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Review

Subcortical processing in auditory communication

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ABSTRACT

The voice is a rich source of information, which the human brain has evolved to decode and interpret. Empirical observations have shown that the human auditory system is especially sensitive to the human voice, and that activity within the voice-sensitive regions of the primary and secondary auditory cortex is modulated by the emotional quality of the vocal signal, and may therefore subserve, with frontal regions, the cognitive ability to correctly identify the speaker's affective state. So far, the network involved in the processing of vocal affect has been mainly characterised at the cortical level. However, anatomical and functional evidence suggests that acoustic information relevant to the affective quality of the auditory signal might be processed prior to the auditory cortex.

Here we review the animal and human literature on the main subcortical structures along the auditory pathway, and propose a model whereby the distinction between different types of vocal affect in auditory communication begins at very early stages of auditory processing, and relies on the analysis of individual acoustic features of the sound signal. We further suggest that this early feature-based decoding occurs at a subcortical level along the ascending auditory pathway, and provides a preliminary coarse (but fast) characterisation of the affective quality of the auditory signal before the more refined (but slower) cortical processing is completed.

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1. Introduction

Emotional stimuli command vast cognitive resources and benefit from privileged processing across a distributed network of brain regions (Rolls, 1999). Much of the emotional quality of the human voice can be inferred by the physical features of the vocalisation, and by the sonic properties of one's speech. Nonverbal expressions, for example, communicate affective meaning and information about the speaker's state of mind independently of linguistic cues, as shown by cross-cultural studies (Scherer et al., 2001; Pell et al., 2009). The human auditory system is especially sensitive to the human voice. Specific voice-selective areas have been repeatedly reported in the right and left superior temporal

cortex (Belin et al., 2000), with peaks of activation varying considerably across individuals. The networks implicated in the processing of vocal affect includes superior temporal, inferior frontal, and limbic regions (Grandjean et al., 2005; Sander et al., 2005; Schirmer and Kotz, 2006; Bach et al., 2008; Wiethoff et al., 2009; Leitman et al., 2010; Ethofer et al., 2012; Fecteau et al., 2007; Frühholz et al., 2012; Frühholz and Grandjean, 2013a; Wildgruber et al., 2009 for a review). Within the auditory cortex, the voice-sensitive areas have been shown to respond more strongly to emotional as opposed to neutral voices (Frühholz and Grandjean, 2013b), suggesting that information about vocal emotion is already available at the perceptual level of processing. It is however unclear whether this information may also be available prior to reaching the sensory cortex. Hence, a central question in auditory affective communication is at which level of processing the human brain extracts the earliest information relevant for the identification of the voice's affective quality.

Recent models (Schirmer and Kotz, 2006; Wildgruber et al., 2009; Brück et al., 2011) have emphasised the role of the auditory cortex, and proposed that emotionally relevant acoustic information is extracted in the superior temporal gyrus and integrated in

List of abbreviations: BG, basal ganglia; CN, cochlear nucleus; EEG, electroencephalography; fMRI, functional magnetic resonance imaging; IC, inferior colliculus; MGB, medial geniculate body of the thalamus; PAG, periaqueductal grey; SOC, superior olivary complex; STRF, spatio-temporal receptive field

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the superior temporal sulcus. Here we elaborate on these models by focussing on the first stage (the extraction), and propose that the earliest emotion-relevant information may also be available prior to the cortical level, at early stages of auditory perceptual processing. For the purpose of this work, we use the term 'perception' to denote a modality-specific sensory processing, independently of whether or not this is reportable and/or consciously perceived – as, for example, in cortical deafness (Graham et al., 1980).

Our model builds on the notion that emotional states can modulate vocal features of the human voice (e.g. intensity of fundamental frequency, energy distribution across frequency bands, distribution of harmonic frequencies) through changes in the peripheral vocal production structures (Banse and Scherer, 1996). Early animal studies have shown a link between the motivational state and the physical structure of the vocalisations emitted in a social context (motivation-structural rules, Morton, 1977). For example, birds and mammals use harsher (covering a wider-frequency band, as opposed to pure-tone-like), lower-frequency vocalisations in hostile contexts compared to friendly settings (Morton, 1977). It has been proposed that these primitive aspects of affective expression have been retained even after the evolutionary transition from basic animal vocalisation to the more sophisticated human language (Grandjean et al., 2006). For example, the physiological changes induced by emotional arousal (e.g. in muscle tone, heart rate, and respiration) may affect the characteristics of the human voice, resulting in an emotional modulation of the vocal expression (Bachorowski, 1999; Bachorowski and Owren, 2003).

Studies have shown that some emotional states share similar influence on vocal features. For example, both in speech (Scherer et al., 1991; Banse and Scherer, 1996; Johnstone and Scherer, 2000) and non-speech vocalisations (Szameitat et al., 2009, 2011; Sauter et al., 2010), anger, fear, and joy have all been associated with increased pitch. However, despite these commonalities, different emotional states are typically associated with distinct overall patterns (Patel et al., 2011), that is, distinct combinations of features. For example, anger has been associated with increased pitch and loudness; fear with increased pitch and speech rate; joy with increased pitch, loudness, and speech rate; sadness with decreased pitch, speech rate, and loudness (Scherer et al., 1991; Banse and Scherer, 1996; Johnstone and Scherer, 2000; Szameitat et al., 2009, 2011; Sauter et al., 2010). The resulting unique vocal profile helps to differentiate the affective quality of the vocalisation, and respond with the appropriate behaviour (e.g. differentiating anger from fear enables responding appropriately, i.e. approaching rather than avoiding, Marsh et al., 2005).

