and Psychophysical Perspectives (Watanabe, T., ed.), pp. 187–211, MIT Press

38 Knill, D.C. and Richards, W., eds (1996) *Perception as Bayesian Inference*, Cambridge University Press

39 Nowlan, S.J. and Sejnowski, T.J. (1994) Filter selection model for motion segmentation and velocity integration *J. Opt. Soc. Am. Ser. A* 11, 3177–3200

40 Nowlan, S.J. and Sejnowski, T.J. (1995) A selection model for motion processing in area MT of primates *J. Neurosci.* 15, 1195–1214

41 Simoncelli, E.P. and Heeger, D.J. (1998) A model of neuronal responses in visual area MT *Vis. Res.* 38, 743–761

42 Stoner, G.R., Albright, T.D. and Ramachandran, V.S. (1990) Transparency and coherence in human motion perception *Nature* 344, 153–155

43 Stoner, G.R. and Albright, T.D. (1994) Visual motion integration: a neurophysiological and psychophysical perspective, in *Visual Detection of Motion* (Smith, A.T. and Snowden, R.J., eds), pp. 253–290, Academic Press

44 Koechlin, E., Anton, J.L. and Burnod, Y. (1999) Bayesian inference in populations of cortical neurons: a model of motion integration and segregation in area MT *Biol. Cybern.* 80, 25–44

45 Snowden, R.J. and Braddick, O.J. (1989) The combination of motion signals over time *Vis. Res.* 29, 1621–1630

46 Smith, A.T., Curran, W. and Braddick, O.J. (1999) What motion distributions yield global transparency and spatial segmentation? *Vis. Res.* 39, 1121–1132

47 Braddick, O.J. *et al.* (1998) Brain areas differentially activated by coherent visual motion and dynamic noise *NeuroImage* 7, S322

48 Marshak, W. and Sekuler, R. (1979) Mutual repulsion between moving visual targets *Science* 205, 1399–1401

49 Niemann, T., Ilg, U.J. and Hoffmann, K.P. (1994) Eye movements elicited by transparent stimuli *Exp. Brain Res.* 98, 314–322

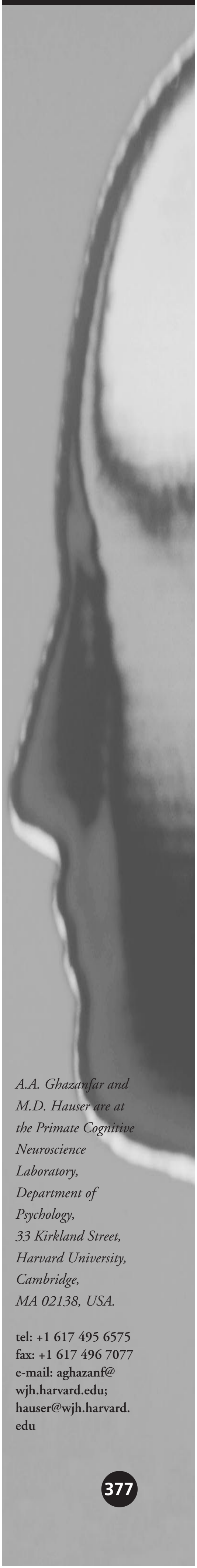
The neuroethology of primate vocal communication: substrates for the evolution of speech

Asif A. Ghazanfar and Marc D. Hauser

In this article, we review behavioral and neurobiological studies of the perception and use of species-specific vocalizations by non-human primates. At the behavioral level, primate vocal perception shares many features with speech perception by humans. These features include a left-hemisphere bias towards conspecific vocalizations, the use of temporal features for identifying different calls, and the use of calls to refer to objects and events in the environment. The putative neural bases for some of these behaviors have been revealed by recent studies of the primate auditory and prefrontal cortices. These studies also suggest homologies with the human language circuitry. Thus, a synthesis of cognitive, ethological and neurobiological approaches to primate vocal behavior is likely to yield the richest understanding of the neural bases of speech perception, and might also shed light on the evolutionary precursors to language.

