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How to cite

FRÜHHOLZ, Sascha, GRANDJEAN, Didier Maurice. Processing of emotional vocalizations in bilateral inferior frontal cortex. In: Neuroscience and biobehavioral reviews, 2013, vol. 37, n° 10 Pt 2, p. 2847–2855. doi: 10.1016/j.neubiorev.2013.10.007

This publication URL: https://archive-ouverte.unige.ch/unige:84143

Publication DOI: 10.1016/j.neubiorev.2013.10.007

Neuroscience and Biobehavioral Reviews 37 (2013) 2847–2855

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

Processing of emotional vocalizations in bilateral inferior frontal cortex

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A R T I C L E   I N F O

Article history:
Received 10 April 2013
Received in revised form 9 August 2013
Accepted 14 October 2013

Keywords:
Voice
Emotional vocalizations
Prosody
Inferior frontal cortex
fMRI

A B S T R A C T

A current view proposes that the *right* inferior frontal cortex (IFC) is particularly responsible for attentive decoding and cognitive evaluation of emotional cues in human vocalizations. Although some studies seem to support this view, an exhaustive review of all recent imaging studies points to an important functional role of both the *right* and the *left* IFC in processing vocal emotions. Second, besides a supposed predominant role of the IFC for an attentive processing and evaluation of emotional voices in IFC, these recent studies also point to a possible role of the IFC in preattentive and implicit processing of vocal emotions. The studies specifically provide evidence that both the right and the left IFC show a similar anterior-to-posterior gradient of functional activity in response to emotional vocalizations. This bilateral IFC gradient depends both on the nature or medium of emotional vocalizations (emotional prosody versus nonverbal expressions) and on the level of attentive processing (explicit versus implicit processing), closely resembling the distribution of terminal regions of distinct auditory pathways, which provide either global or dynamic acoustic information. Here we suggest a functional distribution in which several IFC subregions process different acoustic information conveyed by emotional vocalizations. Although the rostro-ventral IFC might categorize emotional vocalizations, the caudo-dorsal IFC might be specifically sensitive to their temporal features.

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http://dx.doi.org/10.1016/j.neubiorev.2013.10.007

1. Introduction

The lateral inferior frontal cortex (IFC) mainly consists of the inferior frontal gyrus (IFG) and the frontal operculum (fOP). Besides several functions related to executive processes that generally regulate other cognitive functions, activity in the IFC is strongly involved in the processing of human vocal utterances, such as speech (Friederici, 2012). The IFC is also consistently involved in the processing of nonverbal and speech-based vocal intonations, such as speech prosody (Frühholz et al., 2012; Frühholz and Grandjean, 2012; Schirmer and Kotz, 2006) (see Fig. 1). Linguistic prosody refers to the suprasegmental intonational contour during verbal utterances and seems to mainly activate the right IFC (Bryan, 1989; Friederici and Alter, 2004). Similarly, emotional prosody, that is, the emotionally influenced tone of a voice (Banse and Scherer, 1996), elicits strong and replicable right IFC activation (e.g. Buchanan et al., 2000; George et al., 1996; Wildgruber et al., 2004). This finding supports early proposals of the critical involvement of the right hemisphere in prosody processing in general (Ross, 1981) and specifically emotional prosody (Ross and Monnot, 2008, 2011; Ross et al., 1997; van Lancker, 1980). Thus, compared with the predominant syntacto-semantic processing in the left IFC (Friederici, 2012), the right IFC is thought to be strongly involved in the processing of the dynamics of vocal emotional intonations. This has also been recently put forward as the final stage of a multi-stage model of emotional prosody processing (Schirmer and Kotz, 2006), specifically serving the explicit and cognitive controlled evaluation of vocally expressed emotions (Bruck et al., 2011; Wildgruber et al., 2009).

However, the right IFC seems not to have a sole and unique role in the processing of prosody, especially emotional prosody. First, many recent studies found bilateral (Beaucousin et al., 2007; Ethofer et al., 2006; Frühholz et al., 2012; Kotz et al., 2003; Morris et al., 1999) or even specific left IFC activity (Bach et al., 2008; Fecteau et al., 2005; Mitchell, 2006; Wildgruber et al., 2004) in response to emotional prosody in several subregions of the IFC (see Fig. 2). This observation is also supported by recent clinical studies showing impaired vocal emotion processing in patients with left IFC brain lesions or brain atrophy (Adolphs et al., 2002; Rohrer et al., 2012). A second surprising finding is that even voice melody in nonverbal vocal expressions (Fig. 1A, upper panel), devoid of any language-like syntacto-semantic features, can activate some subregions of the left IFC language areas (Fecteau et al., 2005). Although nonverbal expressions are different because they are not superimposed on speech or speech-like utterances and are usually less temporarily extended, they might figure as precursors to emotional intonated speech (Arnold and Zuberbuhler, 2006; Belin et al., 2008a; Hauser, 1997; see also Section 4). Accordingly, nonverbal expressions have many acoustic features in common with emotional prosody (Banse and Scherer, 1996; Patel et al., 2011; Sauter et al., 2010), from which listeners infer the emotional state of the speaker. The left IFC thus might also decode emotional cues from nonspeech vocalizations, indicating that left IFC activity is not exclusive to syntacto-semantic speech processing, but serves more general functions during the processing of human utterances. Finally, although the IFC has been proposed to be involved in the explicit decoding of emotional prosody when attention is directed to the emotional cues in voices, IFC activity has also been found when attention is directed away from emotional cues in voices (Belin et al., 2008a; Fecteau et al., 2005; Frühholz et al., 2012; Morris et al., 1999; Wildgruber et al., 2004, 2005) or during passive listening (Mitchell et al., 2003). This contradicts some proposals that the IFC is predominantly involved in the explicit evaluation of emotional voices or when attention is directly focused on the emotional value of voices (Bruck et al., 2011; Schirmer and Kotz, 2006; Wildgruber et al., 2009).

