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# Do anger perception and the experience of anger share common neural mechanisms? Coordinate-based meta-analytic evidence of similar and different mechanisms from functional neuroimaging studies

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A B S T R A C T

The neural bases of anger are still a matter of debate. In particular we do not know whether anger perception and anger experience rely on similar or different neural mechanisms. To study this topic, we performed activation-likelihood-estimation meta-analyses of human neuroimaging studies on 61 previous studies on anger perception and experience. Anger perception analysis resulted in significant activation in the amygdala, the right superior temporal gyrus, the right fusiform gyrus and the right IFG, thus revealing the role of perceptual temporal areas for perceiving angry stimuli. Anger experience analysis resulted in the bilateral activations of the insula and the ventrolateral prefrontal cortex, thus revealing a role for these areas in the subjective experience of anger and, possibly, in a subsequent evaluation of the situation. Conjunction analyses revealed a common area localized in the right inferior frontal gyrus, probably involved in the conceptualization of anger for both perception and experience.

Altogether these results provide new insights on the functional architecture underlying the neural processing of anger that involves separate and joint mechanisms. According to our tentative model, angry stimuli are processed by temporal areas, such as the superior temporal gyrus, the fusiform gyrus and the amygdala; on the other hand, the subjective experience of anger mainly relies on the anterior insula; finally, this pattern of activations converges in the right IFG. This region seems to play a key role in the elaboration of a general meaning of this emotion, when anger is perceived or experienced.

## 1. Introduction

### 1.1. Understanding anger

Anger is one of the core emotional experiences that characterize our lives and that is often aroused during interpersonal interactions (Grecucci et al., 2013a,b,c; Gilam and Hendler, 2015; Mattevi et al., 2019; Frederickson et al., 2018). These interactions can involve different situations characterized by frustration or personal offense, such as goal obstruction episodes, violation of rules, norms and promises, or status and power derogation (Bies and Tripp, 2004; Aquino et al., 2006; Grecucci et al., 2013a,b,c; Gilam and Hendler, 2015; Mattevi et al., 2019).

This evidence shows that, among other negative valenced emotions, anger is characterized by an approach rather than an avoidance inclination (Berkowitz and Harmon-Jones, 2004) that leads us to respond to difficult situations. This approach-oriented motivational inclination is suggested to be the result of a brain "low road" linked to uncontrollable anger and rapid aggression (Alia-Klein et al., 2020) that can be eventually down-regulated (Berkowitz and Harmon-Jones, 2004; Frederickson et al., 2018; Grecucci et al., 2013c; 2015; 2017; 2020; Mattevi et al., 2019).

Experimental studies on anger and on its neural bases have been conducted in the last years to better understand these processes. However, the heterogeneity of experimental paradigms used to study this topic did not always lead to similar results. Different reviews suggest interesting hypotheses on the neural bases of anger (see for example Gilam and Hendler, 2015; Alia-Klein et al., 2020), however, literature lacks a meta-analytic approach. One useful distinction to better understand this emotion is to separate the perception of anger from the experience of anger. *Anger perception* involves the perception of a stimuli expressing anger (perception of anger conveyed by faces or voices of others), whereas, *anger experience* refers to the elicitation of the experience of anger in the observer. While in the first case the emotion is stereotypical represented "within" the stimulus, in the second case, the stimulus is intended to evoke the emotion within the observer. The aim

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of this paper is to find similarities and differences in the neural bases of these two facets of anger. Beside anger, the issue of separating the neural mechanisms of the perception of emotions from ethe experience of emotions, is of great theoretical interest for advancing our understanding of emotions, as it is yet a confused chapter in the affective neuroscience literature.

### 1.2. Anger perception

Anger perception (AP) has been investigated studying the perception of stimuli characterized by anger, such as faces or voices. Angry faces, categorized as "negative" or "threatening" stimuli, elicit a heightened startle response when compared to neutral, happy and even fearful faces (Springer et al., 2007; Dunning et al., 2010). Other physiological responses during the perception of angry faces and voices include among others, increased heart rate, skin conductance response and forehead temperature (Dimberg, 1987; Aue et al., 2011; Banks et al., 2012). At a neural level, the view of angry faces elicits activity in regions including different areas of the PFC (OFC, IFG, MFG, ACC), the entorhinal and parahippocampal gyrus, subcortical regions and occipito-temporal areas (Fusar-Poli et al., 2009; K.A. Lindquist et al., 2012; Gilam and Hendler, 2015). In particular, the superior temporal gyrus seems to play a key role when considering the processing of social signals (e.g. angry faces, voices, gestures) and contextual information that individuals use to interpret others' behaviors (Seok and Cheong, 2019; Baldwin, 1992; McArthur and Baron, 1983). Further, in a study investigating both the perception and expression of anger, the STG was found to mediate the relation between the amygdala reactivity and aggression, probably because of a higher attribution of hostility to other's intentions (Buades-Rotger et al., 2016). Accordingly, the amygdala is reactive to the view of angry facial expressions, especially when considering idiosyncratic personality differences and arousal (Passamonti et al., 2008; K.A. Lindquist et al., 2012). Finally, different areas of the ventral prefrontal cortex, especially in the right hemisphere, seem to play a key role in the recognition and the classification of perceived emotions, including anger (Jastorff et al., 2015; Lieberman et al., 2007; Adolphs, 2002; Hornak et al., 1996; Blair et al., 1999).

### 1.3. Anger experience

Anger experience (AE) has been investigated through paradigms designed to elicit the emotion of anger in participants. Although perceiving a face or voice conveying anger has been supposed to elicit a certain quantity of anger in the observer (Penton-Voak et al., 2013), the experience of anger cannot be evoked exclusively by the perception of an angry stimulus (Gilam and Hendler, 2015). Among the set of paradigms to elicit anger in participants, social interactive games with an opponent are commonly used. Classic economic games such as the Ultimatum or Dictator games (Guth et al., 1982; Sanfey et al., 2003; Grecucci et al., 2013a,b,c; 2015; G. Gilam et al., 2018; De Panfilis et al., 2019; Grecucci et al., 2020) based on unfair monetary offers have been extensively used, as well as games based on provocation (Taylor Aggression Paradigm, Taylor, 1967), or exclusion (Radke et al., 2018; Chester et al., 2018b; Dewall et al., 2011). Another common way to elicit anger involves the retrieval of autobiographic episodes characterized by the experience of anger (cf. Gilam and Hendler, 2015).

At a physiological level, anger is associated with heightened heart rate, skin conductance responses, respiratory rate, and muscle activity that represent the arousal characteristic of this emotion (Potegal et al., 2010; Kreibig, 2010). These physiological changes have a functional value to motivate individuals to face physically or socially caused harm.

About the neural bases of anger experience, studies using interpersonal provocative paradigms (such as the Ultimatum and the Dictator games, or the Taylor Aggression Paradigm), have been shown to increase brain activity during provocation or unfair situations in dACC, insula, ventrolateral, dorsolateral and dorsomedial PFC, precuneus, temporal pole, TPJ, and visual regions including the FFG (Wagels et al., 2019; Weidler et al., 2019; Repple et al., 2017; Feng et al., 2015). Paradigms involving the recollection or the imagination of personal autobiographic memories characterized by anger have shown different brain activations, such as in the PFC, the medial temporal lobe, the anterior insula, the orbitofrontal cortex, the IFG, the amygdala and the putamen/caudate (Blair, 2011; Fabiansson et al., 2012; K.A. Lindquist et al., 2012; Gilam and Hendler, 2015). Finally, a new interesting kind of paradigm was proposed by Denson and colleagues (T.F. Denson et al., 2009; 2013; 2014). It consists in an actual interpersonal induction of anger through an insult by a rude experimenter. These studies found brain activity related to anger in the ACC, the dorsomedial PFC, the SFG, MFG, the Insula, the Thalamus and the Amygdala.