The species-specific vocalizations of non-human primates are crucial for their social interactions, reproductive success and survival[1,2], and some have argued that speech has played a similar role in human history[3]. Investigating the perception and social use of vocalizations in extant non-human primates might be the most direct route to understanding the substrates underlying the evolution of speech and language. It follows, therefore, that investigating the neural processes underlying the vocal behavior of primates might yield important insights into the neurobiology of speech.

Neuroethological research has already added much to our understanding of how natural selection shapes brain-design for complex behaviors such as echolocation in bats[4], song learning in birds[5–7], and mate-choice in frogs[8]. Likewise, in the visual behavior of primates, faces are highly relevant stimuli in their day-to-day social interactions and specialized regions of the temporal lobes appear to be dedicated to face processing[9]. Based on the consistency with which behavioral adaptations are mediated by specialized neural systems in the animal kingdom, we hypothesize that the design of the



A.A. Ghazanfar and M.D. Hauser are at the Primate Cognitive Neuroscience Laboratory, Department of Psychology, 33 Kirkland Street, Harvard University, Cambridge, MA 02138, USA.

tel: +1 617 495 6575
fax: +1 617 496 7077
e-mail: aghazanf@wjh.harvard.edu; hauser@wjh.harvard.edu

1364-6613/99/$ – see front matter PII: S1364-6613(99)01379-0

primate auditory system should reflect the specialized functions that it has evolved to carry out: communication between conspecifics. It stands to reason that neurobiological studies of primate auditory function must adopt a cognitive ethological perspective[2,10].

Recent work in this area has revealed remarkable similarities between primate vocal behavior and human speech. Many primates have vocalizations that appear to be functionally referential in that they convey meaningful information about objects and events in their environments[11–13]. Some primate species show hemispheric biases in the perception of conspecific vocalizations[14,15], attend to the temporal aspects of such calls[16,17], and show plasticity in the usage and comprehension of their species-typical calls[18]. In this paper, we review current understanding of the vocal behavior of non-human primates (hereafter, 'primates'), with a special focus on problems that can benefit from neurobiological investigations as well as inform cognitive ethologists about neurobiologically significant problems. We hope to convince the reader that primate vocal behavior represents an excellent model system for studying the substrates of speech perception in particular, and the neural basis of complex biological signal recognition in general.

The ethology of primate vocal communication: problems for the neurosciences

Temporal processing of vocal signals

Humans use temporal cues such as the duration, interval and order of acoustic features to distinguish among categories of speech sounds[19,20]. For example, humans distinguish /pa/ from /ba/ on the basis of voice onset time, and /sa/ from /sta/ on the basis of the silent time between consonants and vowels. Based on these data and studies of language-impaired children, it has been suggested that speech perception is based on the rapid processing of temporal information[21].

Do primates perceive their own vocalizations in a categorical fashion, and if so, do they base their perceptual classifications on temporal features? In an early study of primate communication, Green characterized the vocal repertoire of the Japanese macaque (*Macaca fuscata*)[22]. He found that Japanese macaques used subtle differences in the acoustic structure of their calls to distinguish between types that covary with particular contexts. For example, among the affiliative 'coo' call, the 'smooth early high' (SE) type was given by young individuals isolated from companions, while the 'smooth late high' (SL) type was given by subordinate animals to more dominant troop members. Green's diagnostic for distinguishing these types was the temporal position of the fundamental frequency peak, which in the SE coo occurred in the first two-thirds of the call, and in the SL coo occurred in the final third[22]. This temporal cue could be an acoustic feature that Japanese macaques use to distinguish between these two calls.

As humans use specialized neural circuitry to parse speech sounds based on temporal cues[21], perceptual experiments on Japanese macaques investigated whether they too are able to discriminate these two call types using temporal features of the signal[17,23,24]. Japanese macaques, as well as several closely related Old World monkeys, were trained on two discrimination tasks, one using peak fundamental frequency position and the other using initial frequency as the relevant parameter. Results revealed that Japanese macaques, but not the other species, were better able to discriminate between the two coo types using peak position than using the initial frequency. In contrast, the other species performed better using the initial frequency of the coos than using peak position[23,24]. When individual acoustic elements of each coo vocalization were edited out, results showed that for Japanese macaques, the temporal position of the peak frequency was the most significant feature for discriminating between the coos[17]. Thus, at least one non-human primate species appears to have specialized neural mechanisms for categorizing conspecific vocalizations on the basis of temporal cues.