Both the left and the right IFC are thus considerably active in response to emotional vocalizations across different levels of attentional processing, allowing no clear hemispheric distinction. However, the recent literature on the neural basis of vocal emotion decoding seems to show that instead of a left and right IFC distinction, a rostral-to-caudal distinction exists in the bilateral

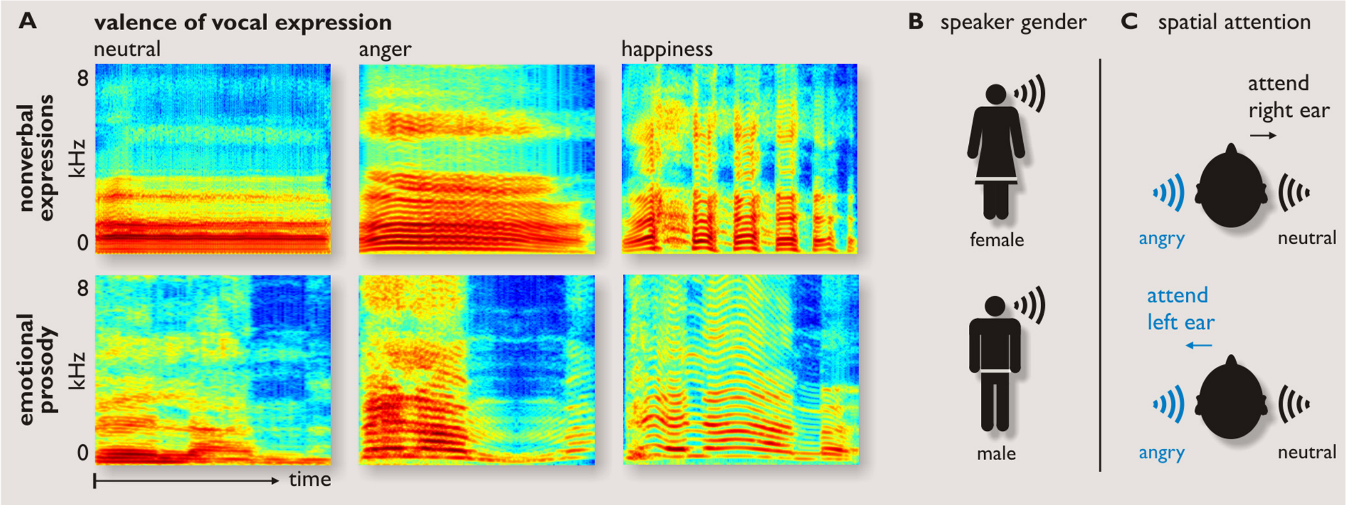

Fig. 1. (A) Studies investigating the processing of emotional cues from voices use either nonverbal vocal expression (upper row; the examples shows spectrogram of stimuli taken from the MAV database; see Belin et al., 2008b) or emotional intonations superimposed on speech or speech-like utterances, referred to as emotional prosody (lower row; spectrograms on the pseudo-word "belam"; see Frühholz et al., 2012). Although nonverbal expressions and emotional prosody are different in nature, they share common acoustic features (such as pitch or intensity level and variation), from which listeners decode the emotional meaning of vocalizations. (B) Besides the differences related to the stimulus material, studies often use different tasks to manipulate the focus of attention during the processing of emotional vocalizations. The latter can be experimentally manipulated such that emotional cues in voices can be presented inside or outside the focus of attention. When emotional voices are presented inside the focus of attention (which we refer to as explicit attention or task), participants have to make a decision on the emotional valence of voices (as shown in A), allowing a cognitively controlled processing of emotional cues in vocalizations. The presentation of emotional voices outside the focus of attention (which we refer to as implicit attention) requires, for example, that participants focus on the gender of the speaker (left panel) (e.g. Frühholz et al., 2012), or that they direct spatial attention to another source away from the spatial location of emotional voices (e.g. Grandjean et al., 2005) (right panel, upper part; the lower part shows attention toward the spatial location of emotional voices). During an implicit attentional focus or task, it is assumed that the emotional tone of a voice is still processed on an implicit level.

