Functional imaging of brain regions sensitive to communication sounds in primates

Christopher I. Petkov\textsuperscript{1} & Benjamin Wilson\textsuperscript{1}

\textsuperscript{1}Institute of Neuroscience, Newcastle University, U.K.

chris.petkov@ncl.ac.uk, benjamin.wilson1@ncl.ac.uk

Abstract

There is considerable brain imaging evidence on the neural substrates of speech in humans, but only recently has data for comparison become available on the brain regions that process communication signals in other primates. To obtain insights into the relationship between 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. We note a striking general correspondence between the primates on the pattern of brain regions that process species-specific vocalizations and the acoustics related to voice identity.

Index Terms: human, monkey, chimpanzee, comparative, evolution, communication, speech, vocalizations, imaging, fMRI, auditory cortex, auditory processing

1. Introduction

Recently a number of groups have imaged the brains of nonhuman primates while the animals listened to different types of sounds, including communication signals [1,2,3,4]. These developments raise the interesting question of, how does the processing of communication signals by the brains of human and nonhuman primates relate? We first consider how human speech and voice information might be related to the communication signals of other animals, before comparing the neuroimaging data for communication across the 3 primate species. Some aspects of these comparisons were initiated and have been considered in more detail elsewhere [5,6,7].

It is difficult to know what ‘speech-like’ vocalization would be like without human animals. It is unlikely that the spectro-temporal aspects of speech can map directly onto those present in the vocalizations of other animals, for the following reasons. Human vocal production has changed considerably from that of other primates during language evolution and speech is a very elaborate spectro-temporal acoustical signal [8], making direct comparisons between human vocalizations and those of the other primates difficult. Also, many animal species are able to modify their vocalizations to better negotiate environmental noise and to ensure the acoustics of the vocalizations are distinct from those of other animals; this can occur several times over the lifetime of the animal or as a result of evolutionary forces that have affected many generations. Moreover, to the extent that some animal vocalizations refer to environmental events [8,9,10], acoustics might predict a particular type of referential signal for a particular species [11], but another species may use an acoustically very different vocalization to refer to the same event.

A way forward might be to consider the behavioral context affecting vocalization production and perception. Under similar contextual conditions one might expect comparable evolutionary forces to have affected vocalization behavior. Experimentally the behavioral information can be used to organize sounds into different categories. Then the brains of the participants can be scanned with the different sound categories to reveal if and how the brain differentially responds to them. Since each individual vocalization can contain rich amounts of information, the advantage of this approach is that categories of sounds can be designed to emphasize comparisons of interest (e.g., conspecific vocalizations, heterospecific vocalizations, etc.) and to control for other aspects, by either balancing the category for these (e.g., varying the meaning as much as possible by including calls of different types) or including sounds to act as acoustical controls. A number of neuroimaging studies use this approach.

There are certainly some instances in which acoustics are closely related and can be compared across the species, such as when the vocalizations of different animals are produced in a similar way and for the same purpose, or if the animals cannot easily affect the acoustics present in their vocalizations. For example, the vocal tract creates resonant frequencies in the vocalizations of animals that cannot easily be hidden or disguised. The resonant frequencies are indexical cues of vocal-tract length, are known to correlate with body size, and can provide information about voice identity by way of the size of the individual [12,13,14,15,16].\textsuperscript{1}

Following the above logic, the neuroimaging data in humans, chimpanzees and macaques were grouped into results that have used categories of sounds to reveal preferences for species-specific vocalizations, and those studies that have revealed the brain regions involved in processing the non-linguistic aspects of voice information. Thus, we were able to compare the results from several noninvasive brain imaging studies in humans to those that have recently been obtained from macaques and chimpanzees, using functional magnetic-resonance imaging (fMRI) or positron emission tomography (PET) to study brain function, the same techniques commonly used with humans. In brief, the results of these comparisons reveal a number of general correspondences in how the brains of each of the species process vocalizations, that differ in form from what may have been predicted by the classical language model based on left hemisphere lateralized brain regions involved in processing speech based on the pioneering work of Carl Wernicke and Paul Broca, see below.

