other prefrontal regions of the brain such as the dorsolateral prefrontal cortex, generally lauded as regions of decision-making and executive control (Miller and Cohen, 2001).

The IFC is a heterogeneous gyral complex and its subregions differ in morphology, cellular architecture, and function (Amunts et al., 2010; Anwender et al., 2007; Clos et al., 2013; Frühholz and Grandjean, 2013b; Gerbella et al., 2010; Petrides and Pandya, 2002). Therefore, it is likely that the mid and posterior IFC plays multiple roles during the explicit evaluating of emotional expressions. The IFC is generally seen as the locus of integration of perceptual and emotional/motivational information held in posterior cortical association areas and subcortical regions, respectively (Gilbert and Burgess, 2008; Lee et al., 2014; Petrides, 2005; Petrides and Pandya, 2009). This form of cognitive control is necessary for the active retrieval of information and the deliberative decisions towards goal-directed behavior (Abraham et al., 2010; Gilbert and Burgess, 2008; Koechlin et al., 2003; Sakagami and Pan, 2007).

The left IFC has long been associated with language production and comprehension (Clos et al., 2013; Saur et al., 2008), as well as with short-term and long-term memory (e.g. (Badre and Wagner, 2007; Nee et al., 2013; Riès et al., 2016; Rottschy et al., 2012)). Semantic memory consists of long-term knowledge of facts, word meanings and object properties. When accessing such knowledge, the left mid IFC supports a post-retrieval selection process meant to solve competition among similar active semantic representations (Bokde et al., 2001; Dal Monte et al., 2014; Liakakis et al., 2011; Poldrack et al., 1999; Thompson-Schill et al., 1997). Furthermore, the left mid IFC is involved in the storage and maintenance of information in the working memory

(Barbey et al., 2013; Liakakis et al., 2011; Rottschy et al., 2012; Rypma et al., 2002), possibly via subvocalizations (Swick et al., 2008; Vigneau et al., 2006; Vigneau et al., 2011). When explicitly evaluating an emotional expression, one needs to keep several choice options in the short-term memory, retrieve the semantic representation associated with those emotional constructs, and covertly label the emotion perceived.

The right IFC has been associated with encoding and implementing abstract rules (i.e. stimulus-response contingencies; (Koechlin et al., 2003; Wallis et al., 2001)), as well as with motor and cognitive inhibition (Aron et al., 2004; Cai et al., 2014; Levy and Wagner, 2011), including the inhibition of one's self-perspective when reasoning about others (Aboulafia-Brakha et al., 2011; Abraham et al., 2010; Apperly et al., 2004; Saxe et al., 2006; Schurz and Tholen, 2015; Shamay-Tsoory et al., 2009; Spunt and Lieberman, 2012). In particular, the suppression of one's perspective is believed to be crucial in identifying others' false beliefs and the general tracking of their mental states. Inhibiting the self-perspective allows for the disengagement of the self onto others and the increase of attentional resources to focus on others (Hartwright et al., 2012; McCleery et al., 2011; Mitchell, 2011; Samson et al., 2005; Samson et al., 2015; Schurz and Perner, 2015; Van der Meer et al., 2011). Ineffective inhibition of one's self, in the form of egocentric biases, have been directly linked to limited inhibitory control (Carlson et al., 2004), and have been shown in young children (Carlson and Moses, 2001; Sommerville and Woodward, 2005), adults suffering from brain damage (Apperly et al., 2004; Gregory et al., 2002; Rowe et al., 2001; Samson et al., 2005; Samson et al., 2015), and psychiatric patients (Corcoran et al., 1995; Langdon et al., 2006; Langdon et al., 2002; Leslie and Thaiss, 1992). Furthermore, studies using event-related potentials have also shown that inhibiting and disengaging one's perspective occurs prior to switching perspectives (McCleery et al., 2011; Thirioux et al., 2014) and reasoning about mental states (Zhang et al., 2009). It has been proposed that mindreading consists of two components that can be differentiated at a neural level: inhibiting one's own perspective and reasoning about the mental state of another (Hartwright et al., 2012; Samson et al., 2005; Van

der Meer et al., 2011). The IFC would then play the important role of inhibiting and disengaging from one's own perspective, while the dmFC would account for the second component of mindreading, namely perspective-taking (Samson et al., 2005; Van der Meer et al., 2011) and reasoning about mental states (Hartwright et al., 2012; Ruby and Decety, 2003). When perceptual cues alone are not sufficient to attribute or infer emotions and other mental states, additional brain regions are recruited at this stage, such as the temporoparietal junction (Decety and Lamm, 2007; Van Overwalle, 2009).

