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Communication and the primate brain: Insights from neuroimaging studies in humans, chimpanzees and macaques

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Abstract

Considerable knowledge is available on the neural substrates for speech and language from brain imaging studies in humans, but until recently there was a lack of data for comparison from other animal species on the evolutionarily conserved brain regions that process species-specific communication signals. To obtain new insights into the relationship of the substrates for communication in primates, we compared the results from several neuroimaging studies in humans with those that have recently been obtained from macaque monkeys and chimpanzees. The recent work in humans challenges the longstanding notion of highly localized speech areas. As a result, the brain regions that have been identified in humans for speech and non-linguistic voice processing show a striking general correspondence to how the brains of other primates analyze species-specific vocalizations or information in the voice, such as voice identity. The comparative neuroimaging work has begun to clarify evolutionary relationships in brain function, supporting the notion that the brain regions that process communication signals in the human brain arose from a precursor network of regions that is present in nonhuman primates and used for processing species-specific vocalizations. We conclude by considering how the stage now seems to be set for comparative neurobiology to characterize the ancestral state of the network that evolved in humans to support language.

Keywords

Human; primate; monkey; macaque; chimpanzee; comparative; evolution; communication; language; vocalizations; brain imaging; electrophysiology; fMRI; auditory cortex; auditory processing

Introduction

Human speech and language are communication abilities that are without parallel in the animal kingdom, suggesting that they have had relatively short evolutionary histories. Some scientists have argued that the pursuit of language precursors in extant nonhuman species would be a fruitless endeavour (Pinker et al., 1990). For instance, if the key aspects of language evolved within the ~5 million years since our last shared ancestor with chimpanzees (one of the closest evolutionarily related species to humans) then nonhuman primates would not be expected to be able to conduct more than rudimentary behavioural computations that humans rely on for language, or their brains would support such computations in fundamentally different ways than the brains of humans.

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Alternatively, if a number of brain and behavioural adaptations have gradually taken place to support language over a longer period of time, then it is likely that some nonhuman animals would possess behavioural capabilities, not necessarily tied to their communication abilities, which could be linked to simple language-related abilities in humans. Hauser, Chomsky and Fitch (2002) define this as the 'language faculty in the broad sense'. Furthermore, we might expect that such abilities would be supported by brain networks whose function resembles that of the network in humans, e.g., similar patterns of brain activity for comparable tasks would suggest that the mechanisms upon which these behaviours are based are evolutionarily conserved. Alternatively, different networks might be used, suggesting evolutionary divergence since the last common ancestor of the species under study.

To lead us toward new insights on the origins of language, we extend the previous discussions by proposing that empirically based comparative neurobiology can make greater advances by objectively considering both, 1) the behavioural capacities of the animals that can be related to certain basic abilities that humans use for language, and 2) how the brains of different species support such abilities. Ideally then, upon an established behavioural correspondence, data on brain function would be obtained in nonhuman animals using the same brain imaging techniques and experimental paradigms used with humans. To take us closer toward this goal, we consider the neuroimaging studies in macaque monkeys and chimpanzees that are now available on the processing of communication signals by the brains of primates. These studies are compared to recent neuroimaging work in humans on the processing of communication signals by the human brain. As we consider the current state of research in the field, these comparisons allow us to make some initial observations on the brain regions that process communication signals in primates and how they appear to relate across the species. Upon this basis, the gaps in our knowledge and the paths ahead become easier to see.

In this review, we first compare the results from several functional magnetic-resonance imaging (fMRI) studies in humans to those that have recently been obtained from macaque monkeys and chimpanzees, using either fMRI or positron emission tomography (PET). This comparison reveals a number of general correspondences in how the brains of each of the species process communication signals. Some aspects of these comparisons were initiated and have been considered in more detail elsewhere (Petkov, 2010; Petkov et al., 2009; Petkov et al., 2010). In the second part of the review, we describe ongoing efforts to better integrate behavioural and neurobiological approaches that might more directly address issues related to the neurobiology of language evolution.