Of all brain activations, the insula seems to play a key role in the experience of anger as it is commonly found in the above-mentioned studies. Indeed, its activity has been linked to the arousal and visceral sensations of the experience of anger (Ochsner and Gross, 2014; K.A. Lindquist et al., 2012; Penfield and Faulk, 1955), it is modulated when anger is down-regulated by cognitive strategies (Grecucci et al., 2013b,c), and it is increased during angry rumination and retaliation (T.F. Denson et al., 2009; Emmerling et al., 2016). Moreover, being the anterior insula a part of the salience network, may help detecting situations characterized by subjective pain and emotional experience (Gilam and Hendler, 2015). In addition, this region plays a key role in representing core affective feelings and emotional awareness (Craig, 2009); therefore, it might represent the "core affect" of anger experience. Supporting this hypothesis, Lindquist and colleagues (K.A. 2012) in a meta-analysis of different emotions found that, while other brain regions associated to core affect such as the amygdala were not specific for anger, the activity of some voxels of the left insula was found especially during anger experience when compared to other emotions. In line with the above findings, we hypothesize that while the amygdala's role in core affect might be more related to the attribution of saliency to external stimuli (i.e. anger perception), the insula's role in core affect might be more related to the subjective feelings of anger (i.e. anger experience).

Other key regions involved in anger experience, especially when interpersonally provoked, are the ventral regions of the PFC, probably associated with the regulation of anger and aggressive expression. More precisely, the vlPFC may be implicated in cognitive control, whereas, the vmPFC may be involved in the evaluation of the possible outcomes of anger (Gilam and Hendler, 2015; Ochsner and Gross, 2014). Notably, the vmPFC has been proposed as a key region for the generation of affective meaning, whose activity is critical when affective behavior is modulated by conceptual information about specific outcomes (Roy et al., 2012). However, medial and lateral prefrontal regions may interact in the generation and regulation of anger. Accordingly, affective labeling shows greater activity in the right vlPFC (BA 45,47), which in turn reduces the response of limbic regions through the mediation of vmPFC (Lieberman et al., 2007). In sum, the vmPFC may play a role in anger regulation, by taking into account the expected value of the behavioral outcomes of expressing anger (Gilam et al., 2015; G. 2018; Gilam and Hendler, 2015).

### 1.4. Anger conceptualization

Beside the differences in anger perception and anger experiences, commonalities may exist too. Thus, after looking for distinct and specific mechanisms for anger perception and anger experience, we also aim to explore possible overlaps between the two. We expect to find prefrontal brain regions such as the right IFG (Lieberman et al., 2007) or the vmPFC (Roy et al., 2012), to be involved in both aspects of anger, possibly related to the conceptualization of anger. According to the constructionist view of emotion, conceptualization is a fundamental part of every emotion. In Barrett words (2006): "people experience an emotion when they conceptualize an instance of affective feeling. In this view, the experience of emotion is an act of categorization, guided by embodied knowledge about emotion. […] We experience an instance of emotion in ourselves, or see it in others, when we conceptualize an ongoing, basic affective state via the process of categorization ". Although other perspectives do not assign such a causal role to conceptualization, mainly all theories consider a conceptual level to be part of the emotional experience (see for example, Damasio et al., 2000).

### *1.5. Aims of the present study*

The neural correlates of anger are still under investigation, and the knowledge discovered so far is based on different and hard to compare paradigms. When taken separately the individual imaging studies showed contrasting finding. In addition to some interesting reviews (Alia-Klein et al., 2020; Gilam and Hendler, 2015), meta-analyses on emotions (Fusar-Poli et al., 2009; K.A. Lindquist et al., 2012; Kirby and Robinson, 2017 Nov) hold the power to make the neural bases of anger clearer. However, the past neuroimaging studies and meta-analyses on emotions focused on the perception of emotional faces (Fusar-Poli et al., 2009) or on the experience of the induced emotions (Kirby and Robinson, 2017 Nov), without making comparisons between the two. Understanding whether emotion perception and emotion experience differ at a brain level, is of fundamental importance for advancing knowledge on affective processes. For the first time, we aim to offer a more complete view of neuroimaging studies on anger by analyzing separately anger perception and anger experience in order to detect possible similarities and differences. To this end, we performed a meta-analysis of the available neuroimaging data to unveil: 1) the neural bases of the perception of anger in others; 2) the neural bases of the subjective experience of anger; 3) eventual common mechanisms behind the two processes.

We expect that anger perception studies would elicit brain activity in emotional perceptual areas such as the amygdala and temporal regions. On the other hand, we expect that anger experience would elicit brain activity in spreader fronto-temporal areas involving the insula and the ventrolateral PFC that seem to be involved in the subjective experience, and the evaluation and control of the situation, respectively. Finally, we expect that a frontal brain region such as the vmPFC (Roy et al., 2012) or the rIFG (Lieberman et al., 2007) could emerge from the conjunction analysis, as a common substrate of conceptual categorization for both anger perception and experience. Notably, the present study is not aimed to solve theoretical questions on how emotions (and anger) are or are not localized, or distributed, nor constructed in the brain. The aim is to find possible distinct and common mechanisms of anger perception and experience.

## 2. Methods

### *2.1. Rationale of the meta-analytic approach*

There are different reviews on the neural bases of anger that compare different paradigms or different phases of anger processing, from provocation to regulation (Gilam and Hendler, 2015; Alia-Klein et al., 2020; Blair, 2011; T.F. Denson et al., 2009). However, quantitative evidence from meta-analytic studies is still needed to identify the most consistent findings and to overcome the limitations of single neuroimaging studies.

Therefore, the aim of this paper is to identify the brain regions consistently associated with anger perception and with anger experience. We defined "anger perception" a situation in which participants consciously perceive a stimulus characterized by anger and "anger experience" a situation in which either a socially-related anger is induced through social interactive games or a situation of experiencing anger is evoked through imagination or recollection.

In addition, we hypothesize that some brain regions may be involved in both processes when considering emotional categorization, given that conceptual knowledge allows emotions (perceived or experienced) to become meaningful (Barrett et al., 2006). To quantify the overlap between the neural bases of anger perception and anger experience we performed a third ALE analysis addressing the conjunction between these two processes. The rationale of this choice rests on the fact that almost all studies on anger are limited to perceptual or experiential paradigms, rarely relying on both of them. Therefore, a comparison between these conditions is necessary to understand whether there is a brain area involved in anger perception and anger experience. This would allow us to relate the associated brain areas to the aspects of conceptualization of this emotion rather than on a specific process (perception or experience).

Based on current suggestions on ALE meta-analyses (Muller et al., 2018; Eickhoff et al., 2016), we aimed to include at least 17–20 experiments in each condition (anger perception and anger experience) to achieve sufficient power and to ensure that results would not be driven by a few or a single experiment (Arioli and Canessa, 2019). To this purpose, first a literature search was performed in order to check whether there were enough studies containing our conditions of interest. Then, a selection of papers was done in order to select experiments that fulfilled all inclusion criteria (see 2.2.1 and 2.2.2 for more details). Finally, to avoid errors in the data, a double-checked extraction of the necessary information for the analyses was performed, including the coordinates, the sample size and the acquisition space (Muller et al., 2018).