Behavioral asymmetries in the processing of vocal signals

A classic feature of language processing is its neural lateralization. Although there is no clear general dichotomy of function between the cerebral hemispheres, perceptual experiments, studies of brain-damaged patients and functional imaging studies have indicated that speech perception is usually lateralized to the left temporal lobe[21].

One indication of left-hemispheric specialization for speech processing in intact humans is the performance advantage exhibited by the right ear for the identification of speech sounds, and the lack of, or left-ear, advantage for non-speech sounds[25]. Behavioral experiments under laboratory and field conditions reveal that primates also exhibit similar asymmetries in the perception of their vocalizations. Data from the perceptual experiments on Japanese macaques described above, and from other studies, revealed a right-ear advantage when discriminating coo calls according to their species-specific, communicative relevance. No ear advantage was shown for discriminations based on initial frequency[15,23]. Based on the fact that the coos were of functional significance to the Japanese macaques, and that the other primate species tested showed no ear advantage in their performance (save for one vervet monkey, *Cercopithecus aethiops*), the observed asymmetry in perception could be attributed to the communicative valence of the signals and not particular acoustic characteristics.

To explore further the problem of hemispheric asymmetries in acoustic perception, Hauser and colleagues ran a series of field experiments on the closely related rhesus monkey (*M. mulatta*). Playback experiments using 12 different call types associated with coarse-grained emotional states (affiliation, aggression and submission), and several socioecological contexts, revealed that most adult rhesus monkeys turned their heads right when orienting towards a vocalization emitted from a hidden speaker placed 180 degrees behind them[14] (see Fig. 1). Thus, this species also shows a right-ear bias in the perception of conspecific vocalizations[14,16]. Hauser and colleagues suggested that this orienting bias is the result of left-hemisphere dominance for the processing of conspecific vocalizations. Interestingly, infant rhesus monkeys failed to show any orienting bias to conspecific calls (Fig. 1), similar to the absence of perceptual asymmetries of speech sounds in human children with specific language impairment[21].

The relationship between temporal cues and neural lateralization can be revealed by manipulating vocal signals and measuring behavioral performance. Using the dichotic listening paradigm, the magnitude of the right-ear advantage exhibited by humans can be altered by speeding up or slowing down formant transitions within a speech syllable[26]. Similarly, temporally manipulating rhesus-monkey calls can abolish the right-ear bias observed in the field[14,16]. By contracting or expanding the inter-pulse duration of three pulsatile vocalizations beyond the species-typical range, the right-ear orienting bias for conspecific vocalizations was abolished for two of the three vocalizations ('grunt' and 'shrill bark'), resulting in a no-ear or left-ear bias[16]. These results support the hypothesis that, like human brains, some non-human primate brains are specialized to process conspecific vocalizations, and that efficiently parsing temporal cues might be one of the critical processing components.