Our bilateral activation throughout the mid and posterior IFC suggests the simultaneous recruitment and cooperation of both hemispheric functions when explicitly evaluating emotions of others. The left IFC could support selection of semantic representations about the emotional categories, maintenance of possible choice options in the working memory and covert labeling of perceived expressions. In return, the right IFC could ensure self-perspective inhibition and increased attentional resources to the other. In light of the functional and structural complexity of the IFC, however, we do not claim an exhaustive coverage of the possible roles that the IFC might play.

4.3. *Amygdala*

The only structure recruited across all forms of emotion perception, namely explicit evaluation, incidental perception, and passive perception, was the amygdala. Such a finding is not surprising since this subcortical region has a long history of association with processing emotional versus neutral stimuli (Phelps and LeDoux, 2005). In the auditory domain, particularly, amygdala plays a central role in decoding emotional meaning from sound across a variety of domains, including verbal and nonverbal emotional expressions, and musical pieces (Fruhholz and Grandjean, 2013; Frühholz et al., 2014; Pannese et al., 2015; Trost et al., 2015). Furthermore, patients with amygdala damage demonstrate difficulties in processing emotional voices, especially in a

multimodal stimulation (Milesi et al., 2014), and globally reduced processing of emotional voices in the ipsilesional auditory cortex (Frühholz et al., 2015b).

In addition, our results show that the peri-amygdala, a structure surrounding the amygdala, was uniquely recruited during explicit evaluation of emotional stimuli, especially emotional faces. The peri-amygdala is often mislabeled by researchers as simply “amygdala” despite being visibly more anterior (e.g. Vuilleumier et al., 2001). Other times, researchers include the peri-amygdala into a larger heterogeneous anatomical structure labeled the “peri-amygdaloid cortex” (Ethofer et al., 2006; Frühholz et al., 2010; Morris et al., 1998). Regardless of the nomenclature, studies with similar coordinates as those found by our meta-analysis point to a potential role of the peri-amygdala in the accurate retrieval of emotional faces (Kensinger and Schacter, 2005), especially fearful faces (Dolan et al., 2001; Morris et al., 1996). It is possible, therefore, that the explicit evaluation of emotional expressions could trigger peri-amygdala activation via mnemonic processes. Future functional neuroimaging studies with higher spatial resolution can provide more insight into the exact role of this structure.

4.4. Lack of activation in somatosensory-related cortices

We note that we did not find activations in somatosensory-related cortices when explicitly evaluating emotional expressions from the face, the voice or from the combination with body expressions. This appears to contradict several findings from lesion studies (Adolphs et al., 2002; Adolphs et al., 2000; Adolphs et al., 1996) and neuroimaging studies (Heberlein and Saxe, 2005; Winston et al., 2003). We believe that these differences lie in the task demands. In our meta-analysis, the majority of studies used emotion labeling and emotion matching, whereas the literature involving somatosensory-related cortices predominantly use computationally difficult rating tasks that call for internal simulation. For example, Adolphs and colleagues asked patients to rate the intensity of six basic emotions from facial and vocal expressions on a six-point scale

with respect to six attributes (Adolphs et al., 2000; Adolphs et al., 1996) or eight attributes (Adolphs et al., 2002). Similarly, neuroimaging studies that found increased activity in somatosensory-related cortices use some variation of the rating task, such as rating point-light body movement stimuli on a four-point scale (Heberlein and Saxe, 2005) or deciding which face from a pair of morphed facial expressions is more emotionally intense (Winston et al., 2003). Arguably, the task of gauging the intensity of an emotion, especially on a scale that seems counterintuitive (e.g. anger on a happiness scale), requires additional resources compared to simple recognition and labeling of emotions. Indeed, the task of labeling emotions was impaired more often among patients with lesions in bilateral IFC and the right STG than somatosensory regions (Adolphs et al., 2002). Furthermore, recognizing complex social emotions such as guilt, pride and boredom recruits somatosensory cortices more than recognizing basic emotions does (Alba-Ferrara et al., 2011). It is possible, therefore, that more difficult tasks such as assessing the intensity of an emotion can benefit from an online somatosensory representation via internal simulation in order to be performed successfully (Goldman, 2008).