### *2.2. Literature search and study selection*

A systematic online database search was performed in January 2018 on PubMed (https://www.ncbi.nlm.nih.gov/pubmed/) by entering all possible combinations of search items as detailed in the next subsections.

#### *2.2.1. Anger perception*

In order to find studies investigating the neural underpinnings of anger, a systematic online database search was performed in January 2019 on PubMed (https://www.ncbi.nlm.nih.gov/pubmed/) using the following terms: ((anger) OR (angry) OR (basic emotions) OR (frustration) OR (aggression)) AND ((fMRI) OR (PET) OR (positron emission tomography) OR (functional magnetic resonance imaging) OR (functional MRI)), and setting a range of dates between January 1st 1995 and January 28th 2019. This research revealed 1839, which were processed to see whether they met the following criteria:

1) Papers originally published in English.
2) Functional neuroimaging studies performing univariate whole brain analyses. Hence, studies using only region of interest (ROI) analyses or multivariate analyses were excluded.
3) Studies including adult (age-range: 18–55 years), non-clinical, and drug-free participants.
4) Studies reporting the MNI or Talairach coordinates of the activations.
5) Studies investigating brain activity related to the perception of anger in the visual or auditory modality. To this purpose, we selected only the specific contrasts reporting angry > neutral stimuli. This allowed controlling the variability associated with different experimental paradigms, given that we included only studies in which the baseline condition was represented by the same angry stimuli but with a neutral valence, excluding rest and fixation baseline (Stark and Squire, 2001). Studies failing to report this information were excluded.

This method allowed us to identify 35 studies investigated anger perception (297 foci, 778 participants, 430 M, mean age $26.23 \pm 8.97$). The most used paradigm in the anger perception condition was the presentation of emotional vs. neutral visual (angry vs. neutral faces) or auditory (angry vs. neutral prosody) stimuli. We have also added in the supplementary materials the analyses (not considered in the discussion given the smaller number of studies) on these two main conditions included in anger perception - visual vs auditory stimuli.

### 2.2.2. Anger experience

In order to find studies investigating the neural substrate of anger, a systematic online database search was performed in January 2019 on PubMed (https://www.ncbi.nlm.nih.gov/pubmed/). The Boolean expression used in the search was: ((anger) OR (angry) OR (basic emotions) OR (frustration) OR (aggression)) AND ((fMRI) OR (PET) OR (positron emission tomography) OR (functional magnetic resonance imaging) OR (functional MRI)), and setting a range of dates between January 1st 1995 and January 28th 2019. This research revealed a total of 1839 studies, which were processed to se whether they met the following criteria:

1) Papers originally published in English.
2) Functional neuroimaging studies performing univariate whole brain analyses. Hence, studies using only region of interest (ROI) analyses or multivariate analyses were excluded.
3) Studies including adult (age-range: 18–55 years), non-clinical, and drug-free participants.
4) Studies reporting the MNI or Talairach coordinates of the activations.
5) Studies investigating brain activity related to the experience of anger in social interaction games or during imagery tasks. To this purpose, we selected only the specific contrasts reporting anger > neutral or provocative> non provocative

conditions, excluding studies that used rest or fixation baseline as control conditions rather than neutral stimuli, in order to reduce the effect of different baseline conditions (Newman et al., 2001) in our meta-analysis. Studies failing to report this information were excluded. We acknowledge the fact that our inclusion criteria are strict, but this was done for the sake of clarity. Future meta-analysis can explore other specific aspects of anger not considered here (Table 1).

This method allowed us to identify 26 studies investigating anger experience (310 foci, 724 participants, 407 M, mean age 24.88±6.90). In the anger induction paradigm, the most used paradigms were different interpersonal games with an opponent (e.g. Taylor Aggression Paradigm, Ultimatum Game, Cyberball Paradigm) or the imagination of a situation characterized by anger (e.g. with scripts, vignettes or recollection of autobiographical memories). Even if not all the studies included in our meta-analysis assessed the level of anger in each trial, it has been previously demonstrated that anger is enhanced with provocative or unfair situations of the Taylor Aggression Paradigm (Wagels et al., 2019; Repple et al., 2018; Repple et al., 2017) and of the Ultimatum Game (G. Gilam et al., 2018; Srivastava et al., 2009) and with social exclusion of the Cyberball paradigm (Radke et al., 2018; Seidel et al., 2013; Chow et al., 2008).

Therefore, given the need to consider as many similar studies as possible for the meta-analysis purpose, we have decided to include all the papers emerged in our PubMed search that used these kinds of paradigms and reported the contrast provocative versus not provocative situations (considering as provocative also unfair offers and social exclusion situations). Instead, imaginative tasks considered in this meta-analysis usually reported the specific and/or the level of the experienced emotion during each situation. We have also added in the supplementary materials the analyses (not considered in the discussion given the smaller number of studies) on the two main processes included in anger experience - interpersonal games vs imagination.

### 2.3. Activation likelihood estimation

All analyses were performed with the software GingerALE v3.0.2 (http://brainmap.org/). This software uses activation likelihood estimation method (Eickhoff et al., 2009; S.B. 2012; Turkeltaub et al., 2012) to identify spatial convergence across the foci reported in the selected studies. The first step consisted in converting all foci in Talairach coordinates; in order to perform this step we used the "ConvertFoci" function included in GingerALE. Then, we performed all the analyses.

Activation foci were initially used to build three-dimensional maps applying an empirically derived full-width half-maximum blur depending on the sample size used in the study. Hence, the foci were considered centers of three-dimensional Gaussian probability. These maps were then combined finding the maximum across each focus' Gaussian (Turkeltaub et al., 2012) to produce a modeled activation map. Then, voxel-wise ALE scores describing the convergence of results at each brain voxel are computed combining all the individual modeled activation maps. The ALE scores were compared with an empirically defined null distribution, reflecting a random spatial association between experiments, using a permutation test (Turkeltaub et al., 2012; Arioli and Canessa, 2019).

For each set of studies (anger perception, anger experience) we performed the meta-analysis applying a cluster-level family-wise error correction using on the voxel-level uncorrected threshold of $p<0.001$, 1000 permutations and a cluster-level threshold of $p < 0.05$. This is considered the most reasonable approach according to current indications (Eickhoff et al., 2016; Muller et al., 2018).

The second step was to unveil the common and specific contributions of anger perception and experience to the neural processing of this emotion. To this purpose, direct comparisons and a conjunction analysis were performed comparing the two processes, within GingerALE. Specifically, two ALE contrast images were created and compared by directly subtracting one input image from the other for direct comparisons. Otherwise, the conjunction image was created using the voxel-wise minimum value of the ALE images, to display the similarity between the data sets. To avoid biases due to sample size differences in the compared studies, GingerALE software computed a simulation of data, pooling the original data and randomly sorting them into two new groupings equivalent in size to the original data sets, and calculated ALE maps for the new datasets. These simulated images were then compared with the true data. After 1000 permutations, a voxel-wise p-value image was computed, indicating where the specific value of each voxel was placed on the value distribution of each specific voxel. Values were converted into z-scores. These results were thresholded with $p < 0.001$ uncorrected and a cluster size > 200 $mm^3$, since input data for this conjunction analysis were already corrected for multiple comparisons. Anatomical labels of final cluster locations are provided by the Talairach Daemon (Lancaster et al., 1997; 2000) and Yale MNI-Talairach Converter (http://sprout022.sprout.yale.edu/mni2tal/mni2tal.html) while results are visualized using Mango (http://ric.uthscsa.edu/mango/mango.html).

