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Review article

A comparative neurological approach to emotional expressions in primate vocalizations

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ABSTRACT

Different approaches from different research domains have crystallized debate over primate emotional processing and vocalizations in recent decades. On one side, researchers disagree about whether emotional states or processes in animals truly compare to those in humans. On the other, a long-held assumption is that primate vocalizations are innate communicative signals over which nonhuman primates have limited control and a mirror of the emotional state of the individuals producing them, despite growing evidence of intentional production for some vocalizations. Our goal is to connect both sides of the discussion in deciphering how the emotional content of primate calls compares with emotional vocal signals in humans. We focus particularly on neural bases of primate emotions and vocalizations to identify cerebral structures underlying emotion, vocal production, and comprehension in primates, and discuss whether particular structures or neuronal networks solely evolved for specific functions in the human brain. Finally, we propose a model to classify emotional vocalizations in primates according to four dimensions (learning, control, emotional, meaning) to allow comparing calls across species.

Contents

1. Introduction

Notwithstanding the potential differences in affect or the phenomenological aspect of feeling a particular emotion, that is, being consciously aware of it (Dawkins, 2000), which we do not address in this review, it is now well established that animals have an emotional life (Bekoff, 2007; Davila-Ross et al., 2011; de Waal, 2011; Panksepp, 2011a,b; Parr et al., 2005). This understanding is particularly crucial for studies related to animal welfare and can be used to influence policies on the treatment of farm animals (Briefer, 2012). Additionally, it is also currently held that many, if not all, animal vocalizations convey emotional content, understood as both the fact that these vocalizations reflect the emotional state of the caller, and the fact that emotional information may be extracted by the listener (Briefer, 2012; Fichtel et al., 2001; Owren et al., 2011; Seyfarth and Cheney, 2003). The study of emotions has

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also been of much interest in the recent literature on nonhuman primates (henceforth, primates) at a more fundamental level, particularly because of their close proximity to humans. The possibility that primate vocalizations bear a strong emotional content has nevertheless mostly been considered in discussions related to the evolution of human language, usually as opposed to the presumed unique characteristics of human language. More precisely, nonhuman primate vocal communication systems have been considered similar to human emotional vocal production but different and potentially evolutionary unrelated to human speech, as opposed to their more controlled gestures (Tomasello, 2008). For instance, Tomasello (2008) states that primate vocalizations are "...tightly tied to specific emotions, and broadcast indiscriminately to everyone in the immediate vicinity" (p. 8). In this approach, the focus is put on the fact that primates may not be as capable as humans in controlling their calls or vocalizations, in stark contrast to the flexibility offered by human language and potentially available to other primates in gestural communication (Arbib et al., 2008).

Nevertheless, some studies also suggest that it may be incorrect to label all primate vocalizations as uncontrollable expressions of their emotions. Some of them undoubtedly are (Tomasello, 2008), but so are some equally uncontrollable human vocalizations such as screaming, groaning, crying, or laughing (Groswasser et al., 1988; Mariani et al., 1980). However, primates may also have more control over intentional calls (calls that are produced with the aim of fulfilling a goal) or referential calls (calls that indicate something to someone), which both fulfill a complementary communicative role to the conveying of emotions (Crockford et al., 2012; Liebal et al., 2014; Sievers and Gruber, 2016); finally some calls may have a learnt component (e.g. Watson et al., 2015). Call characteristics probably also depend on the intended audience. For instance, a call aimed at one's own community has different acoustic characteristics than a call intended for intergroup communication (Liebal et al., 2014). Similarly, low- and high-frequency vocalizations are believed to serve different purposes during aggressive interactions (e.g. Ordóñez-Gómez et al., 2015). Interestingly, neurological research in primates has shown that directed and non-directed types of calls recruit different cerebral structures (Ghazanfar and Eliades, 2014; Ghazanfar and Logothetis, 2003).

In this review, our goal is to conciliate both views stemming from research on emotion and on the evolution of language, including the controversial topic of intentional vocal production in primates and other animals, to propose a unifying framework to analyze emotional vocalization in primates. We first give a comparative overview of the cerebral structures involved in the communicative and emotional processes before discussing the higher order cognitive bases of emotional communication across primates, particularly the processes of categorization (distinguishing A versus B) and discrimination (distinguishing A versus non-A). In this review, we will mainly focus on vocal expression and perception of emotions, but we will also connect our discussion to data from visual studies on facial expression or perception of emotions when points of convergence can be underlined. Additionally, we will address aspects about both production and perception of vocalizations and emotions to underline similarities and differences in the two systems across primates to converge towards a model of emotional vocalizations in primates.