Brain imaging of vocalization- and voice-sensitive regions in primates

Humans share with other social animals many communication abilities that can be crucial for survival and mating. As examples, many social animals distinguish and differently respond to the calls of conspecifics relative to those from other animals or sound producing sources (e.g., Seyfarth et al., 1980; Zoloth et al., 1979). Many animals can also identify different calling individuals by voice (Fitch et al., 2006; Gentner et al., 1998; Ghazanfar et al., 2007; Rendall et al., 1998), and use different vocalizations to initiate group movement, social interactions (e.g., affiliative, aggressive, sexual, etc.) and to warn conspecifics of different types of predators (Arnold et al., 2006; Hauser et al., 1993; Seyfarth et al., 1980), for reviews see: (Fitch, 2000; Hauser et al., 2002a; Seyfarth et al., 1999). Recent developments in the technology necessary to conduct brain imaging studies in nonhuman animals (Logothetis, 2008; Logothetis et al., 1999; Ogawa et al., 1992; Poirier et al., 2009; Van Meir et al., 2005) have allowed several groups to reveal how various aspects of communication signals are processed by the brains of monkeys (Gil-da-Costa et al., 2006;

Petkov et al., 2008b; Poremba et al., 2004) and apes (Tagliabata et al., 2008; Tagliabata et al., 2009). Moreover, because the brain imaging technology is often the same as that which is being used to image the human brain, direct comparisons of the human and nonhuman animal neuroimaging data have become possible. Although many human neuroimaging studies on the neurobiology of communication have focused on the unique aspects of speech and language (such as studies on the brain activity response associated with speech intelligibility or specific linguistic tasks), more recent neuroimaging studies have considered the processing of speech with regards to its acoustical features. For instance some of the work has studied how the brain processes the sub-lexical and stimulus-bound acoustical aspects of speech sounds and speech tokens (Dehaene-Lambertz et al., 2005; Liebenthal et al., 2005; Obleser et al., 2007; Obleser et al., 2006; Rimol et al., 2005), or the non-linguistic information in the voice of conspecifics, as a group (Belin et al., 2000b) or the voice of individuals (Belin et al., 2003; von Kriegstein et al., 2003). This has allowed us to make closer comparisons to the nonhuman primate studies that have evaluated how the acoustical aspects of communication sounds are being preferentially processed by the brains of nonhuman primates.

In these summary comparisons, we obtained the stereotactic coordinates of the peaks of activity for specific conditions that were reported in the original work (or mapped these to a common reference frame). See Table 1 for further details on the summarized studies and Fig. 1 for the results of the summaries. In humans, the studies were summarized and categorized into those that have evaluated where the sub-lexical elements of speech (i.e., human 'species-specific' vocalizations) elicited greater activity than non-speech sounds and acoustical controls (purple circles in Fig. 1A, Table 1). We distinguish these from those results that have shown where the non-linguistic aspects of human voice information are processed either generally (orange circles in Fig. 1A), or specifically for identifying the voice of different human speakers (red circles in Fig. 1A). Similarly for the macaque and chimpanzee brains, we first summarized and categorized the studies that have reported where species-specific vocalizations elicited greater activity than various control sounds (see purple circles in Fig. 1B-C). We also summarized results that reveal where voice information is preferentially processed, separate from the potential meaning of the vocalizations. Here, the nonhuman primate neuroimaging work is further (as with the human work) subcategorized into two types: We first summarized the results indicative of brain regions sensitive to voice information in general, which is contrasted with the activity elicited by, for example, other animal vocalizations (see orange circles in Fig. 1C); these studies often use 'voice' categories consisting of many vocalization types as produced by many different conspecifics, which has the effect of blurring the meaning of any one particular vocalization. Second, we summarized the results of brain regions that are specifically sensitive to the acoustical information associated with the identity of different conspecifics (i.e., the 'voice' of individuals, see red circles in Fig. 1C).

Main observations

Regardless of the colour of the categorization schemes used to summarize the studies (Fig. 1), a prominent general observation is that humans, chimpanzees and macaques all seem to show preferential processing of vocalizations and voice-information that involves a large portion of the superior temporal lobe, often in both hemispheres (see the next section for specifics on the lateralization results). Such results for humans have been previously noted in several other reviews on the processing of speech and how the human brain supports speech perception (Hickok et al., 2007; Poeppel et al., 2004; Rauschecker et al., 2009; Scott et al., 2003). These results certainly cannot support the existence of highly localized functional areas that have specialized for processing communication signals. Yet, since the human processing of communication signals is seen to be so distributed, these observations

better correspond to the data obtained from chimpanzees and macaques, which also show evidence of broadly distributed processing for communication signals in the temporal lobe.