## 3. Results

### 3.1. Anger perception

The meta-analysis on anger perception revealed five significant clusters (see Fig. 1 and Table 2). Two clusters were located bilaterally in the amygdala and in the left rhinal cortex, while the other two were located in the right hemisphere at the level of the inferior and the lateral orbito-frontal gyri and the superior temporal gyrus.

In particular, cluster 1 was located in the left hemisphere, in particular 58.8% Limbic Lobe, 37.1% Sub-lobar, 2.1% Frontal Lobe, 2.1% Temporal Lobe

(56.7% Amygdala, 13.4% Lateral Globus Pallidus, 11.3% Medial Globus Pallidus, 6.2% Brodmann area 34, 6.2% Brodmann area 28, 4.1% Putamen, 2.1% Brodmann area 13); cluster 2 was located in the right hemisphere, in particular 92.3% Temporal Lobe, 7.7% Parietal Lobe (65.4% Brodmann area 42, 19.2% Brodmann area 22, 7.7% Brodmann area 41, 7.7% Brodmann area 40); cluster 3 was located in the right hemisphere, in particular: 100% Limbic Lobe (86.3% Amygdala, 8.2% Brodmann area 28, 5.5% Brodmann area 34); cluster 4 was located in the right hemisphere, in particular: 100% Frontal Lobe (75% Brodmann area 45, 20% Brodmann area 47); cluster 5 was located in the right hemi-

**Table 1**
Overview of the 35 studies on anger perception and the 26 studies on anger experience included in the meta-analysis.

| N° paper | Author | Subjects | Age | fMRI or PET | Stimuli | Contrast |
|---|---|---|---|---|---|---|
| Anger perception studies | | | | | | |
| 1 | (Rymarczyk et al., 2018) | 46 (21F, 26 M) | 23.7+−2.5 | fMRI | face perception | angry>neutral |
| 2 | (Lassalle et al., 2017) | 21M | 19.70+−7.74 | fMRI | face perception | angry>neutral |
| 3 | (Chan et al., 2016) | 54 hc (38.9% M) | 23+−2.4 | fMRI | face perception | angry>neutral |
| 4 | (Morawetz et al., 2016) | 60(30F) | 30.48+−11.10 | fMRI | face perception | angry>neutral |
| 5 | (Mccloskey et al., 2016) | 20(12 M) | 32.8 | fMRI | face perception | angry>neutral |
| 6 | (Wabnegger et al., 2015) | 22 (11 M) | 51.8+−9.8 | fMRI | face perception | angry>neutral |
| 7 | (Wheaton et al., 2014) | 24 (54.2%F) | 25+−5.6 | fMRI | face perception | angry>neutral |
| 8 | (Ihme et al., 2014) | 48 (23F) | 24+−3 | fMRI | face perception | angry>neutral |
| 9 | (Pawliczek et al., 2013b) | 33M | 22.3+−2 | fMRI | face perception | anger>neutral |
| 10 | (Weisenbach et al., 2012) | 17M | 31.2+−14.2 | fMRI | face perception | anger>neutral |
| 11 | (Passamonti et al., 2012) | 30(17F) | 25.1+−3.2 | fMRI | face perception | angry>neutral |
| 12 | (Jehna et al., 2011) | 15 (5 M) | 30.3+−10.6 | fMRI | face perception | angry>neutral |
| 13 | (Jehna et al., 2011b) | 30(21F) | 36.3 ± 14.3 | fMRI | face perception | angry>neutral |
| 14 | (Chakrabarti et al., 2006) | 26(13 M) | 23.4+−4.23 | fMRI | face perception | angry>neutral |
| 15 | (Hurlemann et al., 2008) | 14(7) | 25.4+−2.4 | fMRI | face perception | anger>neutral |
| 16 | (Chiao et al., 2008) | 14M | students | fMRI | face perception | angry>neutral |
| 17 | (Jollant et al., 2008) | 16M | 34.3+−9.8 | fMRI | face perception | angry>neutral |
| 18 | (Beaver et al., 2008) | 22(13F) | 26.2+−7.6 | fMRI | face perception | angry>neutral |
| 19 | (Lee et al., 2006) | 18(9F) | 26 | fMRI | face perception | angry>neutral |
| 20 | (Rauch et al., 2007) | 20(10 M) | 25.3+−2.1; 24.5+−3.1 | fMRI | face perception | angry>neutral |
| 21 | (Britton et al., 2006) | 12(6F) | 21.4+−2.2 | fMRI | face perception | angry>neutral |
| 22 | (Sato et al., 2004) | 10(5F) | 24.4+−7.8 | fMRI | face perception | anger>neutral |
| 23 | (Kilts et al., 2003) | 13(9 M) | 24.5(22–26 range) | PET | face perception | angry>neutral |
| 24 | (Blair et al., 1999) | 13M | 25.3 | PET | face perception | angry>neutral |
| 25 | (Sprengelmeyer et al., 1998) | 6(2 M) | 23.5+−1.3 | fMRI | face perception | angry>neutral |
| 26 | (Castelluccio et al., 2015) | 8(3 M) | 22.68+−3.84 | fMRI | voice perception | angry>neutral |
| 27 | (Mitchell et al., 2016) | 27(14F) | 21.5+−3.89 | fMRI | voice perception | angry>neutral |
| 28 | (Ceravolo et al., 2016) | 17(8 M) | 24.29+−4.87 | fMRI | voice perception | angry>neutral |
| 29 | (Smith et al., 2015) | 17(10 M) | 26.5+−5.95 | fMRI | voice perception | angry>neutral |
| 30 | (Frühholz et al., 2014) | 15(8F) | 23.67+−3.5 | fMRI | voice perception | angry>neutral |
| 31 | (Maurage et al., 2013) | 12 (5F) | 23.4+−4.21 | fMRI | voice perception | angry>neutral |
| 32 | (Mothes-Lasch et al., 2011) | 24(16F) | 22.7+−1.49 | fMRI | voice perception | angry>neutral |
| 33 | (Ethofer et al., 2009) | 24(12 M) | 26.3 | fMRI | voice perception | angry>neutral |
| 34 | (Sander et al., 2005) | 15(7 M) | 24.4+−4.6 | fMRI | voice perception | angry>neutral |
| 35 | (Grandjean et al., 2005) | 15(7F) | | fMRI | voice perception | angry>neutral |
| *Anger Experience Studies* | | | | | | |
| *N°paper* | *Author, year* | *Subjects* | *Age* | *fMRI or PET* | *Stimuli* | *Contrast* |
| 1 | (Weidler et al., 2019) | 52M | 24.86+−3.92 | fMRI | Taylor Aggression Paradigm (modified) | *Parametric modulation: provocation intensity* |
| 2 | (Gilam et al., 2018) | 25(15F) | 26.16+−3.63 | fMRI | Anger Infused Ultimatum Game | Unfair>Fair offers (High provocation > Low provocation) |
| 3 | (Repple et al., 2018) | 42(22 M) | F24.77 (2.8); M27.45(9.3) | fMRI | Taylor Aggression Paradigm | High provocation > Low provocation |
| 4 | (Chester and Dewall, 2018a) | 61 (27.87% M) | 18–22 | fMRI | Taylor Aggression Paradigm | High provocation > Low provocation |
| 5 | (Repple et al., 2017) | 29M | 23.6+−3.2 | fMRI | Taylor Aggression Paradigm | Aggression after high provocation > aggression after low provocation |
| 6 | (Skibsted et al., 2017) | 19 (8 M) | 24.6+−2.9 | fMRI | Point subtraction aggression paradigm | Provocation event > Monetary Response (High provocation > Low provocation) |
| 7 | (Buades-Rotger et al., 2017) | 36F | 22+−4 | fMRI | provocative fight or avoid task | High>low selection (High provocation > Low provocation) |
| 8 | (Emmerling et al., 2016) | 15M | 22.33+−2.35 | fMRI | provoking, aggressive reaction, retailation (340) | Aggressive reaction to provoking opponent > non aggressive reaction to non-provoking opponent (High provocation and aggression > Low provocation) |
| 9 | (Dambacher et al., 2014) | 15M | 22.33+−2.35 | fMRI | Taylor Aggression Paradigm (modified) | Provocation > No provocation (High provocation > Low provocation) |
| 10 | (Minamoto et al., 2014) | 35(11F) | 23.05+−2.53 | fMRI | frustration (ego blocking) | Ego blocking > Neutral condition (High provocation > Low provocation) |