4.5. Proposed mechanism for evaluating emotions

In light of all the evidence presented above, we propose that the explicit evaluation of emotional expressions of others starts in a network of brain regions specialized in extracting the sensory information from visual and auditory cues (**Fig. 9**). We showed that these regions were also active during passive perception and, to a much lesser degree, during incidental perception of emotional expressions. We argue that, via a series of structural and functional connections (Fairhall and Ishai, 2007; Frühholz and Grandjean, 2012; Haxby et al., 2002), the result of this sensory processing is forwarded to the pSTS, which extracts representations about the perceived expression that generalize across sensory inputs but do not yet extend to more abstract, inference-based representations. The connections between sensory areas and the pSTS reflect a shared mechanism between explicitly evaluating and passively attending to the emotions of

others, a mechanism that is necessary to recognize and understand emotions (Haxby et al., 2002). We further argue that explicit evaluation of emotions additionally recruits bilateral IFC in order to integrate information from sensory processing regions and possibly the amygdala. Through the cooperation of left and right IFC functions, semantic representations about the emotional categories are accessed and selected, possible choice options are maintained in the working memory and self-perspective is inhibited while attentional resources are allocated towards the perceived individual. Following the inhibition of one's own perspective, the right IFC initiates a spontaneous process of inferring the mental states of the perceived individual that is later finalized in the dmFC (Apperly et al., 2004; Samson et al., 2005). Strong structural (Frühholz et al., 2015a; Sallet et al., 2013; Seltzer and Pandya, 1989, 1994) and functional connections (Bzdok et al., 2013; Frühholz and Grandjean, 2012; Spunt and Lieberman, 2012) have been established between the IFC, dmFC and the pSTS, which would allow the necessary exchange of information between these regions at different stages of processing.

Interestingly, Wolf and colleagues (Wolf et al., 2010) used tensor probabilistic component analysis to show that, during a naturalistic task, the mindreading network is divisible in three circumscribed, statistically independent but functionally and temporally connected networks, consisting of sensory processing regions as a first component, the pSTS as the second component, and the IFC and dmFC as part of the third network component. It is worth noting that the authors found some spillover between components, such that some pSTS activity was encountered in the first component and some IFC activity was encountered in the second component. These spillovers might reflect, on one hand, the difficulty of precise fractioning of the functional roles that each brain structure plays and, on the other hand, that both feedback and feedforward connections between these structures might shift the temporal courses of these structures' activity.

We note that the idea of emotion understanding requiring some degree of mindreading has already been proposed by several researchers (Frith and Frith, 2006; Goldman, 2008;

Mitchell and Phillips, 2015; Van Kleef, 2010). It is widely believed that higher-order mindreading regions, including the dmPFC, are recruited when people perceive complex social emotions (Alba-Ferrara et al., 2011) or when perceptual cues alone are not sufficient to infer an emotion (Olsson and Ochsner, 2008). However, several other authors view emotion understanding as a necessary prerequisite for showcasing a fully-fledged mindreading ability, both ontologically (Mitchell and Phillips, 2015; Saxe et al., 2004a) and within the temporal course of the mindreading ability (Pineda and Hecht, 2009). Furthermore, the tasks included in the current meta-analysis did not require participants to incorporate cues from context in order to evaluate the emotions (i.e. tasks more likely to induce emotion attribution). In fact, the vast majority of stimuli were naturalistic, without noise or any systematic manipulation, and the perceptual cues alone should have been sufficient to reach a decision about which emotion is being perceived. Despite these elements, however, it appears that explicit evaluation of emotional expressions based on perceptual cues still involves a considerable amount of mindreading. This suggests that the observers' knowledge about emotions is represented in coherent lay theories, which comprise of consistent relationships between situations, emotions, and behaviors (e.g. if you get what you want, then you will be happy). Observers then use this knowledge to decipher other people's behavior and signals such as facial expressions in a manner similar to rational inference in other domains (Ong et al., 2015).