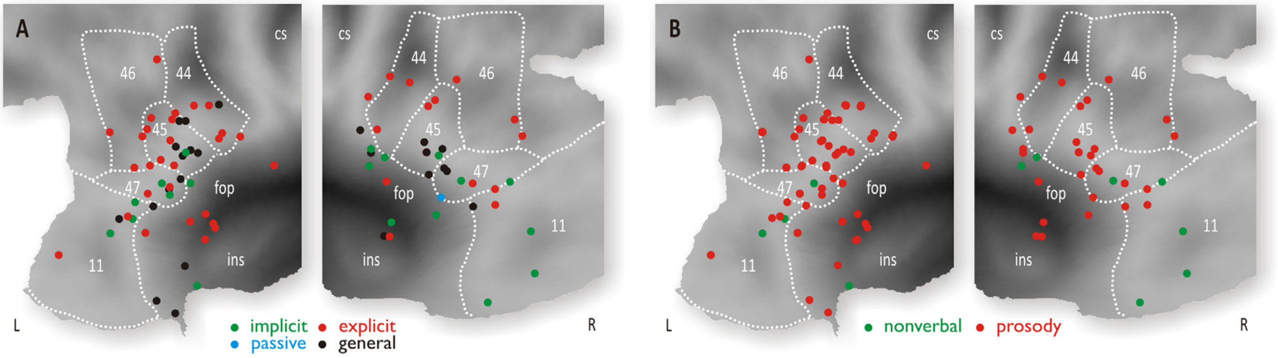

Fig. 2. Activation foci in the inferior frontal cortex (IFC) (A) according to the attentional focus (explicit attention or task (red), implicit attention or task (green), passive listening (blue)) and (B) according to the medium of vocal expressions (nonverbal, emotional prosody). For activation foci according to attentional focus, one activation focus in right inferior BA 47 was found during passive listening to emotional vocalizations (triangle; Mitchell et al., 2003). Black dots in A indicate peak activations taken from studies for which general IFC activity was found independent of attentional focus. Peak activation foci are rendered on the human PALS atlas as implemented in the CARET atlas (Van Essen et al., 2001). We included only activation foci, which were derived from a clear functional comparison between experimental conditions that allowed a clear functional specification; activation foci resulting from a comparison against a baseline condition with no auditory stimulation were not included (see Supplement S1 for the studies included here). The white dotted lines and the white numbers denote Brodmann areas (BA) taken from the same CARET atlas. Abbreviations: *cs* central sulcus, *fop* frontal operculum, *ins* insula. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

IFC. Based on the nature of vocal intonations (emotional prosody versus nonverbal expressions), as well as on the attentional level in the processing of vocalizations, this distinction resembles a recent notion put forward for the left IFC in speech processing (Hagoort, 2005). The IFC is not a unique brain area, but rather comprises several subregions according to cytoarchitectonic and especially connectivity-based parcellations (see Fig. 3). This rostral-to-caudal distinction in the IFC closely follows the termination areas of the dorsal and ventral auditory pathways originating in different parts of the bilateral superior temporal gyrus (STG). Accordingly, we propose a rostro-ventral to caudo-dorsal distinction in both the left and the right IFC, which likely supports different functional roles during the processing of emotional vocalizations based on different acoustical information provided by different auditory pathways. This proposal is outlined in detail here, along with recent evidence for it. We begin with a general anatomical and functional description of the IFC.

2. Anatomy and functions of the lateral IFC

The lateral IFC is primarily composed of the inferior gyrus consisting of Brodmann areas (BA) 47/12, 45, and 44 from anterior to posterior. Ventrally to BA 44 and 45 lies the fOP, primarily covered by BA 47/12 (Fig. 3). The subdivision of the IFC into different subregions is based on cytoarchitectonic (Amunts et al., 1999; Petrides and Pandya, 2002) and connectivity-based approaches (Anwander et al., 2007; Petrides and Pandya, 2002) and has revealed homologous areas in the nonhuman and the human primate brain (Petrides and Pandya, 2002). BA 45 and BA 47 (in humans), the latter corresponding to BA 12 in the monkey brain, show clear homologues in the primate brain (see Fig. 3). BA 44 is clearly identifiable in the human brain and is thought to be a central brain region for human speech processing (Friederici, 2012). Petrides et al. (2005) recently described a cytoarchitectonically similar area in macaque monkeys. The subregions in the IFC seem to have equal representation in both the left and the right IFC. Although early studies seem to demonstrate a leftward advantage, especially for some components of language-related Brodmann areas (BA 44/45), a review of all available data does not support any strong lateralization (Keller et al., 2009).

Connectivity analyses have shown strong connections between the IFC and lateral temporal cortex areas. The fronto-temporal connections have been described in detail for the left hemisphere as the underlying brain network for speech processing. Connection

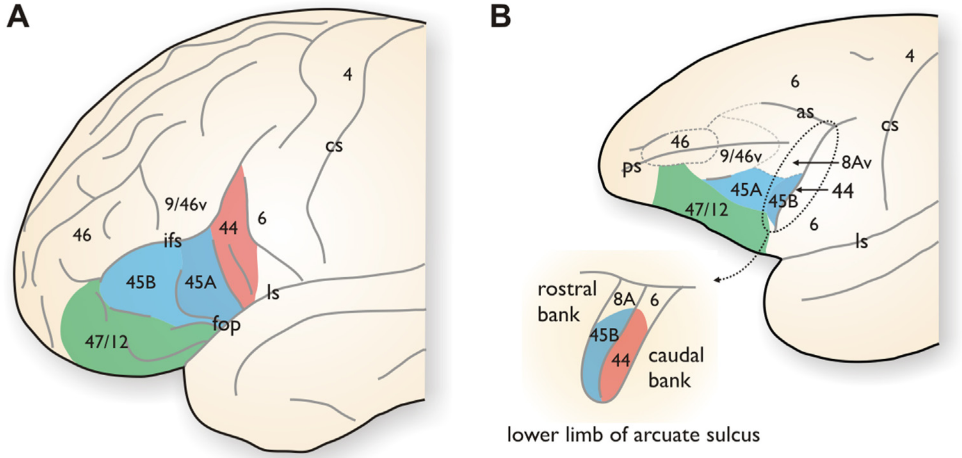

Fig. 3. Maps of the IFC (A) in the human and (B) in the macaque brain. Highlighted are the cytoarchitectonic subdivisions of IFC in BA 47/12, BA 45, and BA 44 as the most dominant language-sensitive brain regions and the regions sensitive to conspecific vocalizations (based on: Petrides and Pandya, 2002). Abbreviations: *as* arcuate sulcus, *cs* central sulcus, *ifs* inferior frontal sulcus, *ls* lateral sulcus, *ps* principal sulcus. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

studies in macaque monkeys have shown connectivity of BA 47/12 to the anterior inferior temporal cortex and of BA 45 to the posterior temporal cortex (Petrides and Pandya, 2002). These connections might be the precursors of the human ventral (from anterior STG to BA 45 and to BA 47/12/fOP) and dorsal speech processing streams (from posterior STG to B44/6) (Friederici, 2012), which gradually develop in the primate lineage (Rilling et al., 2008). A similar fronto-temporal network is thought to exist in the right hemisphere, but the available data are sparse. The right posterior STG seems to be connected to the anterior (Ethofer et al., 2012) and posterior regions of the right IFC (Glasser and Rilling, 2008), but these connections are not reliably identifiable across participants (Glasser and Rilling, 2008).