(*continued on next page*)

**Table 1** (*continued*)

| Anger perception studies N° paper | Author | Subjects | Age | fMRI or PET | Stimuli | Contrast |
|---|---|---|---|---|---|---|
| 11 | (Pawliczek et al., 2013) | 40M | 22.4+−2.2 | fMRI | frustration | Unsolvable > Solvable conditions (High provocation > Low provocation) |
| 12 | (Vieira et al., 2013) | 17 (12F) (low psychopathy… Also high) | 21.24+−2.05 | fMRI | Ultimatum Game | Linear regression: Unfair > Fair (High provocation > Low provocation) |
| 13 | (Lotze et al., 2007) | 16M | 28.6+−6.5 | fMRI | provocation | Parametric modulation: receiving aversive stimuli (provocation) |
| 14 | (Krämer et al., 2007) | 15(11F/20, 5 sbj removed) | 22.9+−2.2 | fMRI | Taylor Aggression Paradigm | High provocation > Low provocation |
| 15 | (Dougherty et al., 2004) | 10 (5F) | 33.90+−11.85 | PET | Autobiographical scripts | Anger>Neutral |
| 16 | (Abler et al., 2005) | 12 (6F) | 21–33 | fMRI | frustration | Frustration > No frustration |
| 17 | (Radke et al., 2018) | 80(40F) | males: $M$ = 24.38 years, SD = 3.37, females: $M$ = 24.69 years, SD = 3.85 | fMRI | Cyberball task | social exclusion> >technical exclusion (High provocation > Low provocation) |
| 18 | (Chester et al., 2018b) | 60(38F) | 20.28+−2.77 | fMRI | Cyberball task | Reject>Accept (High provocation > Low provocation) |
| 19 | (Dewall et al., 2011) | 25(16F) | | fMRI | Cyberball task | Exclusion > Inclusion (High provocation > Low provocation) |
| 20 | (Park et al., 2016) | 16M | 50.06+−6.10 (31–61) | fMRI | induction: audiovisua film clips | Anger > Neutral conditions |
| 21 | (Oaten et al., 2018) | 20(9 M) | 22.2+−2.8 | fMRI | Vignettes | Anger > Neutral conditions |
| 22 | (Pietrini et al., 2000) | 15 (8 M) | 22+−2 | PET | Imagery | Aggression>Neutral |
| 23 | (Damasio et al., 2000) | 11F+ 12M | 24–42 | PET | imagery | Anger > Neutral conditions |
| 24 | (Dougherty et al., 1999) | 8M | 25+−4.4 | PET | imagery | Anger > Neutral conditions |
| 25 | (Marci et al., 2007) | 10 (5 M) | 33.9+−11.9 | PET | autobiographical memory | Anger > Neutral conditions |
| 26 | (Kimbrell et al., 1999) | 8f+10M | 31.25+−8.9F; 34.75+−11.6M | PET | recall | Anger > Neutral conditions |

**Table 2**
Talairach labels of regions of interest, Clusters, maximum ALE value and Brodmann area are shown.

| Analysis | Cluster | x | y | z | ALE | Brodmann | Label (Nearest Gray Matter within 5 mm) |
|---|---|---|---|---|---|---|---|
| Anger Perception | 1 | −18 | −8 | −10 | 0.027 | | Left Amygdala |
| | 1 | −24 | −2 | −10 | 0.024 | 34 | Left Amygdala, Left Entorhinal Cortex |
| | 1 | −30 | 8 | −12 | 0.016 | 13 | Left Inferior Frontal Gyrus/Left Insula |
| | 2 | 58 | −30 | 10 | 0.019 | 42, 22 | Right Superior Temporal Gyrus |
| | 2 | 48 | −36 | 4 | 0.017 | 22, 21 | Right Superior and Middle Temporal Gyrus |
| | 3 | 20 | −4 | −14 | 0.024 | | Right Amygdala |
| | 4 | 48 | 26 | 6 | 0.022 | 45 | Right Inferior Frontal Gyrus, pars triangularis |
| | 5 | 50 | −62 | 2 | 0.022 | 37 | Right Fusiform Gyrus |
| | 5 | 42 | −50 | 6 | 0.016 | 37 | Right Fusiform Gyrus |
| Anger Experience | 1 | −32 | 22 | 2 | 0.027 | 13 | Left Insula |
| | 1 | −40 | 24 | 2 | 0.024 | 47 | Left Inferior Frontal Gyrus, pars orbitalis |
| | 2 | 40 | 28 | 4 | 0.028 | 13, 45 | Right Insula, Inferior Frontal Gyrus, pars triangularis |
| | 2 | 44 | 18 | 12 | 0.019 | 45, 44 | Right Inferior Frontal Gyrus, pars triangularis and opercularis |
| | 2 | 38 | 12 | 10 | 0.017 | 13, 44 | Right Insula, Inferior Frontal Gyrus, pars opercularis |
| Conjunction (Perception & Experience) | 1 | 44 | 26 | 4 | 0.015 | 45 | Right Inferior Frontal Gyrus, pars triangularis |
| | 2 | 46 | 24 | 8 | 0.014 | 45 | Right Inferior Frontal Gyrus, pars triangularis |
| | 3 | 48 | 22 | 8 | 0.013 | 45 | Right Inferior Frontal Gyrus, pars triangularis |