Future work focusing on deconstructing explicit emotion evaluation based on task instructions can shed more light on the specific roles of each functional region in our proposed mechanistic model.

4.6. *Strengths and limitations*

To the best of our knowledge, this is the first quantitative meta-analysis of the neuroimaging literature on emotion perception to differentiate between its levels of processing. Specifically, and in contrast to previously published meta-analyses, we acknowledged the heterogeneity of emotion perception tasks and separately analyzed explicit evaluation, passive perception and incidental

perception of emotional expressions. By doing so, we were able to determine common and distinct brain regions depending on task instructions that would not have been possible had we done a pooled analysis.

Several limitations of the current study should be noted. First, meta-analyses are necessarily based on the available literature and may thus be affected by the publication bias disfavoring null-results. We tried to mitigate this bias by including results on healthy samples from clinical, pharmacological and imaging genetics studies whose main objectives were not to study emotion perception in healthy participants. Moreover, as detailed elsewhere (Rottschy et al., 2012), coordinate-based meta-analyses of neuroimaging data are less susceptible to publication bias than standard meta-analytic approaches that examine effect sizes, as the assessment of spatial convergence across experiments would not be affected by additionally including (observed but not published) null results. We are therefore confident that the validity of our results was not undermined by a publication bias. As a coordinate-based meta-analysis, the ALE algorithm does not consider information such as effect sizes or the extent of activation for each input cluster. Particularly, the former will continue to affect coordinate-based meta-analyses until rigorous standards of data reporting are developed for neuroimaging studies. Although it would be desirable to weigh included studies depending on these criteria, this ideal procedure is difficult to implement and rarely used in practice, because of the need to possess full datasets processed in a homogenous fashion. However, sample size and number of foci reported per individual study are controlled for by the ALE algorithm so that no individual study can significantly bias the ALE analysis (Eickhoff et al., 2009; Turkeltaub et al., 2012).

Another limitation of neuroimaging meta-analyses is that they reflect publication trends and methodological advances. Because research on facial expressions has had a considerable head start compared to research on voices and body postures, our dataset consisted of significantly more studies on facial expressions. Consequently, we were not able to thoroughly test for the influence of perceptual modality on emotion perception and emotion evaluation.

Furthermore, the preponderance of facial stimuli may have also introduced bias into the data and may have limited some of the inferences that could be made from it. However, we were able to dissociate emotion evaluation from facial cues and from vocal cues, as well as emotion evaluation, passive perception and incidental perception from facial expressions alone. The results that we obtained were consistent with the existing literature and previous models of processing emotions from the face and from the voice, and should therefore ensure a degree of confidence in our interpretations.

One might be surprised to find amygdala involvement during explicit evaluation of emotions, given the numerous inconsistent reports claiming either a crucial role (e.g. (Adolphs et al., 1994)) or a supporting role (e.g. (Critchley et al., 2000)). One line of research suggests that implicit forms of emotion perception such as gender discrimination recruit amygdala more so than explicit forms (e.g. (Brück et al., 2011)), while another line of research points to greater amygdala response during non-verbal compared to verbal tasks of emotion evaluation (e.g. (Hariri et al., 2000)). Regarding the latter, it has been proposed that verbalizing the emotion perceived acts as a form of emotion regulation that dampens amygdala activity (Moyal et al., 2013). Our analyses aggregated both verbal and non-verbal tasks of emotion evaluation, thus making it impossible to gauge the contribution of each type of instructions on amygdala activation. Future work can dissociate the effects of verbal and non-verbal evaluation of emotions on amygdala activity. Over and above the involvement of amygdala, a finer analysis of explicit evaluation in terms of task instructions could also reveal potential differences at the level of other brain structures such as IFC and STG. While all explicit tasks of evaluation share crucial characteristics, it is likely that they also diverge in several other aspects.