2. Comparative methods in use to investigate the cerebral bases of behavior in primates

Historically, neuroscience owes much to primate research, particularly because such research has been conducted invasively on species including macaques (genus *Macaca*) and squirrel monkeys (genus *Saimiri*). As was the case for human affective neuroscience, studies of lesions were highly informative in the early days of neuropsychological research (Damasio, 1994). This technique consists of comparing the behavior of a test subject after a stroke or after removal of a brain area for clinical reasons (e.g. tumor or pharmaco-resistant epilepsy). For instance, in monkeys, this technique has been used to study which areas of the brain were necessary for vocal production (Kirzinger and Jürgens, 1982, 1985). Other invasive techniques that offer a direct connection between a given brain area and corresponding behavior are deep electrical stimulation and single-cell recording while an animal is engaged in a task (Jürgens, 2002). Less direct but nonetheless invasive techniques have also been used, such as studying the effect of drugs on neurotransmitters in terms of vocal behavior (Glowa and Newman, 1986). Because of the invasive characteristic of these techniques, little similar research has been conducted on great apes, who are phylogenetically closer to humans. Additionally, the results of lesioning studies in the context of animal vocalizations have been criticized (Ghazanfar and Rendall, 2008). For instance, one major finding of this research in a comparative framework has been that introducing lesions or electrically stimulating primate cortical areas thought to be involved in vocalization has had little effect (Aitken, 1981; Jürgens et al., 1982), as compared with humans who are heavily impaired when Broca or Wernicke's areas are damaged (Groswasser et al., 1988; Mariani et al., 1980). However, these results may benefit from a newer and more informed appraisal based on current knowledge of the primate vocal system (Ghazanfar and Rendall, 2008). The lesion localization approach is also problematic because when a specific region is damaged, all functional activities of connected brain areas to this region are also modified. It is then difficult to disentangle the behavioral impact of damage to a specific brain area from the behavioral impact of modifications induced in all other connected brain areas.

More recent approaches, based on neuroimaging, involve less invasive investigation of the brain processes underlying primate behavior. Following the original postmortem dissections, whose results were affected by mechanisms such as rigor mortis, structural magnetic resonance imaging (MRI) has allowed precise virtual dissections of living primate brains (Rilling, 2006). These studies have shown that human brains are not simply scaled-up versions of primate brains, but have specificities. Compared with other primate brains, human brains have larger neocortices with more numerous cerebral gyri and deeper sulci, their temporal and frontal lobes contain more white matter, and their prefrontal cortices are characterized by higher white matter volume and gyrification (Rilling, 2014). However, human prefrontal cortices may not have undergone specific expansion compared to other primates apart from in absolute number of neurons (Gabi et al., 2016). Diffusion-weighted imaging or diffusion tensor imaging allows researchers to measure the diffusion of water molecules in the brain and to reconstruct major white-matter fibre tracts (Rilling et al., 2008). Functional neuroimaging is also being developed to study brain activation in vivo in primates. Positron emission tomography imaging highlights areas that are active in a task by monitoring the transmission of a radioactive marker. This technique has been used in the study of the production of vocal and gestural signals in chimpanzees (Taglialatela et al., 2008). Electroencephalography has also been used to study reactions of one chimpanzee to emotional and neutral stimuli (Hirata et al., 2013). Finally, while functional MRI (fMRI) studies have been conducted invasively in macaques (e.g. Petkov et al., 2008), they necessitate restraining the test subject, which forbids their use with great apes. In the following paragraphs, we summarize the findings of primate neuroscience research in the domain of vocalizations and of emotions on the basis of the various techniques that we have described here.