3. A general functional role of the IFC

Although the IFC is strongly associated with speech and prosody processing, its functions seem not to be limited to speech processing. Given the general view that the IFC is linked to several first-order executive processes, such as stimulus comparisons or the judgment of stimuli (Petrides, 2005), it might specifically serve several self-referenced or other-referenced social processes, such as the evaluation (Marumo et al., 2009), categorization (Frühholz et al., 2009, 2012), and memory encoding of emotional stimuli (Sergerie et al., 2005). The IFC might also be involved in controlling, overriding, or inhibiting behavioral and emotional responses (Aron et al., 2004; Dillon and Pizzagalli, 2007; Mitchell, 2011), as well as mirroring (Leslie et al., 2004), empathizing (Schulte-Ruther et al., 2007), or imitating the behavior of other individuals (Lee et al., 2006). All of these socially relevant processes can be regarded as first-order executive processes.

Activity in the left but also in the right IFC is thus found for different tasks, especially for nonlanguage tasks, which all involve cognitive processing of first-order executive processes for external or internal verbal and nonverbal social information, especially meaningful social or emotional information. A common perspective for both verbal and nonverbal processing in the IFC might be the general proposal that the IFC integrates (Hagoort, 2005) and performs first-order executive processes (Petrides, 2005). These processes are performed on information, which is represented in posterior association cortices after sensory processing in lower-level sensory regions, particularly in the auditory cortex (Frühholz and Grandjean, 2012). For the case of auditory verbal and nonverbal information, this suggests that the IFC performs executive processes on auditory voice information provided by higher-level auditory regions in the STG.

For the STG, it has been recently suggested that the anterior STG (aSTG) and the posterior STG (pSTG) represent and provide different types of auditory information as part of a dual stream model for auditory processing. A ventral stream originating in primary and secondary auditory regions, passing through the aSTG and terminating in the rostro-ventral IFC, is thought to provide invariant sound representations for perceptual constancy. For example, global acoustic characteristics of emotional vocalizations provide perceptual constancy even when their actual acoustic performance differs (e.g. emotional vocalizations expressed by a male or a female voice). The dorsal stream passing through the pSTG and the inferior parietal lobule (IPL) and terminating in the caudo-dorsal IFC instead provides auditory sequence information for temporally extended sounds (Rauschecker, 2012). The latter might represent different dynamic features of vocal expressions at the temporal frequency of speech segments and on a suprasegmental speech level. This dual stream model has been described only for the left hemisphere, but comparable structural hard wiring in the right hemisphere (Catani et al., 2012; Thiebaut de Schotten et al., 2012) might suggest similar dual stream pathways there, though the evidence for the latter is less consistent (Catani et al., 2007; Rilling et al., 2008). Together with the notion that left and right auditory regions parse the speech signal at different time scales (Giraud et al., 2007; Poeppel, 2003), these observations might suggest that the left and right IFC have access to temporal acoustic information of vocal intonations, which are differently sampled in time. A temporal resolution of the left STG of about 20–50 ms provides high temporal resolution, while the right auditory cortex samples the sensory signal in 100–300 ms time bins, allowing less temporal but improved spectral and pitch resolution (Zatorre and Belin, 2001). Similar to the left and right STG, the left and right IFC have been shown to be predominantly sensitive to slow and to fast dynamics in speech and non-speech sounds, respectively (Husain et al., 2006). Additionally, the right IFC is more sensitive to enhanced pitch variations in speech compared with the sensitivity of the left IFC to more monotonous pitch intonated speech (Merrill et al., 2012).

Intonations superimposed on speech (Banse and Scherer, 1996; Juslin and Laukka, 2003) and paraverbal speech (Patel et al., 2011) and in nonverbal expressions of emotions (Sauter et al., 2010) have global vocal features (i.e. mean intensity or pitch; spectral center of gravity; harmonics-to-noise ratio, HNR), but also show slow and fast dynamic modulations of features. These modulations range from ultrafast dynamic pitch and intensity modulations on a cycle-by-cycle basis (i.e. jitter and shimmer) to fast microstructural spectral, pitch, and intensity irregularities to increased pitch and intensity variability on a segmental and suprasegmental level in speech. While global features might be represented and stored as invariances in the ventral stream, dynamic temporal modulations might be decoded in the dorsal stream by parsing the specific temporal intonation patterns in emotional vocalizations.

The functional role of the IFC might be a unification of these different types of auditory voice information represented in the STG (Hagoort, 2005). The IFC accordingly might perform first-order executive processes on auditory information of emotional vocalizations. Specifically, for emotional voices it has been suggested that the IFC is sensitive to the level of explicitness of the emotional cues and would be more involved in the explicit cognitive evaluation of the emotional value in vocalizations. The available data support the notion of a cognitive controlled evaluation. But this seems not to be restricted to an explicit attentive focus on the emotional cues in voices, given that IFC activity was also found when the emotional value of voices was processed preattentively, such as when it was presented outside the focus of attention (Belin et al., 2008a; Buchanan et al., 2000; Fecteau et al., 2005; Frühholz et al., 2012; Morris et al., 1999; Sander et al., 2005; Wildgruber et al., 2004, 2005).