Another limitation is the use of gender discrimination as the sole representative of incidental processing of emotions. Although we stand by our choice, this may have led to an underrepresentation of the wider range of incidental tasks used in the affective neuroscience

literature. Finally, focusing on emotion effects and task effects preclude us from looking into valence-specific effects.

5. Conclusions

Our study is the first systematical attempt to look at the brain regions involved in actively evaluating the emotions of others. We found that, when we deliberate over which emotions others express, we do not merely perceive those expressions but we also recruit brain regions involved in the correct inference of another individual's mental state. This finding has several theoretical and practical implications for the research on emotional expressions. First, it questions the assumption that emotion perception and emotion evaluation activate the mirror neuron system rather than mindreading systems (Goldman, 2008). Our results show that clear perceptual cues trigger activations in mindreading brain regions in even the simplest emotion evaluation paradigms. Second, it reinforces the recommendation that experimenters be aware that even simple paradigms of emotion recognition would spontaneously recruit mindreading brain regions. Several studies already specifically use passive perception or incidental perception of emotional stimuli to study emotional processing. Consequently, studies on clinical populations (i.e. borderline personality, schizophrenia, autism) using paradigms of explicit emotion evaluation might not reflect impairments in emotion recognition per se but rather impairments in the more general mindreading system for accurately attributing beliefs and mental states to others (Brüne, 2005; Sharp et al., 2011). Third, our findings may help explain how interpersonal perception occurs, such as in zero acquaintance scenarios or when forming first impressions. Studies have shown that person perception occurs fast and accurately based on a limited number of cues (Engell et al., 2007; Waroquier et al., 2010; Wood, 2014). Transient characteristics of another person met at first encounter, including emotional expressions, are spontaneously extrapolated into defining personal traits (Rim et al., 2009; Willis and Todorov, 2006). For instance, a happy

person may be judged at first encounter as having an extraverted or boisterous personality, whereas a sad individual might be labeled as generally gloomy and sulky. The more or less automatic process of interpreting transient affective states as personality traits may reflect the spontaneous mindreading processes behind even the simplest emotion evaluation tasks.

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Fig. 1. Results of the individual ALE meta-analysis of neuroimaging experiments assessing explicit evaluation of emotional expressions from the face, voice, or body posture. The activation map resulting from the ALE analysis was corrected for multiple comparisons using a cluster-level FWE threshold of $p < 0.01$ and cluster-forming threshold of $p < 0.0001$. Notes. IFC = inferior frontal cortex, pSTS = posterior superior temporal sulcus, dMFC = dorsomedial frontal cortex, Amy = amygdala, MFG = middle fusiform gyrus, IPS = intraparietal sulcus, Thal = thalamus, Vis = visual association areas.

Fig. 2. Results of the individual ALE meta-analysis of neuroimaging experiments assessing explicit evaluation of emotional expressions from the face only. The activation map resulting from the ALE analysis was corrected for multiple comparisons using a cluster-level FWE threshold of $p < 0.01$ and cluster-forming threshold of $p < 0.0001$. Notes. IFC_{tri} = pars triangularis of the inferior frontal cortex, pSTS = posterior superior temporal sulcus, dMFC = dorsomedial frontal cortex, Amy = amygdala, MFG = middle fusiform gyrus, IPS = intraparietal sulcus, Thal = thalamus, Vis = visual association areas.

Fig. 3. Results of the individual ALE meta-analysis of neuroimaging experiments assessing explicit evaluation of emotional expressions from the voice only. The activation map resulting from the ALE analysis was corrected for multiple comparisons using cluster-level FWE threshold of $p < 0.01$ and cluster-forming threshold of $p < 0.0001$. Notes. IFCtri = pars triangularis of the inferior frontal cortex, mSTG = middle superior temporal gyrus, dMFC = dorsomedial frontal cortex, fOp = frontal operculum.