3. Brain mechanisms involved in vocal production and perception in primates

3.1. Vocal communication: production

The structures responsible for vocal production can be investigated at three levels: respiratory, laryngeal, and supralaryngeal (Jürgens, 2002; Liebal et al., 2014). Whether the human larynx is truly different from that of other animals – particularly great apes – and whether this has any direct consequences for the uniqueness of human speech is under debate (Ankel-Simons, 2007; Fitch, 2012); thus, we assume here that the basic mechanisms of vocal production are similar in all primates, including humans (Ghazanfar and Rendall, 2008). Processes in the larynx and supralaryngeal vocal tract are controlled by several nuclei located in the pons and medulla that project through subcortical regions (e.g. basal ganglia) to the larynx and other articulatory structures such as the tongue, mouth, and upper face (Jürgens, 2002; Liebal et al., 2014). The activity of the motor nuclei is controlled in the medulla, itself mediated by the periaqueductal gray of the midbrain (Jürgens, 2002; Liebal et al., 2014). Several studies have been published, including empirical evidence and theoretical frameworks, that have highlighted the importance of complex cortical and basal ganglia loops in the production and perception of emotional vocalizations (e.g. Paulmann et al., 2009; Péron et al., 2013). These structures may explain much of primate vocalizations, assuming that they are innate, as voluntary control over communicative signals requires the involvement of cortical structures, particularly the dorso and mediofrontal cortices, including the anterior cingulate gyrus and the supplementary and pre-supplementary motor areas (Jürgens, 2002). This view is additionally supported by the fact that there is no direct connection between the motor cortex and the basal motor nuclei in primates, which are solely controlled by the reticular formation of the medulla. In contrast, in humans, there is a direct connection between the nucleus ambiguus and the motor cortex, providing a direct means for the cortex to control the larynx without relying on the medulla network (Jürgens, 1976). Although some cortical areas (e.g. anterior cingulate gyrus) in monkeys have been connected to the learning of vocalizations in particular food-based paradigms (Gemba et al., 1995), whether they are truly connected to the voluntary characteristic of vocal production or instead to the motivation to obtain the food reward remains unclear (Aboitiz et al., 2006; Liebal et al., 2014). More recent findings suggest that neurons in the prefrontal cortex mediate voluntary vocalizations in monkeys (Coudé et al., 2011; Hage and Nieder, 2013) although this control may disappear with age suggesting a different evolutionary pathway compared to humans (Hage et al., 2016).

It is not clear at this stage whether the connectivities responsible for vocalization production in great apes are more similar to those in humans or to those in monkeys. The use of noninvasive neuroimaging techniques in great apes allowed Taglialatela et al. (2008, 2011) to show activations of the inferior frontal gyrus (IFG) in communicative situations involving both vocal and gestural communication, particularly in the context of producing attention-getting sounds. Liebal et al. (2014) interpret these results as suggesting that cortical structures are directly involved in the production of some vocalizations in chimpanzees. However, because these activations have so far been found only in the context of attention-getting sounds, it remains unclear as to whether they also occur during other vocalizations (Liebal et al., 2014). Interestingly, many of these attention-getting sounds were either nonvocal or idiosyncratic sounds developed by only a few individuals through their extended contacts with human caretakers and thus potentially socially learned (Taglialatela et al., 2012). This opens the possibility of these structures being involved only in the case of learned vocalizations, much like human language, as opposed to more innate and emotionally-based vocalizations.

3.2. Vocal communication: perception

Although the frequency range is known for only a few species so far (e.g. N = 19, Heffner, 2004), the best frequencies for hearing in these species range between 1 and 10 kHz, with a few outliers; in the high frequencies, most primates are able to hear vocalizations ranging up to 35–45 kHz, with prosimians able to hear in much higher frequencies (circa 60 kHz, Ramsier et al., 2012), but humans and chimpanzees limited to lower frequencies (17–29 kHz, Heffner, 2004). Auditory signals are processed similarly in both humans and primates: they are first transformed into neural signals at the basilar membrane of the inner ear, with particular areas of the cochlea sensitive to various frequencies (tonotopy). The specific movement of the basilar membrane triggers a pattern of discharges corresponding to the frequency range that the area is sensitive to by means of hair cells attached to the membrane (Heffner, 2004). The signal is then transmitted to the cochlear nuclei, to the superior olivary complex, and to the ventral nucleus located in the auditory thalamus, which subsequently projects to the auditory cortex of the temporal lobe of the brain (Kaas et al., 1999; Pannese et al., 2015). In the auditory cortex, three areas in the superior temporal plane process the signal: neurons located in the core respond to particular frequencies, while neurons present in the belt and parabelt react to more complex sounds composed of several frequencies or to one that varies over time (Kaas et al., 1999), including neurons that are more sensitive to particular frequencies (rate coding) and others that encode the temporal features of the sound (temporal coding, Brosch and Scheich, 2003). Most neurons in the belt and parabelt respond to more than one frequency and to more than one call type (Ghazanfar and Hauser, 1999). A more temporal pathway appears to be responsible for the identification of the sounds' patterns, while a more parietal pathway is thought to process spatial information, that is where the sounds originate from (Rauschecker and Tian, 2000). fMRI has allowed the isolation and comparison of cortical activations in humans and macaques. Both the lateral sulcus and the superior temporal gyrus (STG) are activated when macaques listen to monkey and human vocalizations. In addition to these two areas, the superior temporal sulcus (STS) is also activated in humans, suggesting a specialization of this area for the treatment of vocalizations in humans (Belin et al., 2000; Joly et al., 2012) or complex organized sounds such as music (Schirmer et al., 2012).