4. Origins of the IFC sensitivity to vocal intonations

Thus, there is abundant evidence for IFC sensitivity to emotional vocalizations. Recent studies suggest that this sensitivity has phylogenetic and ontogenetic precursors. Nonhuman primates already use vocalizations for transmitting socially meaningful information, which quite often involves the signaling of emotional and motivational states (Romanski and Averbeck, 2009). Studies in macaque monkeys have shown that vocalizations can form discrete categories based on their spectro-temporal acoustic profile (Averbeck and Romanski, 2006). These categories might be generated from acoustic cues and represented in the anterior ventral stream (Rauschecker, 2012) and categorized by the IFC (Cohen et al., 2006, 2009; Gifford et al., 2005; Russ et al., 2008b). Indeed, recent animal studies have identified neurons in the IFC (see Fig. 4) that are sensitive to conspecific meaningful vocalizations (Romanski et al., 2005). Instead of low-level auditory features, these neurons seem to

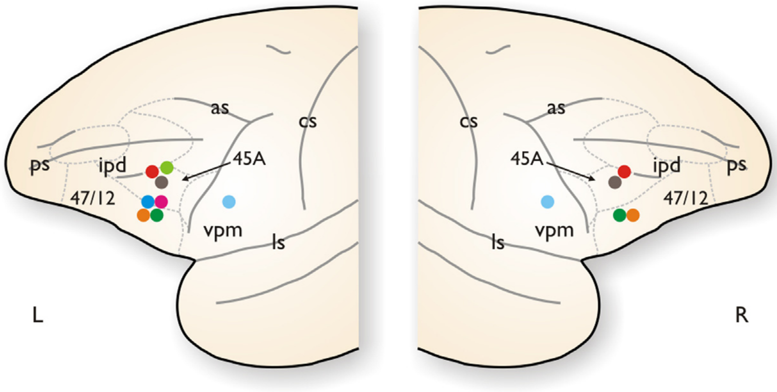

Fig. 4. Approximate locations of single cell recording sites in macaque studies in the left and right IFC, usually referred to as the ventro-lateral prefrontal cortex (vlPFC). Single cell activity was usually recorded in BA 45A and BA 9/46v, both located rostrally to BA 8Av below the principal sulcus. Color-coded dots refer to the following studies: ● (Gifford et al., 2005), ● (Averbeck and Romanski, 2006; Romanski et al., 2005), ● (Cohen et al., 2007, 2009; Russ et al., 2008a), ● (Romanski and Goldman-Rakic, 2002), ● (Cohen et al., 2006), ● (Lee et al., 2009; Russ et al., 2008b), ● (Sugihara et al., 2006), and ● (Gil-da-Costa et al., 2006) for activity in the vPM. Abbreviations: *as* arcuate sulcus, *cs* central sulcus, *ipd* inferior precentral dimple, *ls* lateral sulcus, *ps* principal sulcus, *vpm* ventral premotor area.

decode higher-order information conveyed by those vocalizations (Cohen et al., 2007, 2009). This decoding is probably based on a sensitivity to the acoustic morphology of conspecific vocalizations (Romanski et al., 2005), which help to differentiate several types of vocalizations (Cohen et al., 2006, 2009; Gifford et al., 2005; Russ et al., 2008b). Animal nonverbal vocalizations of primates might figure as precursors of human language (Hauser, 1997), given their comparability of internal structure (Zoloth and Green, 1979) and their functional similarity in social communications (Arnold and Zuberbuhler, 2006), as well as the developmental trajectories in the underlying cortical network (Gil-da-Costa et al., 2006; Rauschecker, 2012; Rilling et al., 2008; Thiebaut de Schotten et al., 2012).

Interestingly, the human IFC is sensitive to animal nonverbal vocalizations (Belin et al., 2008a) and to human nonverbal vocalizations (Fecteau et al., 2005), which share some similarities with vocalizations of nonhuman primates. This provides evidence for a link in the processing of primate vocalizations across species. Similarly, studies in human infants have shown that the IFC is sensitive to nonverbal features of human speech, especially for emotional intonations (Cheng et al., 2012; Grossmann et al., 2010), suggesting an early ontogenetic sensitivity to conspecific vocalizations. Sensitivity of the human IFC to nonverbal vocalizations might be the final precursor to emotional intonations superimposed on speech utterances, because both share similarities of several features of acoustically encoded emotional cues (Banse and Scherer, 1996; Patel et al., 2011; Sauter et al., 2010) and often appear in the same context.

Both nonhuman and human primate studies seem to indicate that the IFC sensitivity implies lateralization changes during ontogenetic maturation and development, resulting in an increasing leftward lateralization. Nonhuman primates show a major developmental trajectory from bilateral processing to a stronger left hemisphere bias in adults (Hauser and Andersson, 1994) for sensitivity to the communicative valence of vocalizations (Petersen et al., 1984) (but see: Gil-da-Costa and Hauser, 2006). Human infants show a stronger involvement of the right IFC (Cheng et al., 2012; Grossmann et al., 2010), which develops to a bilateral representation in adult humans. Both developmental trajectories in monkeys and in humans thus show that the functional role of the left IFC (relative to the right IFC) becomes more important during development, highlighting the notion that the left IFC plays an equally important role for the processing of vocal emotions. However, training of right IFC activity in adults can also strengthen the right IFC network (Rota et al., 2011), pointing to the possibility that both the left and the right IFC are susceptible to training influences and developmental changes.

5. The functional role of the IFC in processing emotional vocalizations

The IFC thus seems to be sensitive to emotional vocalizations, and this sensitivity seems to have developmental precursors in nonhuman primates and in infants. The IFC is primarily assumed to explicitly and cognitively evaluate the emotional value of voices (Ethofer et al., 2012; Leitman et al., 2010), such as occurs in the evaluation, labeling, or categorization of vocal expressions. This conclusion arises from the fact that studies usually find IFC activity when participants are asked to attentively and explicitly focus on the emotional value of voices (Beaucousin et al., 2007; Ethofer et al., 2006; Mitchell, 2006; Wildgruber et al., 2002), or when the decoding becomes more challenging because of ambiguous acoustic cues (Leitman et al., 2010; Schirmer et al., 2004) or conflicting emotional cues (Leitman et al., 2010; Schirmer et al., 2004). Both conditions, the attentive and explicit task, as well the conditions of more challenging decoding, represent first-order executive processes. These active processes might depend on specific connections of IFC subregions with different subregions in the superior temporal cortex, as defined by the different auditory pathways outlined earlier.