At the most basic level, affective vocalisations consist of sounds, hence their perception relies on the ascending (i.e. afferent) pathway of the auditory system. This pathway originates from the auditory nerve, and terminates in the auditory cortex, via several intermediate relay points (see Gelfand, 2009 for overview). Specifically, auditory nerve fibres terminate in the cochlear nucleus, where they synapse with neurons projecting (mainly contralaterally) to the superior olivary complex. Neurons originating from the olivary complex ascend via the lateral lemniscus to reach the inferior colliculus, and the medial geniculate body of the thalamus, which is the last subcortical station of the auditory pathway. From the thalamus, neurons target the auditory cortex, located in the transverse temporal gyrus. Various structures within the ascending auditory pathway have been shown to respond to the physical features of acoustic signals. Starting from the auditory nerve, virtually all the nuclei along the subcortical auditory system are sensitive to specific sound properties. Here we will discuss specifically the cochlear nucleus (CN), the inferior colliculus (IC), and the medial geniculate body (MGB) of the thalamus. Additional

structures outside the ascending auditory pathway will also be discussed in virtue of their tight anatomical and/or functional connection with the auditory perceptual system or known involvement with affective communication. These are the periaqueductal grey (PAG), the basal ganglia (BG), and the amygdala.

1.1. Cochlear nucleus

The cochlear nucleus (CN) is a highly conserved structure found in all vertebrates (Baird, 1974). It is comprised of diverse and highly specialised neuronal populations (Ramón y Cajal c.1900; Lorente de Nó, 1933, 1981) differing in morphology (Harrison and Warr, 1962; Osen, 1969a; and 1969b; Brawer et al., 1974; Heiman-Patterson and Strominger, 1985; Adams, 1986), response properties (Pfeiffer and Kiang, 1965; Pfeiffer, 1966; Evans and Nelson, 1973; Shofner and Young, 1985; Blackburn and Sachs, 1989; Winter and Palmer, 1990; Marsh et al., 2006), and connectivity with the auditory nerve (Lieberman, 1991, 1993). Each neuronal population in the CN exhibits distinct projections (summarised in Cant and Benson, 2003), some ipsilateral (Cant and Casseday, 1986), others contralateral (Warr, 1966, 1969; Winer and Schreiner, 2005), reflecting the distinct functions of the CN anteroventral (involved in sound localisation) and posteroventral regions (involved in sound discrimination) (Eggermont, 2001).

At the functional level, evidence for a role of the CN in auditory vocal communication comes from animal studies showing that neurons in the rats' ventral CN code the syllables' voice-onset time (Clarey et al., 2004). These findings corroborate earlier results from intracellular recordings (Stevens and Wickesberg, 1999; Pressnitzer et al., 2000) and are consistent with the hypothesis that the hyperpolarisation observed in the CN is due to the stimulation of inhibitory sidebands, which reduces the probability of action potential generation and enhances the salience of the voice onset (Paolini et al., 2001). Although hypothetical, the notion that the salience of vocal features may be modulated by activity in the CN – hence, very early in the afferent auditory pathway – is compatible with anatomical evidence of direct projections from this nucleus to the medial geniculate body (MGB) of the thalamus, i.e. bypassing the inferior colliculus (Woollard and Harpman, 1940; Strominger and Strominger, 1971; Strominger, 1973; Strominger et al., 1977; Malmierca et al., 2002; Anderson et al., 2006). Future studies might investigate the functional role of these pathways in processing voices and voice sound features. Besides anatomical evidence from anterograde tracers, this latter study also showed functional evidence for direct projection: neurons in the medial MGB respond to acoustic stimuli with a latency of less than 6.5 ms, which is too short for a transit through the inferior colliculus (IC), and only possible in the presence of a direct (high-speed) pathway from the CN to the MGB (bypassing the IC). This pathway has been further characterised as constituted by (mostly) contralateral fibres originating predominantly from multipolar T-stellate cells of the ventral (and fewer cells of the dorsal) division of the CN, and terminating on the medial MGB, with most cells sending collateral axons (hence, presumably the same information) to the IC as well (Anderson et al., 2006).

A possible implication of a direct projection that bypasses the multiple auditory nuclei (e.g. superior olive, lateral lemniscus, IC) and enables early (short-latency) medial MGB exposure to the acoustic information is that it provides the thalamus with a "preparatory signal" that facilitates further processing of the acoustic stimulus, whose information will eventually be carried more fully through the main (i.e. passing through IC and all the auditory nuclei) ascending auditory pathway (Anderson and Linden, 2011). Since T-stellate cells display a narrow frequency tuning and encode stimulus envelope (Oertel et al., 2011), it has been suggested that

direct projections from the T-stellate cells to the MGB may provide finely tuned acoustic information, and thus may possibly play a role in the processing of complex sound (e.g. speech) (Schofield et al., 2014). Another implication is that the CN-medial MGB direct connection provides a fast route to eventually reach the amygdala (as the MGB projects to the amygdala, Doron and Ledoux, 1999), and is therefore instrumental for fear conditioning, associative learning (Weinberger, 2007), and the processing of relevant affective vocal signals.