The different subcategories of vocalization and voice-information processing reveal additional correspondences between the species (see Fig. 1). Notably, although just one chimpanzee study was available for summary (Taglialetela et al., 2009), at least in humans and macaques the regions involved in the processing of species-specific vocalizations (purple circles) neighbour or seem to overlap the areas involved in the processing of information in the voice (orange circles), also see (Belin, 2006; Belin et al., 2000b; Petkov et al., 2009; Petkov et al., 2008b; von Kriegstein et al., 2003). This observation is consistent with the results of Formisano and colleagues (2008) who showed using an elegant fMRI analysis procedure (De Martino et al., 2008) that the speech and voice processing regions considerably overlap in the superior parts of the human temporal lobe (Formisano et al., 2008).

Although, some specificity is lost in our comparisons due to the general categorization scheme that was adopted to summarize the different studies, some aspects of the results are rather specific. Namely, in both humans and macaques voice-identity sensitive brain regions are located anterior and superior on the temporal lobe (Belin et al., 2003; Petkov et al., 2008b; von Kriegstein et al., 2003). However, although the anterior voice-identity sensitive region in macaques appears to have a comparable function to the one that has been revealed in humans, there is an important difference. As we have noted previously (Petkov et al., 2009; Petkov et al., 2008b), the anatomical position of the region in humans seems to be lower on the temporal lobe than the monkey variant, which has considerable implications for understanding how the human temporal lobe has differentiated since our last common ancestor with macaques. Interestingly, the comparative summaries show some indication of the peaks of activity for various communication sound processing functions being shifted to lower parts of the temporal lobe in chimps and humans, relative to the peaks seen in macaques, which are very much on the top of the temporal lobe (Fig. 1).

What is special about a voice, or what features might the voice sensitive regions in humans and monkeys be extracting? Reasonable hypotheses with regards to voice identity can be outlined based on behavioural work in humans and monkeys. Macaques, along with humans and many other animals, produce vocalizations that are filtered by the vocal tract (Fitch, 2000). This filtering of the acoustics in vocalizations affects certain formant frequencies in vocal sounds and, depending on the size of the vocal tract length, these acoustical features correlate with speaker size and can provide acoustical cues about the identity of the vocalizing individual (Rendall et al., 1998; Smith et al., 2005). It is now known that macaques, like humans, are sensitive to the formant structure of vocalizations that are indicative of the vocal tract filtering (Fitch et al., 2006) and use this acoustical information to judge the size of vocalizing individual (Ghazanfar et al., 2007). We have used voice morphing software to manipulate the acoustical components of macaque vocalizations and are using these as stimuli during macaque fMRI to evaluate which vocal components the vocalization- and voice-sensitive cortical regions extract (Chakladar et al., 2008; Petkov et al., 2008a). However, the species-specificity of the processing could be questioned because a recent study has shown that many of the human 'voice' regions in the temporal lobe are sensitive not only to the resonant structure of the formants in human vocalization, but also to sounds shaped by other resonant sources besides animal vocal tracts (von Kriegstein et al., 2007). It is an outstanding question whether the processing capabilities of comparable brain regions in nonhuman primates are equally generic in their function, or if the brains of some of these animals have specialized more than others for processing the acoustical features of species-specific vocalizations.

Lateralization issues

In these comparative summaries, communication sounds appear to be processed bilaterally in humans and macaques, which as noted above, are observations that contrast with the classical notion of left lateralized speech and language areas (Broca, 1861; Wernicke, 1874), also see (Catani et al., 2005; Petkov et al., 2009; Wise et al., 2001). In the one chimpanzee study that was available for summary, the preferential processing of species-specific vocalizations was statistically stronger in the right hemisphere (Tagliabue et al., 2009), although without replication it is not clear if this would reflect a true species difference between chimpanzees and other primates (Fig. 1).