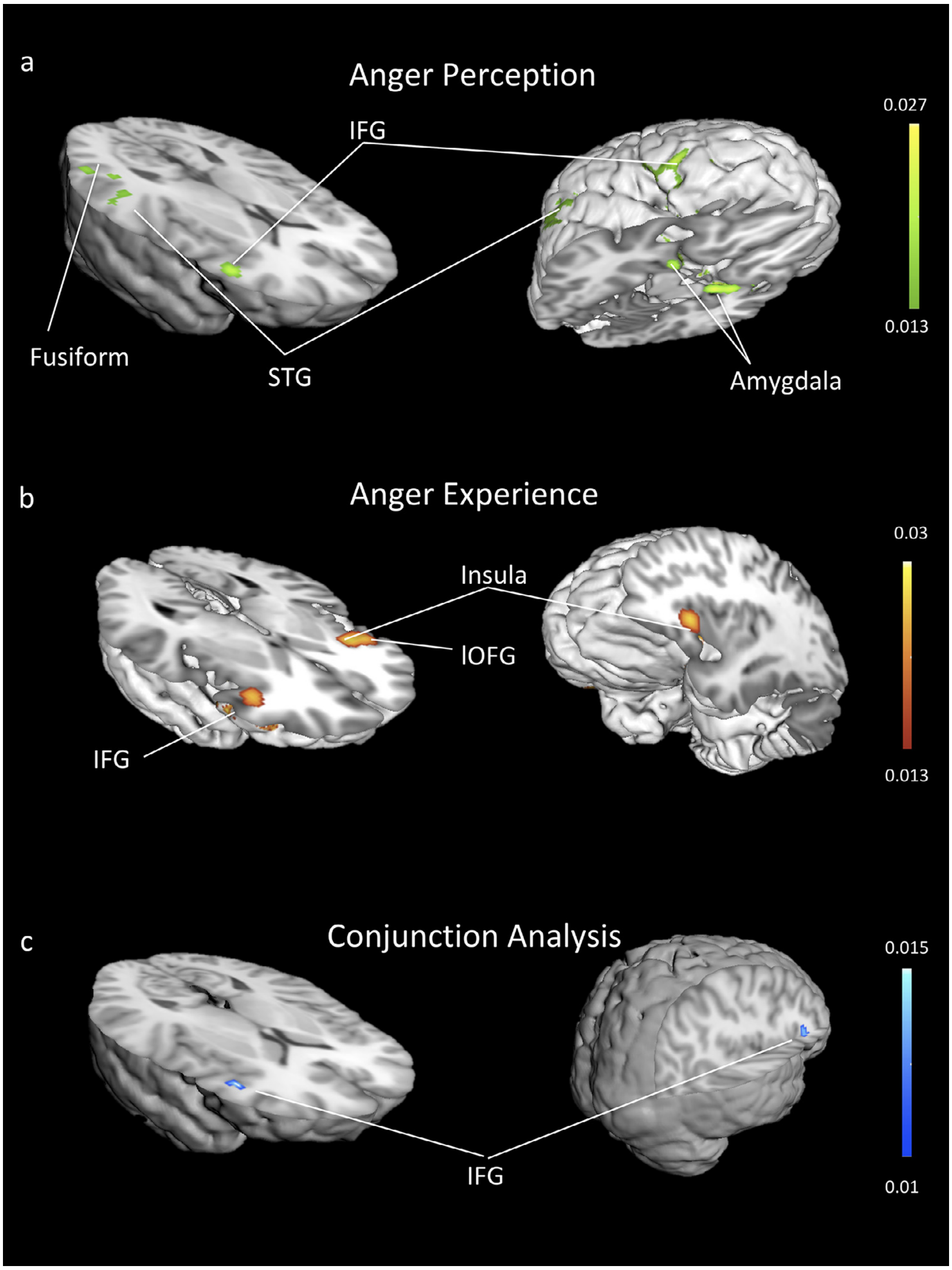


**Fig. 1.** The neural bases of anger perception and anger experience. The figure shows the neural correlates of the first meta-analysis on anger perception, including the superior temporal gyrus (STG), the right fusiform gyrus, the amygdala and the right inferior frontal gyrus (IFG); and, the neural correlates of the second meta-analysis on anger experience, including the insula and the vlPFC - the lateral orbitofrontal cortex (lOFC) and the inferior frontal gyrus (IFG) -. Finally, the conjunction analysis shows a common activation between anger perception and anger experience relying on the right inferior frontal gyrus (IFG).

sphere, in particular: 75% Temporal Lobe (Brodmann area 37), 25% Occipital Lobe.

### 3.2. *Anger experience*

The meta-analysis on anger experience revealed two significant clusters (see Fig. 1 and Table 2). These clusters were located bilaterally at the level of the anterior insula and the ventrolateral prefrontal cortex.

In particular, Cluster 1 was located in the left hemisphere, in particular: 41% Inferior Frontal Gyrus, 39.8% Insula, 10.8% Extra-Nuclear, 8.4% Claustrum (38.6% Brodmann area 47, 33.7% Brodmann area 13, 9.6% Brodmann area 45); cluster 2 was located in the right hemisphere, in particular: 73.3% Inferior Frontal Gyrus, 24.4% Insula, 2.2% Precentral Gyrus (40% Brodmann area 13, 35.6% Brodmann area 45, 13.3% Brodmann area 44, 11.1% Brodmann area 47).

### 3.3. *Contrasts*

The contrasts analyses (anger perception > anger experience, and anger experience>anger perception) did not show significant results.

### 3.4. *Conjunction*

The conjunction analysis (see Fig. 1 and Table 2) showed that both anger experience and anger perception share the activation of one cluster located within the right inferior frontal gyrus, surrounding the horizontal ramus. Clusters were located in the right hemisphere, in particular 100% Inferior Frontal Gyrus (100% Brodmann area 45).

## 4. Discussion

The aim of this paper was to explore the neural bases of anger perception and anger experience. Anger has been studied through different

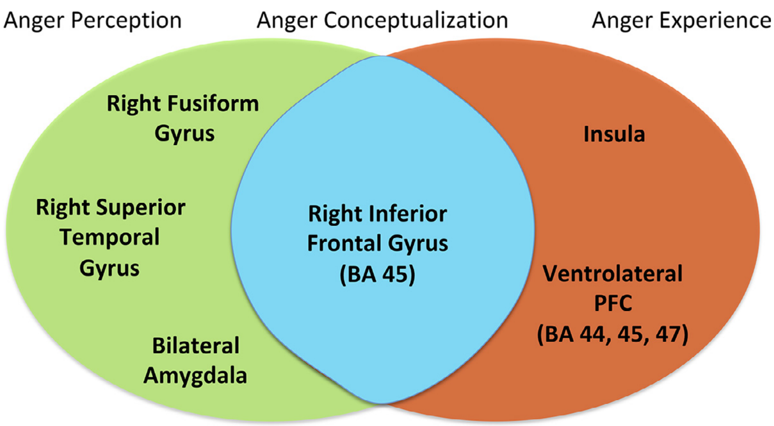


**Fig. 2.** An integrated neurocognitive model of anger. On the basis of our results, we propose a model on anger processing in the brain. According to this model, the perception of anger would rely on the amygdala, whose activity is related to the emotional significance of a stimulus and threat detection; the fusiform gyrus, whose activity is related to face and emotional stimuli processing; and, the superior temporal gyrus, whose activity is related to memories and social information. On the other hand, the experience of anger relies on the insula, whose activity is related to the arousal and the experience of the emotion, and on the lateral orbitofrontal cortex, probably involved in the evaluation and monitoring of the emotion and its outcomes. Finally, the activity of the right inferior frontal gyrus characterizes both processes, probably underlying a common process of emotion conceptualization.

paradigms, some aimed at investigating the effects of being exposed to angry stimuli (anger perception) and some at eliciting anger in the observer (anger experience) through social interactive games or imagery (Gilam and Hendler, 2015). Therefore, we performed two separate ALE meta-analyses on anger perception and anger experience, in order to show quantitative evidence of their distinct neural bases. Nevertheless, beside the distinct mechanisms, both anger perception and anger experience may rely on common mechanism subserving the conceptualization of this emotion (Barrett et al., 2006). Therefore, we also performed a conjunction analysis to test the presence of brain areas that are recruited during both the perception and the experience of anger.