1.2. Inferior colliculus

The inferior colliculus (IC) forms a major convergence region within the auditory system, as it receives feed-forward projections from the auditory brainstem (Oliver, 1984, 1987; Glendenning et al., 1992; Saint Marie et al., 1997), feedback projections from the auditory cortex (Winer et al., 1998; Winer, 2006; Stebbings et al., 2014 for a comprehensive review), and commissural connections from contralateral structures (Aitkin and Phillips, 1984). In turn, the IC sends descending fibres to a variety of brainstem nuclei (Huffman and Henson, 1990), and ascending projections to the auditory thalamus (Andersen et al., 1980). Consequently, the IC has been characterised as a major locus of integration of excitatory and inhibitory inputs (Eggermont, 2001).

Three functionally distinct structures have been identified within the IC: the central nucleus, which is exclusively auditory (Aitkin et al., 1994); the lateral (or external) cortex, which is multisensory (Aitkin et al., 1978), and receives considerable non-auditory input (Morest and Oliver, 1984); and the dorsal cortex (Winer et al., 1998), which receives instead a large proportion of descending (top–down) projections from the auditory cortex (Winer et al., 1998; Winer, 2006). The different types of cells represented within the central nucleus (each characterised by distinct electrophysiological properties and discharge patterns) enable highly precise representation of complex auditory signals (Peruzzi et al., 2000). Animal studies have shown that the central nucleus receives ascending (bottom–up) projections from various brainstem nuclei (summarised in Baumann et al., 2011) – including the dorsal and posterior ventral cochlear nucleus (Warr, 1969; Oliver, 1984) – and is tonotopically organised along the dorso–ventral axis (Schreiner and Langner, 1997; Malmierca et al., 2008; Baumann et al., 2011; Cheung et al., 2012). Evidence for a tonotopic organisation within the central nucleus has been found in humans as well, where high-resolution functional magnetic resonance imaging has identified a dorsolateral-to-ventromedial gradient preferentially responding to low-to-high frequencies (De Martino et al., 2013).

Based on the convergence of ascending and descending inputs, this structure is thought to play a key role in auditory learning (Bajo et al., 2010). In animal models, this hypothesis is corroborated by empirical observations of modulation in IC activity following short-term auditory training (Suga and Ma, 2003; Sun et al., 2007; Suga, 2008), as well as evidence of impaired auditory learning following IC lesion (Bajo et al., 2010). In humans, where non-invasive studies of auditory learning have mostly focussed on cortical areas, evidence compatible with a role for the IC has also recently been reported (Chandrasekeran et al., 2012).

Hence, through its various subdivisions, the IC is connected with the visual system (superior colliculus), the somatosensory cortex, the cerebellum, and a variety of regions involved in vocalisation and attention (Huffman and Henson, 1990). This dense and varied network of connections with other sensory and cognitive processing regions suggests that the IC may play a key role in the analysis of different aspects of the vocal signal, and in the discrimination of its affective quality. Evidence in this direction comes from the observation that the IC decodes and integrate

spectral (Portfors and Felix, 2005) and temporal information (Baumann et al., 2011). For example, different populations of IC neurons have been shown to display distinct discharge patterns (e.g. sustained, adapting, and onset-bursting, Xie et al., 2008), and unique temporal responses and directional selectivity for frequency modulated (FM) sweeps (Andoni et al., 2007; Pollak et al., 2011). These feature-specific responses in the IC are also observed at higher levels of complexity, for example in terms of over-representation of species-specific vocalisations (Portfors et al., 2009). Further indication that the IC plays a central role in linking sonic features of vocalisations with behaviourally relevant affective meaning comes from evidence of innervation and modulation of IC responses by serotonin (Thompson et al., 1994; Hurley and Pollak, 1999; Hurley and Thompson, 2001; Hurley et al., 2002), a neurotransmitter known for its involvement in social interaction. Combining behavioural observation (e.g. where rats were trained to discriminate consonants and vowels) and neural recording in the IC and in the auditory cortex, studies have shown that the brain represents different sounds (e.g. consonants and vowels) at different points in time (Perez et al., 2013). The time lapse between responses in the IC and in the auditory cortex supports the notion that consonant and vowel sounds are represented by neural activity patterns occurring on different timescales (Poepfel, 2003; Carreiras and Price, 2008), and suggests that voice processing operates through the gradual transformation from low-level acoustic information to high-level cognitive category. This transformation follows a temporal frame that reflects the sound's spectrotemporal features. Since vocal tones are characterised by unique spectral and temporal profiles, and since temporal features are known to help distinguish different vocal expressions of emotions (Banse and Scherer, 1996; Sauter et al., 2010; Patel et al., 2011), the IC is a prime candidate as the neural substrate operating an early differentiation of the emotional properties of a vocal utterance based on its spectral and temporal features.