The classical idea of left lateralized regions for communication, although having been considerably refined (Friederici, 2004; Grodzinsky et al., 2006; Hickok et al., 2007; Petkov et al., 2009; Poeppel et al., 2004; Rauschecker et al., 2009; Scott, 2005; Scott et al., 2003), has had a strong impact on the approaches undertaken to study communication signal processing in nonhuman species. Electrophysiological studies in macaques that have pursued the neuronal responses and mechanisms supporting communication sound processing in nonhuman primates have nearly exclusively favoured the left hemisphere for recording (e.g., Cohen et al., 2004; Ghazanfar et al., 2008; Ghazanfar et al., 2005; Gifford et al., 2005a; Gifford et al., 2005b; Rauschecker et al., 1995; Romanski et al., 2002; Sugihara et al., 2006; Tian et al., 2001), but see (e.g., Eliades et al., 2008; Russ et al., 2008). As can be seen in the comparative summaries (Fig. 1) a focus on the left hemisphere for the processing of communication signals would not be supported by the neuroimaging evidence. Figure 1 highlights that the right hemisphere may be as important to study for some aspects of communication sound processing. For instance, the anterior voice-identity sensitive cortex appears to elicit stronger activity in the right hemisphere of humans and macaques, although the left hemisphere also seems to contribute at least in macaques (Petkov et al., 2008b).

Comparative neurobiology of language-related processes

The research presented in the first part of this review has considered how human, chimpanzee and macaque brains process species-specific vocalizations and voice information. Some of the temporal lobe areas highlighted in the neuroimaging data from nonhuman primates may well have involved evolutionary precursors to Wernicke's territory, the classically defined—although not by Wernicke (Petkov et al., 2009; Wernicke, 1874)—posterior temporal/parietal lobe region involved in human speech comprehension. However, the prior experimental paradigms are insufficient to adequately address this and even if brain regions in nonhuman primates that are thought to be anatomical homologues of the classical language areas in humans can be activated by having the animals listen to species-specific vocalizations (Gil-da-Costa et al., 2006), this experimental approach provides little clarity on how the function of such brain regions might relate to that of the human language regions. For instance, the comprehension of human speech requires an understanding of the meaning of words (semantics) and in being able to evaluate the grammatical relations of words in a sentence (syntax). These abilities do not easily lend themselves to comparative study in nonhuman species. We next consider how certain general aspects of language-related processes are being studied in nonhuman species to advance our understanding of the evolutionary precursors of the language regions.

Semantics

How might one reveal precursors to the brain regions in humans that evaluate the semantic aspects of communication signals? Primates use vocalization as referential signals and can respond with an appropriate behaviour to different vocalizations types (Seyfarth et al.,

1980). However, in neurobiological studies a distinction is required between the processing related to the functional category ('meaning') and the processing of the other acoustical features present in vocalizations (Fitch, 2000). Gifford and colleagues showed that cells in the ventral prefrontal cortex (vPFC) of macaques are sensitive to the functional meaning associated with three vocalizations, all of which were acoustically distinct but only two of which were from the same functional category (Gifford et al., 2005b). The responses of vPFC neurons did not distinguish reliably between acoustically different sounds of the same functional category (harmonic-arches and warbles, positive calls relating to desirable or high quality food sources). However, calls related to different putative meanings, in this case high or low quality foods, elicited different responses from the neurons suggesting that neurons in the vPFC can encode functional categories. Using a related approach, we have been recording from neurons in the superior temporal lobe in macaques and using as stimulation two vocalizations with comparable acoustical structures that fall across different functional categories (an affiliative 'grunt' versus an aggressive 'pant threat') and a third vocalization type that is acoustically distinct from these, but falls within the same functional category as one of them (an affiliative 'coo') (Perrodin et al., 2009). However, since the electrophysiological studies require pre-selection of brain sites for recording, whole-brain neuroimaging would be an important complement to, 1) guide the search for the regions throughout the brain to target for further electrophysiological study, and 2) to provide a global perspective on the representation of the functional meaning of vocalizations to compare with how the human brain represents semantic information (Binder et al., 2009).

Syntax

The ability to understand the grammatical relations of words in a sentence is fundamental to human language. As such defined, syntactic ability does not exist in nonhuman species, which highlights the challenge of understanding how linguistic approaches can be adapted to study comparable behavioural computations in other animal species (Hauser et al., 2002a; Marslen-Wilson et al., 2007). However, if we propose that a core aspect of syntactic ability involves an understanding of the structure of meaningful expressions, such as learned sequences of sensory (auditory, visual, etc.) elements, then an appealing hypothesis is generated that can be tested in nonhuman animals, which has the potential to reveal the ancestral state of 'proto-syntactic' brain structures from which the human language regions that support syntactic learning may have evolved.