Fig. 4. Results of the individual ALE meta-analyses of neuroimaging experiments assessing (A) passive perception and (B) incidental perception of emotional expressions from the face, voice or body posture. The activation map resulting from the ALE analysis was corrected for multiple comparisons using cluster-level FWE threshold of $p < 0.01$ and cluster-forming threshold of $p < 0.0001$. Notes. IFCorb = pars orbitalis of the inferior frontal cortex, pSTS = posterior superior temporal sulcus, dMFC = dorsomedial frontal cortex, prGyr = precentral gyrus, Amy = amygdala, MFG = middle fusiform gyrus, IOG = inferior occipital gyrus.

Fig. 5. Results of the contrast and conjunction analysis of the individual ALE maps assessing explicit evaluating of emotional expressions from the face and from the voice. Notes. IFC_{tri} = pars triangularis of the inferior frontal cortex, pSTS = posterior superior temporal sulcus, mSTG = middle superior temporal gyrus, dMFC = dorsomedial frontal cortex, Ins = insula, Amy = amygdala, MFG = middle fusiform gyrus, Vis = visual association areas.

Fig. 6. Results of the contrast and conjunction analysis of the individual ALE maps assessing explicit evaluating and passive perception of emotional expressions from the face and from the voice. Notes. IFC = inferior frontal cortex, IFC_{oper} = pars opercularis of the inferior frontal cortex, IFC_{tri} = pars triangularis of the inferior frontal cortex, IFC_{orb} = pars orbitalis of the inferior frontal cortex, pSTS = posterior superior temporal sulcus, dMFC = dorsomedial frontal cortex, IPS = intraparietal sulcus, Amy = amygdala, pAmy = peri-amygdala, MFG = middle fusiform gyrus, Vis = visual association areas.

Fig. 7. Results of the contrast and conjunction analysis of the individual ALE maps assessing explicit evaluating and incidental perception of emotional expressions from the face and from the voice. Notes. IFC = inferior frontal cortex, IFCtri = pars triangularis of the inferior frontal cortex, pSTS = posterior superior temporal sulcus, dMFC = dorsomedial frontal cortex, IPS = intraparietal sulcus, Amy = amygdala, pAmy = peri-amygdala, Vis = visual association areas.

Fig. 8. Results of the analysis of the individual ALE maps assessing explicit evaluating, passive perception and incidental perception of emotional expressions. Notes. Amy = amygdala

Fig. 9. A multi-stage model for processing the emotional expressions of others. (1) Perceiving the expressions of others starts in a network of brain regions specialized in extracting the sensory information from visual cues (such as the Vis, MFG, and IOG), and auditory cues (such as the mSTG). (2) The result of this sensory processing is forwarded and integrated in the pSTS where a basic form of intentionality is extracted from the perceived emotional expression. These two stages are sufficient for emotion perception and understanding. (3) Whenever there is a necessity to evaluate the perceived emotion, bilateral posterior and mid IFC are additionally recruited to maintain the available choice options in working memory, to access semantic representations associated with the emotional categories, and to inhibit the perceiver's self-perspective. (4) A spontaneous process of inferring the mental state of the perceived individual is then finalized in the dMFC. Notes. Vis = visual association areas, MFG = middle fusiform gyrus. IOG = inferior occipital gyrus. mSTG = middle superior temporal gyrus. Amy = amygdala. pSTS = posterior superior temporal sulcus. IFC = inferior frontal cortex. dMFC = dorsomedial frontal cortex.

Tab. 1. Descriptive statistics of the paradigms included in the meta-analyses

Paradigm	Articles	Experiments	Participants	Foci
Emotion evaluation	98	102	2167	1457
Passive perception	32	33	666	508
Incidental perception	46	47	878	572

Tab. 2. Descriptive statistics of the sensory modalities included in the meta-analysis.

	Emotion evaluation		Passive perception		Incidental perception	
	<i>Experiments</i>	<i>Participants</i>	<i>Experiments</i>	<i>Participants</i>	<i>Experiments</i>	<i>Participants</i>
Faces	75	1742	20	411	37	701
Voices	18	291	5	100	9	166
Body	4	65	4	83	0	0
Mixed	5	69	4	72	1	11

Note: “Mixed” refers to stimuli presented in a combination of cues (i.e. expressions from faces and voices; from faces and body postures).