2. Methods

2.1. Brain imaging of vocalization- and voice-sensitive regions in humans, apes and monkeys

We summarized the results of several neuroimaging studies by obtaining the stereotactic coordinates of the peaks of activity

\textsuperscript{1} The acoustics associated with affective state are another example in which cross-species comparisons of acoustics can be made [17]. However, these are not considered here since there is currently a lack of neuroimaging evidence on the topic for cross-species comparison.
for specific conditions that were reported in the original work, or by mapping the peaks of activity to a common reference frame. These were summarized and categorized, as follows (also see Fig. 1). In humans, the studies were categorized into those that have evaluated where sublexical elements of speech elicit greater activity than non-speech sounds and acoustical controls [18,19,20,21,22], see the purple circles in Fig. 1 for the human brain. We distinguish these from those studies that have evaluated where non-linguistic aspects of human voice information are processed either generally [23], see orange circles in Fig. 1 for the human brain, or specifically for identifying the voice of different human speakers [24,25], see red circles in Fig. 1 for the human brain.

For the nonhuman primate brains, we first summarized the studies that have reported where species-specific vocalizations elicit greater activity than various control sounds [1,2,3,4], purple circles in Fig. 1 for the chimpanzee and macaque brains. We also show experiments that reported where voice information is processed, separate from the potential meaning of the vocalizations. The nonhuman primate work is further subcategorized into two types. In the orange circles in Fig. 1 for the macaques are summarized the results indicative of brain regions sensitive to voice information in general, e.g., experiments that have used many types of vocalization produced by many different conspecifics (blurring the meaning of any one particular vocalization), which were contrasted with the activity elicited by other sound categories such as animal vocalizations [2,3]. The other subcategory, as in humans, summarizes the results which have revealed brain regions that are specifically sensitive to the voice identity of different conspecifics (the ‘voice’ of individuals), see [3] and the red circles in Fig. 1 for the macaques.

3. Results and Discussion

3.1. Main observations

Humans, chimpanzees and macaques all show preferential processing of vocalizations and voice-information that involves a large portion of the superior temporal lobe (when all stimuli are considered together, regardless of the categorization scheme used in Fig. 1). The results for humans have previously been noted in several other reviews on the processing of speech and how the human brain supports speech perception [26,27,28,29]. These distributed processing preferences in humans are seen to generally correspond to observations from the neuroimaging studies of chimpanzees and macaques, which appear to show an equally distributed preference in processing species-specific communication signals. These observations challenge the notion of highly localized functional areas involved in the processing of communication signals.

The different subcategories of vocalization and voice-information processing also show a general correspondence across the species (see Fig. 1). Notably, although just one chimpanzee study was available for summary [1], at least in humans and macaques the regions involved in voice processing (orange circles) neighbor or seem to overlap areas involved in processing other aspects of species-specific vocalizations (dark circles), also see [3,6,23,25,30]. This observation is consistent the results of Formisano and colleagues (2008) who showed using an elegant fMRI multivariate analysis procedure [31] that the processing of the speech and voice areas in humans considerably overlaps [32].

Some specificity is lost in our comparisons due to the general categorization scheme that we have adopted to summarize these diverse studies. However, some aspects of the results are rather specific. Specifically, in both humans and macaques voice-identity sensitive brain regions are located anterior and superior on the temporal lobe [3,24,25]. Yet, although the voice-identity sensitive region in monkeys would seem to have a comparable function to the one that has been revealed in humans, there is an important difference. As we have noted previously [3,6], 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 after the split from the common ancestor to 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).

3.2. Lateralization results

The results presented here suggest that communication sounds appear to be processed bilaterally in at least humans and macaques. In humans this observation has been previously noted and contrasts with the classical notion of left lateralized speech and language areas [33,34], also see [6,35,36]. The one available study on chimpanzees shows that species specific vocalizations more strongly recruit the right hemisphere, although, considering the bilateral human and macaque observations, further research would be necessary to determine if this represents a true difference between chimpanzees and other primates.

4. Conclusions

Following recent advances in developing the imaging technology to study the brain function of nonhuman animals using the same techniques commonly employed in humans, we have begun to see a general correspondence in how the brains of humans, apes and monkeys process communication signals. These observations support 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 for processing species-specific vocalizations.

5. Acknowledgements

We are grateful to W. Marslen-Wilson, J. Obleser, K. Smith, J. Taglialatela and Q. Vuong for valuable discussions on this set of projects. This work was supported by a grant from Newcastle University (Faculty of Medical Science) and the MRC (Strategic Life Skills Award).

6. References


6. Petkov CI, Logothetis NK, Obleser J (2009) Where are the human speech and voice regions and do other animals have anything like them? Neuroscientist 15: 419-429.


Figure 1. Comparative summary of human, chimpanzee and macaque processing of vocalizations. Colored 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 processing of vocal signals in the temporal lobe. See the text for further details. For humans, we summarize the peaks of activity reported in studies of the sublexical 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 chimp sound 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. Tagliazulatela, 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.