4. Lateralization of the brain for vocal and emotional processing in primates

While lateralization has often been presented as a key specificity of the human brain, recent research has found similar effects in other primate brains in a broad array of studies ranging from gestural communication to listening to species-specific vocalizations (for a review, see Hopkins and Cantalupo, 2005). Nevertheless, many of the primate studies solely present behavioral evidence of lateralization and can therefore only be suggestive of the existence of such lateralization at the brain level. Comparative structural neuroimaging has shown that particular areas involved in the processing of human language and known to be leftwardly asymmetric in humans are also leftwardly activated in great apes (Gannon et al., 1998; Hopkins et al., 1998; Pilcher et al., 2001), although the bias is more pronounced in humans (Fitch and Braccini, 2013; Yeni-Komshian and Benson, 1976). Differences between humans and other primates can be found when detailed comparative analyses are conducted. For instance, the arcuate fasciculus, a large white-matter bundle that connects Wernicke's area (posterior portion of the left STG) and Broca's area (a region in the left inferior frontal cortex (IFC)), is present in macaques, chimpanzees, and humans (Rilling, 2014). However, out of the three species, it is only in humans that the arcuate is leftwardly asymmetric, which supports its possible role in language processing (Rilling, 2014).

At the neural level, results in monkeys remain inconclusive: the listening of species-specific calls, compared to a variety of non-vocal sounds and/or heterospecific calls depending on the study, elicited either left-lateralized activity in the temporal pole of the STG (Poremba et al., 2004) or right-lateralized activity (Gil-Da-Costa et al., 2006); other studies found that species-specific vocalizations could not be linked to any side in particular (Joly et al., 2012). In chimpanzees, it may be the function of the call that drives the lateralization of brain activity (Taglialatela et al., 2009). For instance, while long-distance pant hoots did not lead to lateralization of the brain, listening to short-distance social calls such as grunts or barks elicited a right bias in activation. A right-sided activation of the brain was also suggested by research in the emotional domain: monkeys and great apes both show orofacial asymmetries during vocal production, as evidenced by more pronounced grimaces on the left side of the mouth, which is suggestive of right hemisphere dominance (Fernández-Carriba et al., 2002; Hauser, 1993; Hauser and Akre, 2001; Hook-Costigan and Rogers, 1998), as has been documented in humans (Moreno et al., 1990). These leftward orofacial asymmetries have been most often associated with the emotional state of the animal: for instance, in chimpanzees they are found in emotionally loaded expressions such as "silent-bared teeth face," "playface," and "scream face" (Fernández-Carriba et al., 2002). Interestingly, in chimpanzees, a rightward orofacial asymmetry seems specifically associated with learned attention-getting sounds, while a leftward bias is associated with vocalizations such as pant hoots; this suggests that different neural substrates are involved for types of calls that differ in their emotional content (Losin et al., 2008; Wallez et al., 2012). This hemispherical lateralization in chimpanzees may be similar to the hemispherical lateralization described in humans for language processing, with activations in the two hemispheres sustaining various aspects of human language processing (Belin et al., 2000; Schirmer and Kotz, 2006; Zatorre and Belin, 2001). For instance, production of attention-getting sounds led to activations in the left IFG in chimpanzees (Taglialatela et al., 2008).