1.3. Medial geniculate body

The medial geniculate body (MGB) of the thalamus is comprised of three subdivisions: ventral, predominantly auditory; dorsal, involved in auditory integration; and medial, predominantly multisensory (Winer and Schreiner, 2005). Both dorsal and ventral divisions send projections to the auditory cortex (Huang and Winer, 2000), although their targets differ in terms of spatial and functional distributions (Reale and Imig, 1980; Shinonaga et al., 1994). The medial division projects instead to a wide spectrum of auditory (Niimi and Matsuoka, 1979), and non-auditory (Ottersen and Ben-Ari, 1979) targets, including the amygdala (Shinonaga et al., 1994). The subcortical efferent projections from the MGB have been shown to mediate emotional responses (LeDoux et al., 1984), and the thalamoamygdaloid pathway is thought to play a key role in implicit learning from auditory cues (LeDoux et al., 1985). Within the MGB, response latencies vary between the different divisions (Anderson et al., 2006). A large proportion of neurons display sharp tuning and fast-response (Anderson and Linden, 2011). Although the MGB receives its main input from (the central and external nuclei of) the IC (Malmierca et al., 1997) other sources of ascending input – e.g. the cochlear nucleus – may target the MGB without necessarily transiting through the IC (Cant and Benson, 2003).

The fact that the medial MGB projects broadly to the auditory cortex and to the amygdala (LeDoux et al., 1985; Doron and Ledoux, 1999), and is itself the target of direct projections from the cochlear nucleus (see 'Cochlear nucleus' section above), suggests an involvement in the processing and integration of different components of the auditory information *en route* for emotional and cognitive appraisal. Evidence in this direction comes from the

observation that both the IC and the MGB are sensitive to basic spectral features and their variations over time (Nelken, 2008; Baumann et al., 2011), as well as to specific combinations of spectral features (Kanwal and Rauschecker, 2007). Furthermore, the MGB is responsive to complex sounds (Wenstrup, 1999), and its activity is modulated by the task (e.g. it shows adaptation to repeated speech recognition, Von Kriegstein et al., 2008), as well as by the context (e.g. it shows adaptation to repeated exposure to given sounds, Bordi and LeDoux, 1994; Antunes et al., 2010; Antunes and Malmierca, 2011). Animal studies have shown that about 50% of cells in this nucleus respond to conspecific vocalisations (e.g. the guinea pig purr) (Syka et al., 1997), and that neurons in both the ventral and medial MGB display a phase-locked response to the vocalisation's fundamental frequency (Wallace et al., 2007). This indicates that the MGB may play a role in the analysis of auditory communicative signals. Further indications in this sense come from reports of (unspecific) thalamic activation for emotional prosody (Wildgruber et al., 2004), with some areas close to the MGB (Kreifelts et al., 2010). Also, both the medial and dorsal subdivisions of the MGB have been implicated in the auditory processing of affective communicative signals (Bordi and LeDoux, 1994; Cappe et al., 2009; Edeline and Weinberger, 1991, 1992). It is therefore plausible that the IC and the MGB might provide a first acoustic profile of vocal emotions, which is then fed forward into the amygdala for a first differentiation between different vocal expressions based on their acoustic profile.

1.4. Periaqueductal grey

The periaqueductal grey (PAG), a poorly differentiated cell-dense area that encircles the mesencephalic aqueduct (Linnman et al., 2012) plays a central role in both the production and the perception of vocal behaviour (Behbehani, 1995). Stimulation of this region produces vocalisation (Jürgens and Ploog, 1970; Suga et al., 1973; Waldbillig, 1975; Yajima et al., 1980; Lu and Jürgens, 1993), whilst its lesion produces mutism (Adametz and O'Leary, 1959; Jürgens and Pratt, 1979; Esposito et al., 1999). Anatomical observations in the cat showed that neurons in the latero-caudal periaqueductal grey project bilaterally to the nucleus retro-ambiguus in the caudal medulla oblongata, which in turn projects to motor neurons innervating structures involved in vocalisation – e.g. intercostal, abdominal, mouth-opening and perioral muscles, pharynx, soft palate, and tongue (Holstege, 1989). Similarly, single-unit recordings in the monkey have shown that activity in PAG neurons is correlated with activity in laryngeal and respiratory muscles involved in vocal production (Larson, 1991). These and similar findings seemed to point to the PAG as the site of vocal pattern generation (Davis et al., 1996). However, evidence from lesion studies in the monkey (Siebert and Jürgens, 2003), where electric stimulation of vocalisation sites in the caudal midbrain, pons and medulla elicited vocalisation despite chemical lesion of the PAG, suggests that the PAG might instead serve gating functions. Studies in non-human primates have shown a close relation between vocalisation-producing subcortical regions in the midbrain, medulla and pons, and the limbic system, especially amygdala, hippocampus, and cingulate gyrus (Jürgens and Ploog, 1970). Similarly, human neuroimaging studies indicate that the PAG is a key region for the regulation of pain, anxiety, and autonomic functions (Linnman et al., 2012).