Much of the evidence for nonhuman animal syntactic-related capabilities comes from the study of vocal learning in songbirds that naturally learn to sequence different singing motifs to make a song (Gentner et al., 2006; Jarvis, 2004). Since avian neurobiology is considerably different from that of humans (but see Jarvis et al., 2005), songbirds likely evolved syntactic-like abilities independently from humans. Nonhuman primate vocal communication abilities are much more rudimentary than those of songbirds, but it is difficult to dismiss comparative work in nonhuman primates since their neurobiology is in many ways comparable to that of humans.

Ongoing ethological work on primate communication is helping us to better understand how primates communicate. For instance, putty-nosed monkeys have been shown to concatenate their vocalization to refer to different predatory threats and to generate distinctly different behavioural responses with a limited set of vocalizations (Arnold et al., 2006). However, even if many other monkeys and apes are shown to be able to concatenate their communication calls to some extent to generate referential signals in ways that we are currently unaware of, in order to fully understand whether nonhuman primates can learn the grammar of syntactic sequences we may need to look beyond their communication abilities (Hauser et al., 2002a) and consider, for instance, the ability of the animals to sequence sensory information. Several studies have used artificial-language learning paradigms

involving rule-based sequences of complex sound to evaluate which grammatical rules tamarin monkeys can learn. For instance, after exposing tamarins to sequences that follow a pre-defined grammatical rule, the monkeys, within the context of a preferential looking experiment, look longer to ungrammatical sequences that violate certain learned rules than they do to grammatical sequences that follow the rules (Fitch et al., 2004; Hauser et al., 2002b; Saffran et al., 2008). Such paradigms employ implicit learning of the statistical structure of artificial languages, and have also been used with great success to reveal specific syntactic learning abilities in rodents (Murphy et al., 2008), preverbal infants (Marcus et al., 1999; Saffran et al., 1996), and are being used to study adult human language learning in the laboratory with greater precision than is possible with natural languages (Kirby et al., 2008).

Interestingly, human brain neuroimaging following artificial-language learning has revealed that the language-related network of brain areas is also recruited in the processing of the sequence of artificial languages. This includes Broca's region in the inferior frontal cortex which is sensitive to grammatical violations of certain learned artificial-language grammars (Friederici et al., 2006; Makuuchi et al., 2009). However, how such learning is supported by the brains of nonhuman animals is an outstanding issue. We have research in progress combining artificial-language learning with fMRI in macaques. This work aims to identify a nonhuman primate variant of the human syntactic-learning network (Friederici et al., 2004; 2006), at least for the specific types of syntactic-related learning that macaques are able to conduct (Petkov, 2010). Yet, as the comparative summary at the beginning of this paper highlighted, data from one or two species is insufficient to clarify evolutionary changes. For instance, if differences between humans and macaques are noted, as we did above in relation to the voice-identity sensitive brain regions, it is not fair to attribute all of these differences as changes that have occurred within the hominid lineage following the split from a common ancestor with macaques. Therefore, data from other primate, mammalian and avian species is required and will provide a more complete understanding of the origins of specialization in communication systems, including how language, as a highly specialized human communication system, compares to the communication systems of other extant animal species who have evolved and adapted to survive in their environments.

Conclusions

Multidisciplinary efforts which integrate behavioural and neurobiological approaches in novel ways across the species are required to understand the neurobiology of language and its evolutionary origins. The comparative approach is needed to delineate the homologies and specializations in brain function that support communication or communication-related abilities in different animal species, so that we can, at the same time, 1) better understand the communication systems of different animals, in their own right, 2) understand how language evolved, and 3) consider better treatment options for human communication and language disorders.

Following recent advances in developing the imaging technology to study the brain function of nonhuman animals using the same techniques commonly employed in humans, novel insights have emerged on the correspondence between the processing of communication signals by brain structures in humans, apes and monkeys. Even the rather general comparisons that can be made at this point from the neuroimaging data in humans, chimpanzees and macaques have highlighted certain correspondences and potential differences in how the temporal lobes of these species processes communication sounds. Greater specificity will likely be achieved as the available data grow, especially data obtained by using the same stimuli, experimental paradigms and quantitative cross-species comparisons of brain function, structure or connectivity.