Compared with research investigating the evolutionary roots of language, research investigating emotion perception in primates has strengthened the idea of a right bias in lateralization specific to emotion treatment (Lindell, 2013). Several studies using videos of either neutral or emotional stimuli have investigated how chimpanzees react to the emotional content of a given scenario at the behavioral, physiological, or neural level. In particular, Parr and Hopkins (2000) used tympanic temperature as an assay of brain hemisphere activity, with an increased tympanic temperature indicating increased activity. They found that right ear temperature increased in captive chimpanzees when they were watching emotional videos, consistent with greater right hemisphere involvement (Parr and Hopkins, 2000). The rightward hemisphere bias documented in chimpanzees is also found in other species such as baboons or mangabeys during natural interactions, as evidenced by studies investigating the perception of visual emotional stimuli (Baraud et al., 2009; Casperd and Dunbar, 1996; Morris and Hopkins, 1993; Wallez and Vauclair, 2011).

5. Brain mechanisms involved in emotional processing in primates

In the visual domain, initial work done by Ekman in 1992 has suggested that positive and negative facial emotions are both expressed and understood in a universal manner in humans (Ekman, 1992). However, more recent work has revealed several limitations about the universality of emotion perception and the impact of human cultures on relevant visual information for emotional facial expression (Crivelli et al., 2016; Jack et al., 2012). Interestingly, a recent study compared the activation of the STS in humans and in macaques while they processed facial emotional cues (Zhu et al., 2013). The human STS was functionally subdivided in a right posterior area that responded to emotional expression of both species, and a more anterior area in the right middle STS that responded only to human emotions. In contrast, in monkeys, the response was more important to conspecific rather than human emotional expressions, but not as specific as in the human case. The authors concluded that the human STS may have thus specialized to analyze emotional expressions by humans. There is no comparable study available with chimpanzees, who are phylogenetically closer to humans, that would allow assessment of the validity and specificity of this conclusion.

Humans rely heavily on auditory signals to convey emotional content, particularly through the vocal channel (Belin et al., 2004). The emotional content can be expressed through nonverbal means, for instance, with laughter or screams (Sauter et al., 2010; Scherer, 1994; Schrober, 2003; Wattendorf et al., 2013). It can also be expressed through modulation of the prosody, that is, the intonation found in speech utterances (Banse and Scherer, 1996; Grandjean et al., 2006; Patel et al., 2011). The ability to perceive the coarse meaning of nonverbal signals during human interactions across cultures suggests the existence of a basic neuronal network subserving this ability.

Brain stem subregions and subcortical structures, especially the amygdala nuclei and the basal ganglia through dynamic interactions with distributed cortical areas (e.g. insula, orbitofrontal, medial temporal lobe, cingulate, and cortical sensory regions), are thought to be the foundations of such emotional perception (e.g. Nieuwenhuys, 1996). More specifically, a large spectrum of negative emotions expressed during vocal behavior, such as anger, fear, or disgust, and positive emotions, such as happiness, have been found to modulate subcortical regions, especially the amygdala and the basal ganglia, whose activity is modulated during emotional decoding and/or responses (Bach et al., 2008a; Fecteau et al., 2007; Frühholz et al., 2012; Leitman et al., 2010; Phillips et al., 1998; Sander et al., 2005; Scherer, 1994; Schrober, 2003; Wiethoff et al., 2009). Indeed, a complex neural network has been found to be modulated by exposure to vocal emotional expression in humans. The nuclei of the amygdala structure are crucial in this neural network (Bach et al., 2008b; Ethofer et al., 2009; Fecteau et al., 2007; Frühholz et al., 2012; Frühholz and Grandjean, 2013; Grandjean et al., 2005; Leitman et al., 2010; Phillips et al., 1998; Sander et al., 2003a, 2007; Sander and Scheich, 2005; Wiethoff et al., 2009). While their functional roles are still debated in terms of whether they can truly decode the emotional valence of vocal expressions or the extent to which they are involved in emotional responses to emotional vocalizations (Adolphs and Tranel, 1999; Bach et al., 2013; Scott et al., 1997; Sprengelmeyer et al., 1999), the nuclei of the amygdala are sensitive to vocal cues of anger (Bach et al., 2008a), as well as to expressions of happiness (Fecteau et al., 2007; Leitman et al., 2010; Sander et al., 2003b; Sander and