Hence, the PAG is relevant to affective communication because the type of vocalisations in which this region is involved has a distinctly emotional quality. For example, in the rat, PAG lesion has been shown to trigger aggressive behaviour (Chaurand et al., 1972). The PAG has also been associated with a variety of affectively

relevant adaptive functions, such as defensive reactions, reproductive behaviour, pain regulation (Behbehani, 1995), and response to stress. Moreover, the PAG appears to be directly involved in the perceptual aspects of emotionally significant vocal signals. Studies indicate that the ability of the PAG to select and initiate specific motor behaviours that have a social dimension (e.g. courtship, mating) relies on the PAG's capacity to integrate sensory and limbic inputs (Holstege, 1998; Sukikara et al., 2006; O'Connell and Hofmann, 2011), suggesting that the PAG may act as an interface between different sensory and motor modalities (e.g. auditory perception and vocal production). According to this automatic "audio-vocal interface" model, the PAG's role in vocal communication includes not only the non-voluntary production of vocal signals, but also the integration of auditory information about the vocal behaviour of conspecifics. Support in this direction comes from neurophysiological studies on squirrel monkeys, where specific clusters of neurons within the PAG have been shown to exhibit greater activity when an animal both hears a conspecific call and vocalises in response to that call, than when it either only hears or only vocalises (Dusterhoft et al., 2004).

The relevance of the PAG to social communication extends to humans as well, where emotionally significant vocal signals have been shown to elicit PAG-selective neural activity. For example, direct recordings on human adults who had undergone deep brain stimulation have shown that hearing infant vocalisations elicits in the PAG an enhanced activity, compared to the activity recorded in response to acoustically similar natural or synthetic sounds (Parsons et al., 2013). This enhanced response in the PAG is specific both spatially and temporally, as it is not observed in other subcortical structures (e.g. in the thalamus) and it occurs as early as 49 ms after sound onset (Parsons et al., 2013). These results indicate that the PAG plays a central role in the automatic identification of the affective quality of vocal signals, and suggest that this phenomenon may occur at early stages of processing along the auditory pathway.

1.5. Basal ganglia

The basal ganglia (BG) include caudate nucleus, putamen, pallidum, and nucleus accumbens (core structures), as well as the substantia nigra, subthalamic nucleus, ventral anterior nucleus, ventrolateral nucleus, and centromedial nucleus (associated structures) (Parent, 1986). Although the involvement of the BG in communication has so far mostly focussed on their role in the motor component of language and speech production (e.g. Svennilson et al., 1960; Van Buren and Ojemann, 1966; Friston et al., 1993; Démonet et al., 1994), evidence suggests that parts of these structures may also be involved in various aspects of language perception, such as syntactic (e.g. Moro et al., 2001; Friederici et al., 2003), semantic (e.g. Pilgrim et al., 2002; Copland, 2003) and prosodic components (e.g. Brådvik et al., 1991; Breitenstein et al., 1998, 2001; Pell and Leonard, 2003; Péron et al., 2013). The notion that the BG play a role in the processing of emotional prosody is supported by the presence of incoming projections from the superior temporal gyrus (i.e. a region overlapping or in close proximity with the auditory cortex) to the caudate and putamen (Yeterian and Van Hoesen, 1978; Yeterian and Pandya, 1998), as well as from the MGB to the striatum and globus pallidus (Morizumi and Hattori, 1992). Outgoing fibres from the pulvinar to the rostral superior temporal gyrus and sulcus have also been described and are thought to play a role in auditory information processing (Romanski et al., 1997). Those same temporal regions have been shown to also project to the amygdala (Stefanacci and Ameral, 2000, 2002), suggesting that the BG are part of a cortico-

subcortical circuit involved in the affective processing of auditory information.

Studies on patients suffering from Parkinson's disease, a condition characterised by the degeneration of specific structures of the BG, confirm the critical role of these brain regions in the processing of speech prosody (Pell, 1996; Pell and Leonard, 2003). Deep brain stimulation in the subthalamic nucleus (STN) of patients suffering from Parkinson's disease has been shown to alter the processing of affective information at multiple levels (e.g. emotion recognition, arousal, motor expression of emotions), and irrespectively of stimulus valence (positive or negative) and sensory modality (visual or auditory) (Péron et al., 2013 for a review). In the auditory modality, this impairment in emotional processing prevents patients from correctly identifying the affective quality of vocal utterances (emotional prosody) (Péron et al., 2010). Compared to healthy controls, Parkinson's disease patients exhibit deficit in the ability to decipher the emotional quality of speech, both at the level of the type of emotion (Scott et al., 1984; Péron et al., 2014), and at the level of its overall valence (Dara et al., 2008). These impairments could reflect a more general adverse effect of Parkinson's disease on working memory and the executive function (Breitenstein et al., 2001), to which the BG are known to contribute (Brown et al., 1997). The possibility that the STN DBS-induced deficit may be the result of the STN involvement in larger neural networks is also suggested by evidence for an emotion-specific bias to certain acoustic features (e.g. F0, duration, and loudness), which has been interpreted as underlying the inadequate use of acoustic cues as a means for correctly decoding the emotional quality of the vocal signal (Péron et al., 2015).