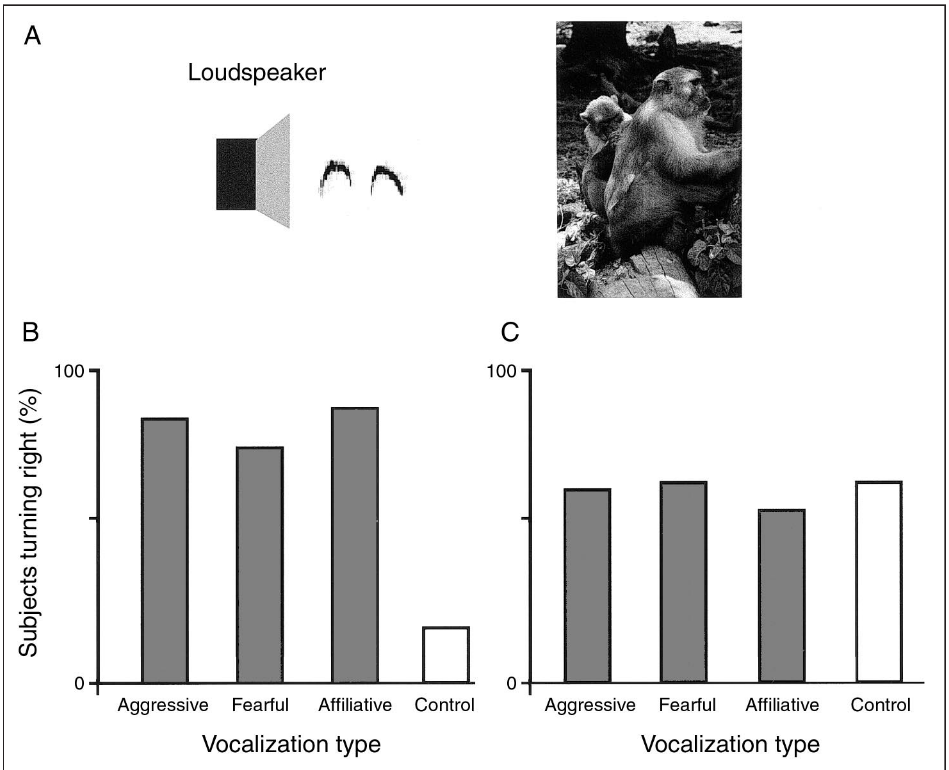


Fig. 1. Left-hemisphere bias towards conspecific vocalizations. Rhesus monkeys (*M. mulatta*) were tested when seated at one of three food dispensers, which provided a consistent context for testing. Vocalizations were played from a hidden speaker placed directly behind the subjects **(A)**. The response assay was to score whether the subjects turned the right or left ear in the direction of the speaker. The graph plots the proportion of adult **(B)** and 4–12-month-old infant **(C)** rhesus monkeys turning the right ear towards the speaker in response to three types of conspecific vocalizations (black bars) and one control heterospecific call (the turnstone's alarm call, a sound the subjects were familiar with) (white bars). Adult, but not infant, monkeys showed a right-ear bias in response to conspecific vocalizations. (Data from Ref. 14.)

Referential communication by monkeys in their natural environments

One of the most important features of human language is its ability to refer to objects and events in the external world. Until 1980, it had been assumed that primate vocalizations simply reflected the caller's emotional state and nothing more[27,28]; different call types were associated with different emotional states (e.g. screams for fear or barks for aggression). Over the last two decades, however, there has been an accumulation of data supporting the claim that many primate vocalizations are functionally referential, providing listeners with information about food, predators, and social relationships.