Scheich, 2005), suggesting a response to high arousal states in general (Frühholz et al., 2014), as has also been suggested in the domain of olfaction (Anderson et al., 2003). The hippocampus is another large subcortical structure of the so-called limbic system that appears to have a role in the decoding of emotions, in particular with respect to memory processes (Frühholz et al., 2014; Maguire, 2001). The hippocampus is thought to act in conjunction with the amygdala, the amygdala providing the evaluation of the stimulus or the related emotional responses and the hippocampus encoding the relevant memory (Frühholz et al., 2014). However, the hippocampus itself appears to have a role in deciphering emotion valence in the auditory context (Alba-Ferrara et al., 2011; Leitman et al., 2010; Phillips et al., 1998; Wiethoff et al., 2008), albeit potentially occurring during more complex emotional situations than for those involving the amygdala (Alba-Ferrara et al., 2011; Frühholz et al., 2014). Other brain areas that have been connected to emotion processing are found in the temporal, frontal, and prefrontal cortices (Banse and Scherer, 1996; Grandjean et al., 2006). Specifically, the STG (bilateral posterior STG (pSTG) (Ethofer et al., 2009; Mitchell et al., 2003; Sander et al., 2005), bilateral mid STG (mSTG) (Bach et al., 2008a; Ethofer et al., 2009; Grandjean et al., 2005; Leitman et al., 2010; Sander et al., 2005), right anterior STG (aSTG) (Bach et al., 2008a)), STS, orbitofrontal cortex (OFC), IFC, and ventromedial and lateral prefrontal cortices appear to be involved in the sensory, emotional, and evaluative decoding of emotional prosody, with different functional roles for these subregions (Schirmer and Kotz, 2006; Wildgruber et al., 2009).

The range of studies found in the domain of emotional vocalization decoding includes different kinds of tasks from passive listening to implicit processing, for example, when the spatial attention of participants is manipulated or when the task of participants is to identify the gender of the speaker while they are exposed to emotional vocalizations (e.g. Grandjean et al., 2005; Sander et al., 2005). Another type of study in this domain involves explicit judgments, in which the participants are asked to evaluate the emotional meaning of the stimuli to which they are exposed (e.g. Bach et al., 2008a). The type of task required from the participants is important to control because variations in the task lead to different modulations of brain activations, suggesting different specific roles of the regions involved. For instance, when the task requires explicit rather than task-independent decoding of emotional prosody, which induces activity in the mid-posterior STG (m-pSTG) (Grandjean et al., 2005; Sander et al., 2005), the activation is shifted to adjacent regions of the right m-pSTG. Explicit decoding induces activity in the pSTG, bilateral IFG, and OFC (Bach et al., 2008a; Buchanan et al., 2000; Ethofer et al., 2009; Mitchell et al., 2003; Sander et al., 2005; Wildgruber et al., 2004; Wildgruber et al., 2005). In contrast, implicit decoding induces activity in the bilateral pSTG, right aSTG, bilateral amygdala, and left IFG (Bach et al., 2008a; Buchanan et al., 2000; Ethofer et al., 2009; Mitchell et al., 2003; Sander et al., 2005; Wildgruber et al., 2004; Wildgruber et al., 2005). Therefore, the different tasks may involve different fronto-temporal networks, in particular during the decoding of angry prosody (Frühholz et al., 2012). Additionally, certain regions, such as the pSTG or the amygdala, appear to be sensitive to specific acoustic cues such as variations of the fundamental frequency or intensity, which are often expressed in emotion-induced calls (Frühholz and Grandjean, 2012; Leitman et al., 2010), whereas the modulation of the IFG or the mSTG, for example, do not seem to be sensitive to these acoustical cues (Frühholz et al., 2012). To date, the emerging picture is that subparts of the STG may provide sensory decoding of emotion-related acoustic cues from voices (Grandjean et al., 2005; Sander et al., 2005). In contrast, the IFG, especially the right IFG, and the OFC, especially its medial part, appear to be involved in categorization and evaluative judgments, respectively, of the affective meaning of prosody (Leitman et al., 2010). In summary, the data suggest specific brain networks of subcortical and fronto-temporal regions for the processing of emotional prosody, with a continual flow between the STG and the IFG regions (Frühholz and Grandjean, 2012).