### 4.1. Anger perception

A previous meta-analysis on emotional face perception found activity related to angry faces in the cingulate, subcortical and frontal brain regions, such as the IFG when compared to baseline condition. Brain activity in the right amygdala and fusiform gyrus was also found when angry faces were compared to disgusted faces (Fusar-Poli et al., 2009). In general, temporal areas have been linked to emotion perception and detection. For example, the right fusiform gyrus and STG are known to be involved in the processing of social signals needed to interpret others' behavior (Seok and Cheong, 2019). Instead, more frontal areas have been linked to the conscious elaboration of the emotion (e.g. recognition and categorization), such as the orbitofrontal cortex and the inferior frontal gyrus (Adolph et al., 2002; Jastorff et al., 2015; Gilam and Hendler, 2015). Consistently with previous studies, our analysis on anger perception showed activation in the right superior temporal gyrus, the right fusiform gyrus, the IFG and the amygdala (Table 2, Fig. 1A, Fig. 2). The role of the amygdala is usually associated with negative affect and negative feelings in response to threatening stimuli (Gilam and Hendler, 2015). Activation of the amygdala has been also found specifically after the presentation of angry faces or angry voices, especially when considering personality differences (Passamonti et al., 2008; Beaver et al., 2008; Sander et al., 2005). Therefore, its activity may be related to the perception of an angry face as a threatening or, more in general, as a salient stimulus (K.A. Lindquist et al., 2012).

The fusiform gyrus is known to be involved in faces processing, but it has also been associated to the arousal and valence of emotional stimuli, as the amygdala (Mattek et al., 2020). Furthermore, it has been found that fast amygdala responses to angry faces modulate STG activity in order to favor aggressive responses (Buades-Rotger et al., 2016). To sum up, the amygdala processes the emotional significance of a stimulus (Sato et al., 2004), in particular signaling whether exteroceptive information is salience (K.A. Lindquist et al., 2012), while the fusiform gyrus and the STG may be involved in processing visual and verbal triggers, in particular when they are linked to emotion expression (Adolphs, 2002). Finally, these processes can be modulated by emotion regulation, which is linked to frontal brain areas (Ochsner and Gross, 2014). For example, a greater IFG-amygdala coupling has been associated to emotion regulation after angry perception (Morawetz et al., 2016). In addition, this coupling is enhanced by serotonin, which seems to facilitate the PFC in suppressing the negative emotions generated in the amygdala (Passamonti et al., 2012). On the other hand, IFG-amygdala coupling has been associated to reduced emotion regulation when considering reappraisal strategy (Wager et al., 2008) and to higher trait anger and traumatic symptoms (Gilam et al., 2017). This suggests a fundamental, but probably differentiated modulatory role of the IFG in affect (Fig. 2).

### 4.2. Anger experience

Previous studies have shown that during anger experience the anterior insula and vlPFC activity can be involved through different kinds of paradigms and processes (Seok and Cheong, 2019; G. Gilam et al., 2018; Tonnaer et al., 2017; Skibsted et al., 2017; Emmerling et al., 2016; Dambacher et al., 2014; Denson et al., 2013; T.F. 2009; Pawlickzek et al., 2013; Fabiansson et al., 2012). Consistently with these results, in our study, anger experience showed bilateral activation of the vlPFC (IFG –BA 45, BA 44- and lOFC –BA 47-) and the anterior insula (Table 2, Fig. 1B, Fig. 2). The anterior insula is one of the brain areas associated with core affect, including motivational states related to subjective feelings and goals (Russell, 2003; K.A. Lindquist et al., 2012; Wager and Barrett, 2017). The insula integrates bottom-up interoceptive signals with top-down predictions, to produce a present awareness state (Gu et al., 2013). Its activity also correlates with the perceived ability to reappraise the emotion after interpersonal provocation (Grecucci et al., 2013a,c). Further, the insula has been linked to anger and aggressive retaliation (Emmerling et al., 2016), and to aggressive behavior (Skibsted et al., 2017; Dambacher et al., 2014). Indeed, its activity is also related to the evaluation of the provocative source/person that elicits anger. For example, when a human being rather than a computer, proposes unfair offers, these elicit lower acceptance rates that are possibly linked to higher negative emotions. This is mediated by anterior insula activity (Sanfey et al., 2003). Furthermore, Seok and Cheong (2019) found a significant reciprocal connectivity between the insula and the lateral OFC during anger experience; since this region seems to have a role in the integration of interoceptive and exteroceptive information (K.A. Lindquist et al., 2012), they argued that while the insula may use this information for the generation and the experience of anger, the lOFC may use it to guide behavior. Indeed, this was the most consistently activated region for anger in previous meta-analyses on different emotions (Murphy et al., 2003; K.A. Lindquist et al., 2012). lOFC may be linked to the subjective experience and evaluation and monitoring of the emotional information in decision making (Beer et al., 2006; Garrett and Maddock, 2006) (Table 2, Fig. 1B, Fig. 2). On the other hand, the activity of OFC has been related not only to fights, aggressive and extrapunitive behavior

(Buades-Rotger et al., 2017; Beyer et al., 2015; Minamoto et al., 2014), but also to anger regulation, especially when considering the medial OFC (Repple et al., 2018; Gilam et al., 2015;G. 2018; Beyer et al., 2015).

Also the vlPFC activity is related to the control of the emotional experience and emotion regulation/inhibition (Aron et al., 2014; Wager et al., 2008; Chester et al., 2018b). However, this area has also been linked to ruminative processes (T.F. Denson et al., 2009; Fabiansson et al., 2012) and to anger experience in high vs. low trait anger individuals (Tonnaer et al., 2017). Accordingly, Wager and colleagues (2008) found that the vlPFC is involved in both generation and regulation of the emotion through different subcortical pathways, and therefore they proposed that this region could be responsible of an appraisal (or reappraisal) process that can lead to opposite outcomes (emotion expression or regulation). Regarding anger regulation, an important brain region is the vmPFC (Gilam et al., 2015; G. Gilam et al., 2018; Y. Jacob et al., 2018), which seems to have bidirectional connections with the IFG. Indeed, Jacob and colleagues (Y. 2018) investigated the influence between brain regions during high vs. low anger, finding that the vlPFC is influenced by both the insula and the vmPFC activity. In another study, the vmPFC mediated the inverse correlation between the right IFG and the amygdala during affective labeling of negative stimuli (Lieberman et al., 2007). Probably, among these interactive regions linked to emotion and emotion regulation, the mPFC could have a more important role in implicit emotion regulation and affective meaning linked to reward and outcomes, while the vlPFC could have a more important role in explicit emotion regulation (such as reappraisal) and affective meaning (such as labeling or appraisal of the situation) (Etkin et al., 2015; Roy et al., 2012; Lieberman et al., 2007; Lieberman, 2011).

To sum up, the neural mechanisms of the experience of anger emerged in this meta-analysis relies on the insula, whose activity is related to the subjective and interoceptive feelings characterizing this emotion, and on the ventrolateral prefrontal cortex (IFG –BA45, BA 44- and lOFC –BA47-), which may be involved in the evaluation of the emotion and in the modulation of the behavioral outcomes in interaction with other prefrontal regions (Table 2, Fig. 1B, Fig. 2).