Compelling evidence from patient studies (Ross and Monnot, 2011), neuroimaging studies (Mitchell et al., 2003), and infant studies (Cheng et al., 2012; Grossmann et al., 2010) supports the view that the right IFC in particular is predominant for this cognitively controlled evaluation of emotional tones of voices. Recent neuroimaging studies found several right IFC peak activations distributed from the posterior to the anterior IFC located in BA 44 (Frühholz et al., 2012; Kotz et al., 2003), BA 45 (Bach et al., 2008; Beaucousin et al., 2007; Ethofer et al., 2006; Sander et al., 2005), and BA 47 (Bach et al., 2008; Beaucousin et al., 2007; Belin et al., 2008a; Ethofer et al., 2009; Frühholz et al., 2012; Mitchell, 2006; Sander et al., 2005), as well as in the fOP (Frühholz et al., 2012; Kotz et al., 2003; Mitchell et al., 2003; Schirmer et al., 2004) (see Fig. 2). Recently, it has been shown that the ability to control activity in the right IFC (BA 45) can improve emotional prosody recognition (Rota et al., 2011). Right IFC activity is also involved during cognitively more demanding emotional decoding in the case of ambiguous acoustic cues in voices (Leitman et al., 2010). Conversely, disrupting activity in the right posterior IFC (fronto-parietal operculum)

(Hoekert et al., 2008) and mid-right IFC (BA 45/46) (Hoekert et al., 2010) can impair the recognition of emotional prosody.

Interestingly, the latter study already provides evidence that disrupting the left IFC (BA 45/46) can also impair emotional prosody recognition, especially for fearful expressions (Hoekert et al., 2010). This suggests that not only the right IFC, but also the left IFC, might have a generic role during the processing of emotional voices. Left hemispheric and particularly left IFC lesions result in impairments during the processing of emotional vocalizations (Pell, 1998), though right hemisphere lesions still show a more pervasive insensitivity to emotional prosody (Pell, 2006). However, it has been suggested that the left compared with the right IFC has only a supplementary processing role, such as prosody-related working memory processes (Ethofer et al., 2009; Wildgruber et al., 2005), linguistic processing (Buchanan et al., 2000; Wildgruber et al., 2004), retrieval of semantic knowledge (Beaucousin et al., 2007), or semantic processing during impaired prosody processing (Mitchell, 2006; Schirmer and Kotz, 2006; Schirmer et al., 2004). Nonetheless, even when controlling for all secondary and language-related task effects, emotional vocalizations still elicit activity in the left IFC (Frühholz et al., 2012; Kotz et al., 2003; Leitman et al., 2010; Sander et al., 2005). Furthermore, the left IFC is active in response to nonverbal expressions without any language-related features (Belin et al., 2008a; Fecteau et al., 2005; Morris et al., 1999). Both facts argue against a simple supplementary or speech-related role of the left IFC.

These results together suggest that both the *left* and the *right* IFC are involved in the processing of emotional value from voices with no clear laterality effects (Kotz et al., 2003). Summarizing the peak activations across all fMRI and PET studies on processing emotional vocalizations provides a clear picture for a bilateral distribution of peak activation (see Fig. 2). Instead of a left-right distinction, it turns out that the nature or the medium of vocal expressions (emotional prosody versus nonverbal expressions), as well as the tasks performed on voices, which manipulated the attentional focus during the processing of vocal expressions, can influence the distribution of these peak activations across different subregions of the IFG.

6. Left and right IFC subregions for the decoding of emotional vocalizations

6.1. Attentional focus: attentive and preattentive processing of emotional vocalizations

Studies on the processing of emotional vocalizations usually use different tasks by manipulating the attentional focus (see Fig. 1). Studies ask participants either to explicitly focus on the emotional value of a voice, which allows cognitive evaluation of the emotional tone of a voice (explicit attentional focus or task), or to focus on another nonemotional feature of the vocal utterance (implicit attentional focus or task). For the latter task, it is assumed that the emotional tone of a voice is still processed on an implicit or preattentive level, given its importance for adaptive behavior. Although the IFC is generally supposed to decode the emotional value of voices when participants are asked to explicitly decode and label its emotional valence, recent studies also consistently found IFC activity when the emotional tone of a voice was presented outside the focus of attention (Belin et al., 2008a; Fecteau et al., 2005; Morris et al., 1999; Sander et al., 2005; Wildgruber et al., 2004, 2005). Early studies on emotional voice processing suggested that an explicit focus is associated with left IFC activity, whereas an implicit focus elicits right IFC activity (Buchanan et al., 2000). This left (Bach et al., 2008) or right lateralization (Wildgruber et al., 2005) is also supported by other studies (Sander et al., 2005). However, some studies do not support clear lateralization, but rather provide evidence for bilateral IFC involvement for both explicit (Beaucousin et al., 2007; Ethofer et al., 2006, 2009; Schirmer et al., 2004; Wildgruber et al., 2002) and implicit tasks (Belin et al., 2008a; Frühholz et al., 2012; Morris et al., 1999), allowing no specific lateralized assignment according to the attentional focus.