6. Integrating brain mechanisms involved in vocal and emotional processing in primates

Our review has shown that much of the brain circuitry at work in the treatment of vocal signals, on the one hand, and emotional signals, on the other, appears to be highly conserved among primates and possibly with a gradient of similarity following the phylogenetic tree, with chimpanzees potentially closer to humans than monkeys to humans. The basic physical properties of the signal appear to be treated similarly across primates, as well as the subcortical structures responsible for their treatment, which have been covered earlier in the text and in other reviews. Here, we focus on the cortical structures that have a larger part to play in the analysis of the emotional content of a call in primates. The general regions of interest that appear both in the vocalization and emotion literature lie in the IFC and superior temporal cortex. The STG appears to be particularly important for the treatment of both vocalizations and emotions among primates. The STS may have additionally been specialized in the human lineage to support properties of language, as well as to decode emotional prosody. Here it is important to note that these aspects have only been compared in humans and monkey species because of the invasiveness of the techniques used. Chimpanzees and bonobos appear to be generally closer to humans in neural organization than to monkeys, and it will be necessary to investigate how close the three species are at the resulting cognitive level (Rilling, 2014). We certainly do not advocate for the use of invasive research with chimpanzees to explore these questions, but suggest that alternative techniques and protocols must be developed in the near future to assess the claimed uniqueness of certain functions and related cerebral structures in humans, especially through comparison with their closest relatives, the chimpanzees and bonobos. In particular, we believe it is of utmost importance to precisely assess the role of the STS and IFG in emotional decoding in chimpanzees, and more generally, in higher order cognitive processes (e.g. Hecht et al., 2013). On the basis of our review and comparable data in humans, we therefore predict that a general STG-STS-IFG functional network that has been highlighted in the treatment of human emotions will be uncovered in the treatment of emotional vocalizations in chimpanzees, particularly in their abilities to discriminate and categorize emotional calls. An informed comparison will allow the precise isolation of the decoding of vocal emotional expressions that evolved solely in the human lineage.

7. Integrating intentional communication with emotional vocalizations in primates

Our review has also shown interesting convergences between the study of emotion and vocalizations in primates, suggesting that several aspects have to be taken into account when evaluating how primates process, evaluate, and categorize the emotional content of the calls they perceive. At the behavioral level, recent research has shown evidence that all primate calls should not be considered equally with respect to their emotional content. In particular, learned vocalizations (such as attention-getting sounds) appear to differ from other vocalizations and may recruit different networks in the brain (Losin et al., 2008; Taglialatela et al., 2008). Considering these results were obtained in captivity, how ecologically valid is this assertion? Primate vocalizations are notoriously fixed in nature, with little description of potential cases of learning, particularly in the wild (Fischer et al., 2015; Watson et al.,