Similarly to Parkinson's disease patients, healthy individuals having suffered from a traumatic lesion of the BG show difficulties in extracting the emotional meaning of prosodic cues (Cancelliere and Kertesz, 1990). This impairment is thought to affect relatively late stages of emotional speech processing, thus compromising behavioural recognition of emotion even when early ERP components (e.g. the P200 component, known to detect emotional salience) is intact (Paulmann et al., 2011). Recent evidence from healthy individuals, where bilateral fronto-striatal activation was found during emotional categorisation tasks on spoken language (especially after elimination of the language's semantic content) (Kotz et al., 2003; Kotz and Paulmann, 2007), further indicates that the basal ganglia play a major function in the processing of affective communication.

1.6. Amygdala

Regions in the limbic system, and the amygdala in particular, have been implicated in processing emotion and decoding affective value in a variety of sensory modalities (e.g. LeDoux et al., 1988, 1990). For example, the amygdala has consistently been shown to respond to stimuli expressing fear across visual and auditory modes of presentation (Phillips et al., 1998).

Anatomically, the amygdala lies at the tail end of the caudate nucleus, and has been shown to receive converging projections from the thalamic and cortical auditory pathways (LeDoux et al., 1987; Doron and Ledoux, 1999). Despite lying outside the sensory auditory system, both amygdalar and striatal areas exhibit auditory evoked responses similar (albeit with longer latencies) to those found in sensory-processing structures in the thalamus and cortex (Bordi and LeDoux, 1992). The amygdala has been shown to respond to acoustic stimulation with activity in neurons in the lateral amygdaloid nucleus (Bordi and LeDoux, 1992). The lateral amygdaloid nucleus is anatomically connected with sensory processing structures in the thalamus (LeDoux et al., 1985; Turner

and Herkenham, 1991) and in the cortex (Whitlock and Nauta, 1956; Jones and Powell, 1970), and is therefore a plausible candidate for the emotional processing of sensory information (Weiskrantz, 1956; Geschwind, 1965). Neurons in the amygdaloid nucleus respond to (simple and broadband) auditory stimuli across a wide range of frequencies, with high sensitivity (e.g. responses are found even at intensities near threshold), and rapid habituation (Bordi and LeDoux, 1992; Frühholz and Grandjean, 2013a).

This wide range of auditory tuning properties suggests a possible role for the amygdala as a direct extension of sensory afferent structures. It is therefore likely that the neuronal activity within the amygdala is modulated by acoustic features of auditory stimuli related to the affective quality of vocal communication. Evidence in this direction comes from animal and human observations. In bats, single neuron recordings from the lateral nucleus of the amygdala have reported selective responsiveness in terms of persistent firing to social vocalisations, especially of negative valence (Gadziola et al., 2012). This persistent firing, which can be reduced by manipulating the spectrotemporal features of the stimuli, and enhanced by chemically activating the MGB (Peterson and Wenstrup, 2012), is a recurrent finding, and is considered a distinctive feature of amygdalar responses to social vocalisations. Studies on mice have shown that neurons in the basolateral amygdala exhibit early excitation to socially-relevant auditory stimuli (conspecific calls), and that this response is modulated by the non-auditory context (e.g. threatening or mating cues) (Grimsley et al., 2013). Importantly, the non-auditory context does not modulate the amygdalar response to non-socially-relevant sounds (e.g. noise bursts), suggesting that some information related to the communicative meaning of auditory signals is already available and/or processed at the level of neurons in the basolateral amygdala. In human studies, the amygdala has been shown to increase activity during the processing of vocally expressed emotions (Wiethoff et al., 2009), particularly when the prosodic signal is processed pre-attentively – i.e. not as an explicitly task-relevant requirement (e.g. Sander et al., 2005; Ethofer et al., 2009; Wiethoff et al., 2009). Based on these findings, it has been suggested that the processing of vocal emotion may follow the (more general) binary model of information processing proposed by LeDoux (1996), whereby following the thalamic stage of sensory processing the signal may be relayed through two distinct neural circuits: a 'high road' – running from the thalamus to the cortex, and on to the amygdala – and a 'low road' – connecting the thalamus directly to the amygdala (i.e. bypassing the cortex). Accordingly, it has been hypothesised that the amygdalar-limbic activation observed during implicit processing of vocal emotion may reflect the 'low road', whereas the more sustained cortical activation observed during explicit processing of vocal emotion may reflect the engagement of the 'high road' (Brück et al., 2011). Evidence from fMRI studies on patients with selective amygdalar lesions, in which fearful stimuli failed to elicit increased activation in the (intact) fusiform and occipital cortices (Vuilleumier et al. 2004; Frühholz et al., 2015) further supports the idea of a functional role of the amygdala as a modulator of cortical activity.

The anatomical and functional evidence reviewed so far indicates that the subcortical components of the auditory system are characterised by a complex connectivity, involving a combination of converging (single auditory centres receive projections from multiple areas) and diverging (single auditory centres project to multiple regions), as well as serial (both feed-forward and feedback) and parallel (starting from the level of the cochlear nucleus) processing.