Explicit and implicit tasks during vocal emotion processing seem, however, to elicit activity in different subregions of the IFC. Whereas explicit tasks are able to elicit activity in all subregions of the bilateral IFC, implicit tasks seem to induce activity only in rostro-ventral IFC areas. These rostro-ventral areas are the main termination areas of the ventral auditory pathway providing access to invariant object or feature information in the aSTG, whereas the dorsal stream provides temporal pattern information (Rauschecker, 2012). This might suggest that the explicit processing of emotional vocalizations relies both on the temporal patterns in emotional voices and on general and global object information of acoustic patterns. The decoding of the temporal pattern is especially necessary for processing emotional prosody, and only prosodic cues extending over several speech units allow valid categorizations of emotional prosodic cues (Pell and Kotz, 2011). Unlike explicit processing, which allows one to temporally follow the dynamic changes in the temporal patterns, implicit processing of emotional vocalizations might rely only on the sound-invariant impression of acoustic patterns in emotional voices.

6.2. The medium of vocal expressions

Attentional focus during the processing of emotional vocalizations figures as a top-down factor, which adjusts the cognitive and the brain systems to prioritize certain features of the stimulus. This top-down factor can influence the distribution of peak activity in the IFC in response to emotional vocalizations, as discussed in the previous section. However, it seems that the medium of vocal expressions as a bottom-up factor can also influence this peak distribution. Concerning this medium or nature of vocalizations, vocal expressions of emotions can be purely nonverbal, such as laughs, cries, or screams (Sauter et al., 2010; Simon-Thomas et al., 2009), but they can also be superimposed on semantically neutral (Ethofer et al., 2009; Kotz et al., 2003; Leitman et al., 2010) and semantically emotional language (Beaucousin et al., 2007; Mitchell, 2006; Mitchell et al., 2003; Schirmer et al., 2004), as well as on pseudospeech (Bach et al., 2008; Frühholz et al., 2012; Sander et al., 2005). Given this distinction between nonverbal vocal expressions and emotional prosody, it might be assumed that emotional intonations superimposed on speech strongly engage the left IFC, whereas nonverbal expressions activate the right IFC (Meyer et al., 2005).

However, for emotional prosody and nonverbal vocal expressions, there is no convincing laterality effect for the distribution of peak activations across studies. Similar to the case for attentional focus, peak activations according to the medium of vocal expression seem to group along a rostro-ventral to caudo-dorsal axis in the bilateral IFC. Whereas emotional prosody elicits activity across all subregions of the IFC, nonverbal expressions elicit activity only in more anterior regions of the IFC. Nonverbal expressions do not reveal any activity in BA 44, but there is more activity in anterior IFC regions extending into ventral regions of the OFC (BA 11) and the fOP. We could assume that, similar to attention-related effects, discrimination for the purpose of categorizing and labeling of nonverbal expressions mainly relies on global invariant information represented in the aSTG, whereas the discrimination and categorization of emotional prosody requires access both to temporal patterns and to acoustic invariant features. A role for the posterior IFC in processing temporal patterns from emotional prosody is also evident in impairments in the processing of emotional prosody and the temporal prosody contour in patients with lesions in the posterior IFC (Adolphs et al., 2002; Rohrer et al., 2012). Furthermore, recent studies point to a possible role of the posterior IFC

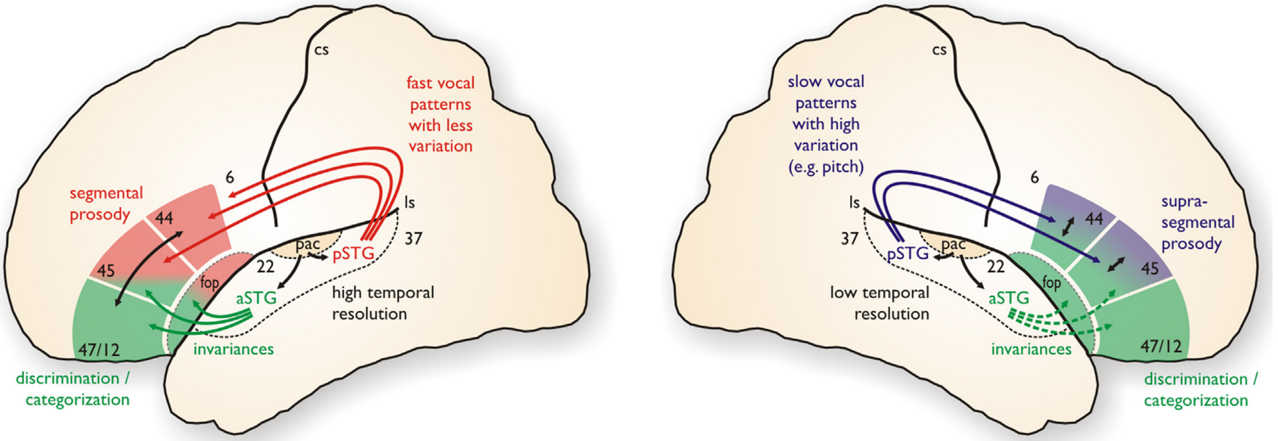

Fig. 5. IFC subregions are thought to have similar functional roles in both the left and the right hemisphere for the processing of emotional vocal intonations. We propose a distinction for the processing of emotional vocalizations in the rostro-ventral and caudo-dorsal IFC in both hemispheres depending on their structural and functional connectivity to the STG in and across the hemispheres. In the left hemisphere, major pathways have been identified for the processing of auditory objects, especially for speech features, along a ventral (green) and dorsal pathway (red). The dorsal pathways primarily terminate in the posterior IFC (BA 6, 44, 45), whereas the ventral pathways terminate in the antero-inferior IFC (BA 47/12, fOP). These pathways are thought to feed temporal auditory patterns and auditory signal invariances, respectively (so-called "chunks"; Rauschecker, 2012; Rauschecker and Scott, 2009), forward to the IFC. The pathways have been described in detail for the left hemisphere, but not for the right hemisphere. Although the structural connectivity in the left and in the right hemisphere is thought to be comparable (Catani et al., 2012), the combined description of the structural and functional connectivity is nonetheless sparse. Studies to date have only described a right dorsal pathway for prosody processing (blue) (Ethofer et al., 2012; Rilling et al., 2008), with no evidence for a right ventral stream (green, dotted). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(Pichon and Kell, 2013) and the caudally adjacent premotor cortex (Warren et al., 2006) in the preparation and execution of (vocal) motor outputs in response to perceived emotional prosody. Unlike nonverbal expressions, emotional prosody more often occurs in conversational settings, and thus a close anatomical link between the posterior IFC and the ventral premotor cortex might support perception-action cycles in emotional conversations.