Efforts are underway with nonhuman animals to reveal how the brains of nonhuman primates evaluate the meaning of vocalizations or support the syntactic learning of artificial-language sequences. These approaches aim to develop new empirical approaches that aim to take us closer toward understanding the origins of language and the neurobiological precursors of the language regions. It is hoped that continuing research in this interdisciplinary field will not only provide information about the ancestral network from which human language may have evolved, but may also reveal which animal species that can be studied with neurobiological approaches that are unfeasible for studying humans can be relied on to model the neuronal mechanisms of the brain regions that support speech and language-related processing in humans. Such an understanding cannot be obtained by information from a few species, nor solely by the non-invasive neuroimaging work in humans, but when comparable techniques are used to establish links between several species, the detail on neuronal mechanisms in the animal models is likely to lead to the development of better treatment options for communication and language disorders.

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Figure 1.

Comparative summary of human, chimpanzee and macaque processing of species-specific communication signals. Coloured circles summarize the stereotactic coordinates of the peaks of brain activity response under specific stimulation conditions, as reported in the original studies, with a focus on the preferential processing of communication signals in the temporal lobe. See Table 1 and the text for further details. For humans, we summarize the peaks of activity reported in studies of the sub-lexical or stimulus-bound aspects of speech (see purple circles), voice sensitive regions (see orange circles) and voice-identity sensitive cortex (see red circles). For chimpanzees we summarize a recent study evaluating chimpanzee vocalization processing. For the macaque brain we show the sensitivity to macaque vocalizations (purple circles), and the voice-sensitive regions (orange circles) including the voice-identity sensitive cortex (red circles). This figure contains rendered human and chimpanzee brain images kindly contributed by J. Obleser and J. Tagliabata, respectively. Abbreviations: MNI, Montreal-Neurological Institute stereotactic coordinate system for humans; IA, inter-aural stereotactic coordinate system; LS, lateral sulcus or Sylvian fissure; STS, superior temporal sulcus.

Table 1

Details of the studies summarised in Figure 1.

<i>Primate</i>	<i>Method</i>	<i>Label in Fig. 1</i>	<i>Category in Fig. 1</i>	<i>Task</i>	<i>Comparison</i>
<i>Humans</i>	fMRI	1	Voice	Passive listening	Human vocalizations > Non-vocalization sounds
		2	Voice Identity	Voice identity recognition	Voice identity > Speech
			Vocalization	Speech recognition	Speech > Voice identity
			Voice	"	Voice > Control sounds
		3	Voice Identity	Passive listening	Voice identity > Syllables
		4	Vocalization	Discrimination task	Phonemes > Non-phonemes
		5	Vocalization	Discrimination task	Phonemes > Spectrally inverted phonemes
		6	Vocalization	Repetition detection	Syllables > Noise
<i>Chimpanzee</i>	PET	7	Vocalization	Vowel detection	Vowels > Band-passed noise
		8	Vocalization	Speech identification	Consonants > Spectrally inverted consonants
		1	Vocalization	Passive listening	Proximal & broadcast chimpanzee vocalizations > Time-reversed vocalizations
<i>Macaque</i>	PET	1	Vocalization	Passive listening (scanned anaesthetized)	Macaque vocalizations > Control sounds
		2	Vocalization	Passive listening (scanned anaesthetized)	Macaque vocalizations > Control sounds
	fMRI	3	Voice	Passive listening (scanned awake or anaesthetised)	Macaque vocalizations > Control sounds
			Voice Identity		Voice identity (fMRI adaptation)

References for human studies

1. (Belin et al., 2000a)
2. (von Kriegstein et al., 2003)

References for nonhuman primate studies**Chimpanzee:**

1. (Tagliatela et al., 2009)

References for human studies	References for nonhuman primate studies
<ol style="list-style-type: none">3. (Belin et al., 2003)4. (Dehaene-Lambertz et al., 2005)5. (Liebenthal et al., 2005)6. (Rimol et al., 2005)7. (Obleser et al., 2006)8. (Obleser et al., 2007)	Macaque: <ol style="list-style-type: none">1. (Poremba et al., 2004)2. (Gil-da-Costa et al., 2006)3. (Petkov et al., 2008b)