2. Towards a subcortical model for emotional auditory processing

So far, the network involved in the processing of vocal affect has been mainly characterised at a cortical level, including superior temporal, inferior frontal, and limbic regions (Sander et al., 2005; Grandjean et al., 2005; Schirmer and Kotz, 2006; Leitman et al., 2010; Frühholz et al., 2012; Ethofer et al., 2012), with the amygdala exhibiting a complex response pattern that includes activation upon first exposure to a given affective utterance, followed by rapid adaptation upon repeated exposure to the same affective voice (Wiethoff et al., 2009; Frühholz and Grandjean, 2013a). However, the wealth of subcortical neural resources reviewed above suggests that a substantial contribution to the overall auditory processing may originate at the subcortical level. Since the processing of affective information is known to command extensive neural and cognitive resources (Davidson et al., 2004), it is plausible that subcortical structures may also supply the neural substrate for the processing of the emotional quality of the auditory input, and, through efferent effects, prepare or fine-tune the processing of information at the cortical areas. Based on the evidence reviewed above, we propose that the human brain distinguishes between different types of vocal emotion by using basic acoustic features, and that this discrimination takes place, in the first instance, early (i.e. at a subcortical level) along the ascending auditory pathway.

Humans are very skilled at interpreting the emotional quality of a communicative signal based on its basic acoustic features (Juslin and Laukka, 2003). The extensive evidence (reviewed above) of IC selective response to specific acoustic features supports a role for the IC in providing a certain degree of representation of vocalisation at subcortical level. Communicative signals are typically characterised by multiple and time-varying acoustic properties (see Suta et al., 2008 for review). Some of the structures along the ascending auditory pathway preserve some of these properties, as evidenced by phase-locking between neural activity and the stimulus waveform (Rose et al., 1967; Rouiller et al., 1979; Johnson, 1980; Kuwada et al., 1984; Palmer and Russell, 1986; Wallace et al., 2004; Liu et al., 2006). Specific sonic features, such as the mean and variability of the fundamental frequency, have also been shown to systematically differ between different emotional expressions, thus enabling their successful perceptual distinction (e.g. Van Lancker and Sidtis, 1992). Furthermore, hemispheric differences in the processing of emotional communication have been identified in terms of temporal resolution. Compelling evidence from intracranial recordings (Liégeois-Chauvel et al., 1999) and fMRI (Zatorre and Belin, 2001) studies have shown that the left hemisphere operates on a finer scale, and is therefore better suited to process rapidly changing sensory information, such as the affective quality unfolding from a communicative vocal signal. However, evidence from brain-lesioned patients has also shown that emotion-relevant acoustic information may be processed differently in different individuals, with high inter-subject variability even at the hemispheric level (e.g. Van Lancker and Sidtis, 1992). This challenges the long-held notion of a hemispheric specialisation in extracting the affective information from a speaker's voice (e.g. Van Lancker and Fromkin, 1973; Mitchell and Crow, 2005), and instead suggests that the prosodic affect is the result of multiple processing functions distributed across cerebral systems. Despite inter-individual differences, the converging evidence (reviewed above) indicates that neurons in the subcortical pathway – especially in IC and MGB – respond selectively to features in vocalisations (e.g. Wenstrup, 1999; Marsh et al., 2006; Holmstrom et al., 2007; Portfors et al., 2009; Pollak, 2011, 2012), and that some of these features (e.g. frequency modulation, Andoni and Pollak 2007, Pollak et al., 2011) are known to affect the meaning of vocalisations by signalling

affective or emotional states. The combined observation of feature-specific affective meaning in vocal utterances and feature-specific neural responsiveness in subcortical structures strongly suggests that the subcortical auditory pathway plays a central role in the processing of affective information, potentially influencing specific auditory processing at the cortical level.

The ability to identify affective cues in vocal utterances is a critical component of a successful social interaction (Wallbott and Scherer, 1986), as different emotional expressions signal different environmental and social circumstances requiring different behavioural responses. The correct identification of the affective quality of a communicative signal is therefore necessary for the emergence of an appropriate behavioural response. Consequently, the ability to identify the vocal affect quickly and accurately enables fast action and increases the chances of survival. The existence of a fast route for the discrimination of emotion in communicative signals would therefore be evolutionarily adaptive. Subcortical regions are phylogenetically old, and are known to control fast, reflexive, and automatic behaviours. They are therefore well positioned to serve as a neural substrate for fast and automatic decoding of affective cues. Our model proposes that a fast route for the affective processing of vocal communication may be achieved through an early 'coarse' decoding of the utterance's acoustic profile, and that this phenomenon may operate at the subcortical level of the ascending auditory pathway.