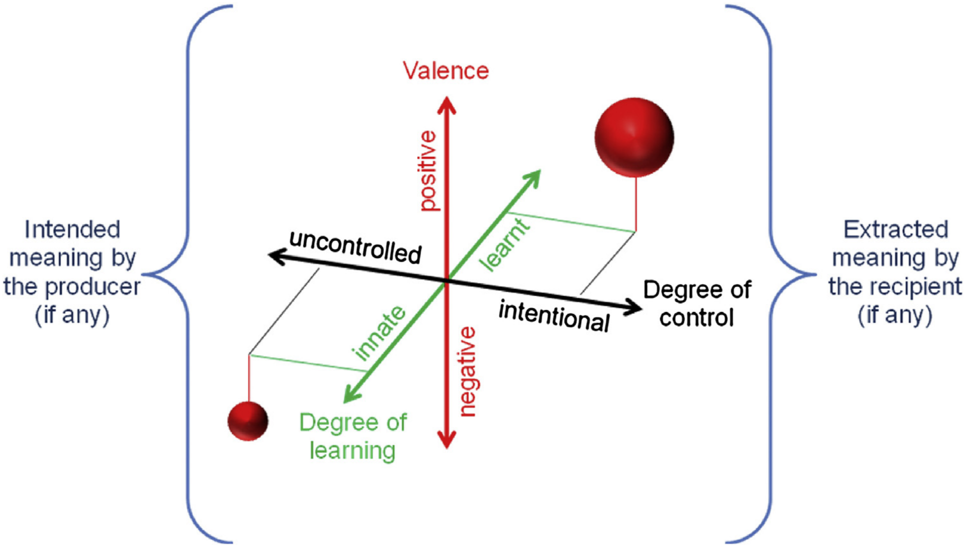

Fig. 1. A schematic representation of the aspects that must be taken into account when analyzing emotional vocalizations in primates. Degree of control (black), degree of learning (green), and valence (red) constitute the axes of a three dimensional space while arousal is represented by the size of the spheres (each symbolizing a different call) in this space. Here, for instance, the rightward vocalization is positively valenced, has a large learnt component, and is produced intentionally while the caller is in a high arousal state; in contrast, the leftward vocalization is negatively valenced, largely innate, and is produced without any control by the caller while in a low arousal state. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2015). Nevertheless, a confounding factor in the previous analysis was the intentional characteristic of the calls analyzed (Losin et al., 2008). Intentional production of calls suggests that animals have control over their vocal tract to produce specific intentional vocalizations; animals thus communicate intentionally a particular content by producing voluntary and recipient-direct signals as a means to reach that goal, modifying the recipient's behavior in the process (Townsend et al., 2016). While still debated, there is now much evidence of such control in primates, particularly chimpanzees (Crockford et al., 2012; Gruber and Zuberbühler, 2013; Schel et al., 2013; Townsend et al., 2016), although this could also constitute cases of contextual learning (Janik and Slater, 2000). An important aspect of the intentional characteristic of a call is that it may not prevent it from bearing emotional content, as is the case in humans. In two recent examples, Crockford et al. (2012) and Schel et al. (2013) showed that wild chimpanzees could control the production of a "snake hoo" alarm call to inform other individuals of the presence of a snake, an upsetting experience for the subject. That is, despite an equivalent external stimulus (either a static or moving snake depending on the study), tested chimpanzees in the two studies were able to modulate their call production depending on whether their audience had previously seen the snake or not. Similarly, Gruber and Zuberbühler (2013) showed that chimpanzees could intentionally control the production of a "travel hoo" to recruit individuals for travel. In doing so, they were making their internal state public ('I'm in the mood for travelling'), but only to a preferred audience.

These two sets of studies, in different contexts, in addition to the other studies reviewed earlier, therefore show that there are at least four aspects that can be taken into account when analyzing emotional calls in primates (Fig. 1): (i) the degree of learning to which they are subjected, (ii) the degree of control that signalers can apply to their production, (iii) the emotional dimensions of the call (i.e. valence and arousal) and (iv) the intended meaning by the producer and inferred meaning by the recipient, if any (see Sievers et al., in press for a discussion of the two last points in the general context of intentional communication). As our review has shown, different subcortical and cortical structures are likely to be involved differentially for each of these dimensions. These different aspects lead us to suggest that emotional calls in primates, including humans, can be of three types: (a) spontaneous and uncontrolled, (b) spontaneous but controllable via voluntary inhibition or amplification of the call, or (c) produced intentionally by the signaler with the intent to induce an emotional state or a specific response in the audience. Here, to distinguish empirically between the different types of call production, it will be necessary to study to the context in which the call is produced, as well as the potential recipient's behavioral response to the production of the call. As such, the more flexibility is found in the interaction between signalers and recipients, the more likely the production of the call is intentional and the interaction an instance of intentional communication (Sievers et al., in press). Note that a specific call is not tied to a specific category and must be analyzed within its context of production to be correctly sorted (e.g. Clay et al., 2015): the same call, e.g. a tantrum scream, can be produced in response to an unlikely event (in this case, uncontrollably, for instance, an adult female bonobo being hit by a falling coconut; Z. Clay, personal communication), can be modified according to the intended audience (Slocombe and Zuberbühler, 2007), or can be produced with the goal of modifying a mother's behavior in chimpanzees (Nishida, 1990). The tantrum example illustrated here in the two *Pan* species can easily be matched to the tantrums produced by human children.

8. Conclusion

To conclude, our review has shown that it is possible to combine the study of emotions and vocalizations in primates, without necessarily having to determine whether the emotional characteristic of primate vocalizations makes them innate by nature and impossible to control for the producer. We have shown that there are highly conserved cerebral structures and possibly patterns of connectivity involved in both the production and the perception of emotions and vocalizations in primates, suggesting that a phylogenetic approach can be useful to the understanding of the two systems. Finally, we propose that, to resolve opposing views about the emotional processing of primate vocalizations, it is necessary to take into account the voluntary characteristic of the calls, that is how intentional the production of these vocalizations is and how intentional the communicative event where a specific vocalization occurs is. Such analysis will allow deciphering between cases where primates have absolutely no control over their vocalizations from cases where they may want to make their emotions public to a specific audience. In this respect, our proposal, exemplified here in the auditory domain, may also be applied in other means of communication such as the visual domain, opening the possibility to analyze the emotional side of primate communication as a whole in the future, as well as its connection with human emotional behavior.

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