### 4.3. Common mechanisms

Some brain regions may be involved in both anger perception and experience (Potegal et al., 2010, p.41), especially when considering the conceptualization of anger (Lieberman et al., 2007). In particular, both categorization of the perceived emotional stimuli (Cunningham et al., 2003; Nomura et al., 2003; Lieberman et al., 2007) and appraisal of the experienced emotion (Grecucci et al., 2013b;c; Buhle et al., 2013) elicit brain activity in the right IFG. In line with the above considerations, our conjunction analysis showed that the right inferior frontal gyrus (BA 45) is the only area shared by both anger perception and anger experience (Table 2, Fig. 1C, Fig. 2). We interpret this as a possible substrate for the conceptualization of anger, necessary for both the perception and the experience of this emotion.

Despite the usual association between the IFG and inhibitory control, Hampshire and colleagues (A. 2009; 2010) found that the rIFG activity is recruited according to the saliency of a stimulus rather than its inhibition. Indeed, the rIFG is also linked to linguistic processing and affective salience (Borod et al., 1992; Nakamura et al., 1999; Rota et al., 2009; Gajardo-Vidal et al., 2018; Sheppard and Hillis, 2018; Gainotti, 2019). Accordingly, the rIFG has been also linked to emotional labeling (Lieberman et al., 2007; Lieberman, 2011), reappraisal (Grecucci et al., 2013a, b, c) and ruminative processes (Fabiansson et al., 2012; Gilam et al., 2017). Therefore, when considering anger, we propose that the rIFG might be responsible of a first linguistic conceptualization of this emotion (perceived or experienced) that can lead to the following modulation of cognition (e.g. reappraisal or rumination) or behavior (e.g. inhibition). This further evaluation and eventual regulation can be performed in interaction with other brain areas; for example, the vmPFC is also involved in the affective meaning in relation to specific outcomes of the situation (Roy et al., 2012). Indeed, the vmPFC mediates the inhibition of the right IFG toward subcortical activity (Lieberman et al., 2007), probably through a modulation of the behavior and of the emotional response.

Therefore, while the vmPFC might have a more direct role in anger regulation linked to the behavioral motivation (indeed its activity is also related to reward and gaining) (Gilam et al., 2015; G. Gilam et al., 2018), the right IFG might have a role more linked to the labeling or appraisal (and reappraisal) that is needed to understand the bottom-up sensory information and to eventually start a regulatory process.

Finally, another meta-analyses on different emotions found that all of them showed activation in the right IFG, suggesting a possible involvement of affective conceptualization, or more in general an interaction of higher cognitive and affective functions (Kirby and Robinson, 2017 Nov). Our results add further evidence to the fundamental role of the right IFG in emotion processing, especially for anger (Fig. 2).

Even if further investigation is needed to clarify the potential role of the right IFG in anger (but also in relation to the general link between emotion perception and experience), we can conclude that it is a key region during anger processing, possibly related to the conceptualization of this emotion.

### 4.4. An integrated neurocognitive model of anger perception and experience

To conclude, on the basis of our results and of the reviewed literature, we propose a model on the brain mechanisms characterizing anger. This model is illustrated in Fig. 2. This model relies on the presence of both distinct and common brain mechanisms responsible for the perception and the experience of this emotion.

The perception of anger, elicited by a triggering stimulus, evokes neural activity in different regions: perceptual areas such as the amygdala, whose response is associated with salient exteroceptive (vs. interoceptive) processing (K.A. Lindquist et al., 2012); the STG and the fusiform gyrus, involved in stimulus processing and linked to social situations; and the right IFG, involved not only in the perception of emotional stimuli (Nakamura et al., 1999), but also in its categorization and possible regulation (Lieberman et al., 2007). Beside the perception of the angry stimulus, anger becomes subjectively experienced thanks to the contribution of the insula and the vlPFC. The insula integrates both bottom-up interoceptive and episodic information from temporal regions and top down predictions and control inputs from the ventrolateral PFC (Gu et al., 2013; Seok and Cheong, 2019).

Therefore, the insula can be related to the interoceptive (vs. exteroceptive linked to the amygdala) experience of anger, while the bilateral vlPFC (IFG and lateral OFG) can be related to a more explicit experience linked to appraisal and anger control.

Finally, the conjunction analysis showed a common activation between anger perception and anger experience in the right IFG. We hypothesize that this area would allow what we defined as "anger conceptualization". In particular, we refer to different processes such as anger labeling, needed to recognize the specific perceived emotion, and appraisal, needed to understand the emotional context of the experienced situation (Lieberman et al., 2007; Lieberman, 2011; Wager et al., 2008).

Indeed, even if more studies are needed to validate and better understand this common mechanism of conceptualization of anger, our results show that they are involved in a common process whose substrate is the rIFG. This demonstrates a possible connection between an emotional subjective experience and its observation in the external world. See Fig. 2.

## 5. Limitations

A first limitation of this study regards that while there was no difference in anger perception and anger experience proportions of male vs. female ($p$ = 0.752), there was a difference in age ($p$ = 0.001), despite the fact that we only selected studies including 18–55 years old individual. Another limitation is inherent in the relevant literature and the selection of papers to include. Indeed, different types of stimuli or conditions are used when studying the neural bases of anger. These include visual versus auditory when addressing the perceptual process, or social games versus imagery when addressing the experiential process. In addition, the criteria of our meta-analysis lead us to exclude some relevant papers that tried to elicit anger through a rude experimenter (T.F. Denson et al., 2009; 2013; 2014); however, given the presence of fixation baseline, we had to exclude this and other studies that emerged in the literature, which can be better understood through a review (Alia-Klein et al., 2020). This exclusion, and the inclusion of many interpersonal games paradigms, may also explain the fact that we did not find brain areas linked to the mentalizing network, such as the mPFC, the PCC and other temporal regions during anger experience (Gilam and Hendler, 2015; Alia-Klein et al., 2020). Another limitation includes the possibility to generate anger from these interpersonal games that we included in our analysis and the decisional process (accept vs. reject) involved in the tasks. Given the need of large samples and controlled experimental conditions (similar contrasts used across different studies) in the meta-analysis, we have decided to include these studies, but only considering the provocative rather than the decision phase; however, our results could be linked not only to anger but also to other processes involved in the comparison between unfair vs. fair offers (for a review on the paradigms used to elicit anger and their implications see Gilam and Hendler, 2015).

Finally, another limitation regards the individual differences that were not addressed in our paper, given the relative small amount of included studies investigating this issue. Future studies are required to provide support to our results, and to compare both individual and experimental differences when more evidence will be available.

## 6. Conclusions

This paper contains a novel meta-analytic evidence of the neural bases of anger, including for the first time a clear separation of anger perception from the experience of anger. Our results highlight not only the presence of different brain areas, but also a common brain area. Differences emerged in the analysis on the perceptual processes, involving the amygdala, the fusiform gyrus and the superior temporal gyrus, or in the analysis on the experiential processes, involving bilateral activations in the insula and the ventrolateral prefrontal cortex. Finally, the right inferior frontal gyrus was identified as a common brain area involved during both processes, representing a possible aspect of categorization and appraisal of anger.

## Declaration of Competing Interest

None.

## Credit authorship contribution statement

**Sara Sorella:** Conceptualization, Methodology, Formal analysis, Writing - original draft. **Alessandro Grecucci:** Formal analysis, Supervision, Conceptualization, Writing - original draft, Writing - review & editing. **Luca Piretti:** Methodology, Formal analysis, Writing - review & editing. **Remo Job:** Supervision, Writing - review & editing.

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## Data and code availability statement

We used a meta-analytic approach in our paper; therefore our data (the papers included in the meta-analyses) are cited in the references.

We have uploaded the GingerALE output files of the meta-analyses in the "Upload Research Data" section of the submission procedure.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.117777.

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