7. Conclusions and future directions

We propose a bilateral rostro-ventral to caudo-dorsal gradient, similar to the left IFC unification gradient proposed by Hagoort (2005) for processing auditory speech. The gradient that we propose reflects a distinction in both the left and the right IFC for the processing of emotional vocalizations (see Fig. 5). This distinction follows the connectivity patterns of the IFC, with auditory processing areas in the STG, providing access to different auditory information depending on the stimulus modality as a bottom-up feature of emotional vocalizations and depending on the attentional focus as a top-down factor. Although this definition of IFC-STG connectivity patterns has been described with much detail in the left hemisphere, especially for the processing of speech and vocal utterances in general, a detailed description of the right hemisphere connectivity pattern based on functional data is largely missing (Ethofer et al., 2012; Glasser and Rilling, 2008). However, a few conclusions can be drawn from the functional distribution in peak activations in the right IFC, which closely resembles the peak distribution in the left IFC. This suggests a similar dual stream pathway model in the right hemisphere to that in the left hemisphere.

In conclusion, the processing of emotional vocalizations seems not to be restricted to the right IFC, as the left IFC shows similar activity in response to emotional vocalizations as the right IFC. Furthermore, unlike the suggestion of laterality effects for attentional task demands (explicit versus implicit) and for the medium of emotional vocalizations (emotional prosody versus nonverbal expressions), both factors determine the same intra-hemispheric peak distribution. Finally, the IFC is not only active during attentive decoding of emotional vocalizations, but more generally serves as a cognitive evaluation unit when the decoding of emotional cues from voices becomes more challenging. This supports the view that the IFC comes into play when first-order executive processes (as defined in Section 3) are needed for the judgment and evaluation of socially meaningful stimuli.

Thus, it seems that broad evidence is available for the functional role of the IFC in processing emotional vocalizations, but that open questions remain, as well as some limitations in the present review, which should be addressed in future studies. The first limitation of the present review is the smaller number of studies on the cortical processing of nonverbal expressions compared with the number of studies on emotional prosody. Although the available studies show some replicable and consistent IFC activity for nonverbal expressions, more imaging studies on cortical processing are strongly needed and should provide more consistent evidence for our proposal of a functional distinction in the IFC. Similarly, more studies are needed on the explicit and attentive processing of nonverbal vocal expressions. Most of the studies on the processing of nonverbal vocal expression use an implicit (Belin et al., 2008a; Fecteau et al., 2005; Morris et al., 1999) or a passive listening approach (Warren et al., 2006). This makes it difficult to compare functional activations for the attentive (explicit) and preattentive processing (implicit) of nonverbal emotional expressions and to completely discern the effects of the attentional focus and the medium of vocalizations. Thus, our conclusions on the processing of nonverbal expressions in the IFC are partly preliminary and have to be taken with some caution. Future studies might provide more supportive and consistent evidence for the decoding of nonverbal expressions in the IFC.

A second open question concerns the vocal feature sensitivity of the IFC. Future studies should investigate which features drive the discrimination and categorization abilities of the IFC. According to nonhuman primate studies, the IFC is rather sensitive to higher-order acoustic information (complex object representations) instead of first-order acoustic properties (simple spectro-temporal features) in vocalizations (Cohen et al., 2007). However, discrimination and categorization of vocal expressions depends on specific features (Banse and Scherer, 1996; Lakshminarayanan et al., 2003; Sauter et al., 2010).

Third, a well-defined IFC-STG connectivity pattern is available, but future studies should define the connectivity patterns of different subregions in the right IFC, especially in combination with specific localizations of functional activations in response to emotional vocalizations. This combined functional-structural approach has led to a detailed description of the left IFC-STG language network (Saur et al., 2008), but a similar detailed description for the right IFC-STG network is lacking (see Rilling et al., 2008).

Fourth, future studies may want to include a better description of the stimuli, especially in terms of the temporal pattern. Several studies already provide some detailed description of the acoustic features of the stimuli, especially in terms of the amount of temporal variation, such as variation of pitch, intensity, and spectrum (e.g. Frühholz et al., 2012; Leitman et al., 2010). Future meta-analyses, however, might derive considerable benefit from providing a detailed description of the carrier or medium material used for the studies on emotional prosody, such as the number of syllables and the temporal dynamic of prosody contour superimposed on this (para-)verbal material.

Finally, there is abundant evidence for forward mapping of sensory information from the STC to the IFC for the processing of different auditory objects, and the pathway model presented here also involves a strong bottom-up perspective for the processing of vocal intonations. However, Rauschecker and Scott (2009) also suggested that the caudo-dorsal IFC in particular, together with the parietal cortex, might be the origin of inverse mapping, allowing, for example, context-dependent selection of the most meaningful information, such as during the processing of competing auditory information. Direct evidence for such mechanisms during the processing of emotional vocalizations is strongly needed.

Acknowledgments

S.F. and D.G. were supported by the Swiss National Science Foundation (SNSF 105314_124572/1 – DG) and by the NCCR in Affective Sciences at the University of Geneva (51NF40-104897 – DG).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neubiorev.2013.10.007.

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