According to recent theoretical models (Schirmer and Kotz, 2006; Wildgruber et al., 2009; Brück et al., 2011), the neural processing subserving the ability to recognise auditory emotion occurs in multiple sequential steps involving an initial low-level analysis of the auditory features, followed by their integration and interpretation through higher-level cognition. This multi-step framework appears to be supported by empirical findings of a functional dissociation between amygdala and voice-sensitive auditory regions, whose activity varies with the stimulus's physical features, and non-specific association regions (such as insula, superior frontal cortex, precuneus, and hippocampus), whose response reflects the stimulus's perceptual attributes (Bestelmeyer et al., 2014). Based on the evidence reviewed above, we suggest that the decoding and interpretation of vocal emotion is the result of multiple incremental processing steps involving distinct neural networks. Given the amygdala's anatomical and functional connection both with early (subcortical) auditory structures (e.g. to the inferior colliculus, Marsh et al., 2002), and with a range of cortical (especially frontal) and subcortical (e.g. hippocampus) regions (Frühholz et al., 2014), we propose that it may serve as a hub for auditory emotional information processing and related behavioural effects. In this model, information about vocal affect is obtained by coupling an early fast extraction of emotional features from low-level sonic features, and a continuous adjustment of this early 'tentative' emotional perception and interpretation based on the progressive accumulation of new sensory and cognitive evidence (Fig. 1).

Our model is compatible with functional neuroimaging evidence indicating that the processing of emotional prosody not only increases the hemodynamic response within the cortical 'voice areas' in the superior temporal regions (Grandjean et al., 2005; Ethofer et al., 2006, 2007, 2009) independently of the type of emotion (Wiethoff et al., 2008), but also enhances the functional coupling of those cortical areas with subcortical structures – e.g. with basal ganglia and thalamus (Ethofer et al., 2012; Frühholz and Grandjean, 2012). The model proposed here is also in line with prior theoretical accounts of auditory processing (e.g. Schirmer and Kotz, 2006; Wildgruber et al., 2009; Brück et al., 2011), and expands their scope to include (and emphasise) the subcortical contribution.

The first stage of Schirmer and Kotz (2006) model consists of low-level acoustic analysis in the primary auditory cortex, followed

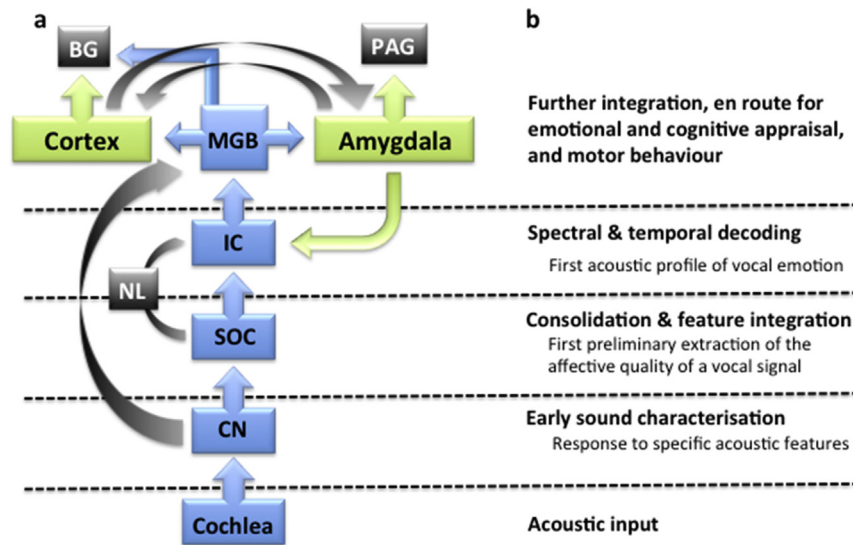


Fig. 1. Schematic representation of the subcortical model for auditory communication. a. Ascending subcortical auditory pathway. The ascending (i.e. afferent) auditory pathway originates from the auditory nerve, and terminates in the auditory cortex, via several intermediate relay points: cochlear nucleus, superior olivary complex, inferior colliculus, and medial geniculate body of the thalamus (last subcortical station of the auditory pathway). Parallel fibres ascend from the cochlear nucleus directly to the medial geniculate body of the thalamus, bypassing the superior olivary complex and the inferior colliculus. b. Information extracted at each stage of the ascending pathway. Nuclei along the subcortical auditory system are sensitive to specific sound properties. We propose that a first preliminary extraction of the affective quality of a vocal signal may occur at early stages of processing along the subcortical ascending auditory pathway, and may rely on the extraction and integration of these sound properties (e.g. spectro-temporal features) at the level of the superior olivary complex and inferior colliculus. In the interest of clarity, only the major ascending projections are shown, and absence of arrows between regions should not be construed as to imply absence of anatomical and/or functional connection. CN: cochlear nucleus; SOC: superior olivary complex; IC: inferior colliculus; MGB: medial geniculate body of the thalamus; BG: basal ganglia; PAG: periaqueductal grey.

by more complex processing and formation of an ‘acoustic object’ within superior temporal sulcus and superior temporal gyrus (both of which receive direct projections from the primary auditory cortex), and eventually culminating in high-level evaluative judgment carried out in frontal areas. Similarly, Brück et al.’ (2011) model characterises the first stage of affective processing of auditory communication as consisting in the extraction of acoustic features, and as taking place in voice-sensitive cortical areas. We propose that a preliminary analysis of acoustic features potentially informative about the sound’s affective quality may take place already in subcortical nuclei early in the ascending pathway, hence prior to the cortical stage, and probably biasing the cortical processing. This fast route would provide a first coarse analysis of acoustic information on the basis of which different vocal affects may be initially discriminated, before undergoing a more thorough (but slower) perceptual processing at cortical (fronto-temporal) level.

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