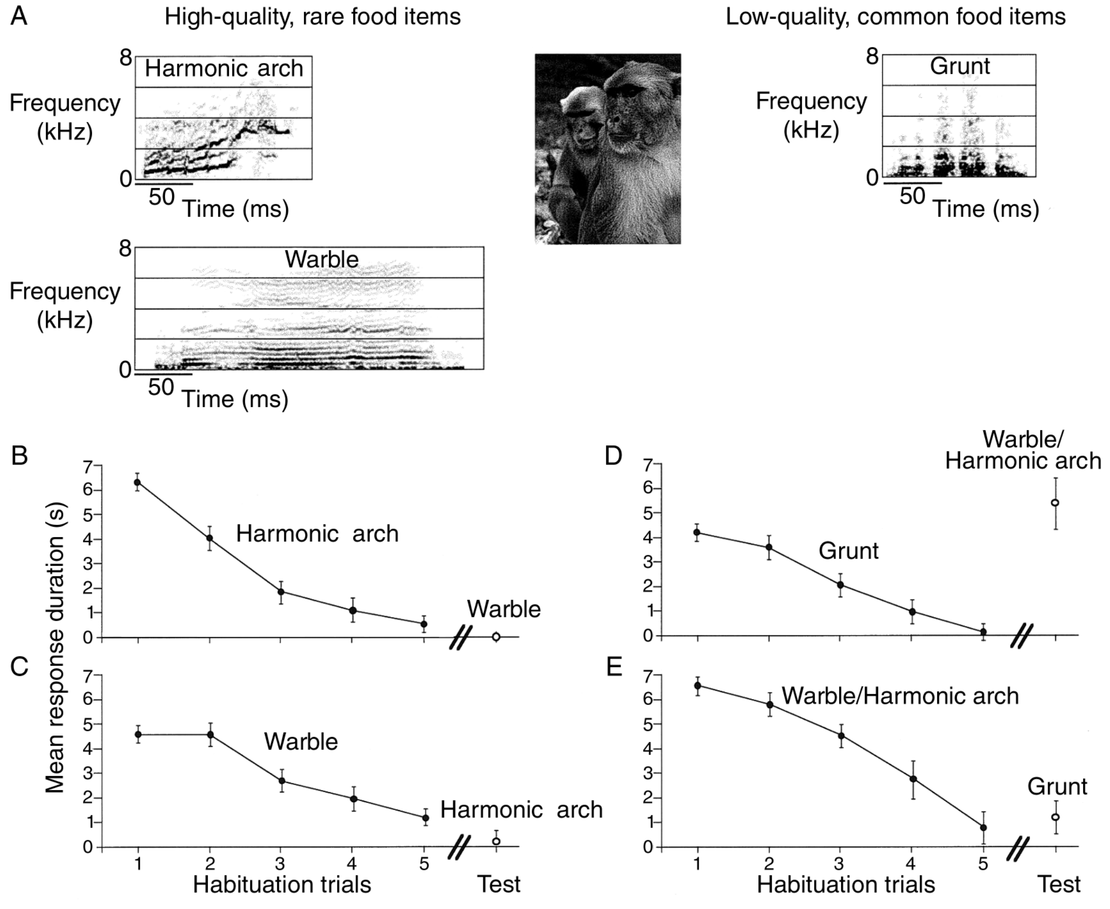
The clearest example of functionally referential signals is the vervet monkey's alarm-call system[11,29]. Vervets produce acoustically distinct alarm calls to their various predators (snakes, eagles, leopards, baboons, humans and small carnivores)[29]. In response to such calls, vervets behave adaptively, responding as a function of the predator's species-typical hunting strategy. For example, when one vervet emits a snake alarm call, other vervets immediately inspect the ground around them; following an eagle alarm call, they look up and/or run into a dense bush, presumably to avoid the eagle's stoop. Playback studies have shown that the acoustics of the alarm call alone are sufficient to elicit predator-specific adaptive responses[11]. Thus, vervet alarm calls are functionally referential signals that convey information about both predator type and the caller's affective state.

These pioneering experiments prepared the way for several other examples of referential signaling by primates in their natural environments[12,30–34]. In rhesus and pig-tailed macaques, field observations and playback experiments have revealed that individuals produce one of five acoustically distinct 'recruitment screams' in order to elicit aid from allies during agonistic encounters[31,35]. The particular call used specifies the particular class of opponent and the level of physical aggression in the encounter. In a different context, toque (*M. sinica*) and rhesus macaques give acoustically distinct vocalizations to refer to different kinds of food, and individuals respond to such calls as if in search of food, often calling back with comparable calls[36,37].

While data on referential signaling in primates reveals some similarities to human words, there are also fundamental differences between these two systems. Unlike human words, there is no evidence that primate calls can reference either the past or the future. Primate vocalizations typically refer to events or objects that are in the present. Furthermore, there is no evidence that whole calls or parts of calls can be strung together to produce more complex utterances with different meanings in the way words or parts of words can[2]. For primates, the call appears to be the primary unit of analysis. Nonetheless, the fact that some non-human primates have the capacity to produce a rudimentary form of referential signal provides an avenue for looking at this system from a cognitive neuroscience perspective, one aimed at revealing the neural substrates underlying conceptual representations.

Perceptual versus conceptual mechanisms of classification

In language, two words, such as 'soda' and 'pop', can mean the same thing but have very different acoustic features. This is one sense in which the acoustic properties of a word are arbitrary relative to its meaning. Although humans can certainly hear the difference between 'soda' and 'pop', they preferentially attend to the referential similarity between these words. Primates also exhibit this capacity[12,32,38].



trends in Cognitive Sciences

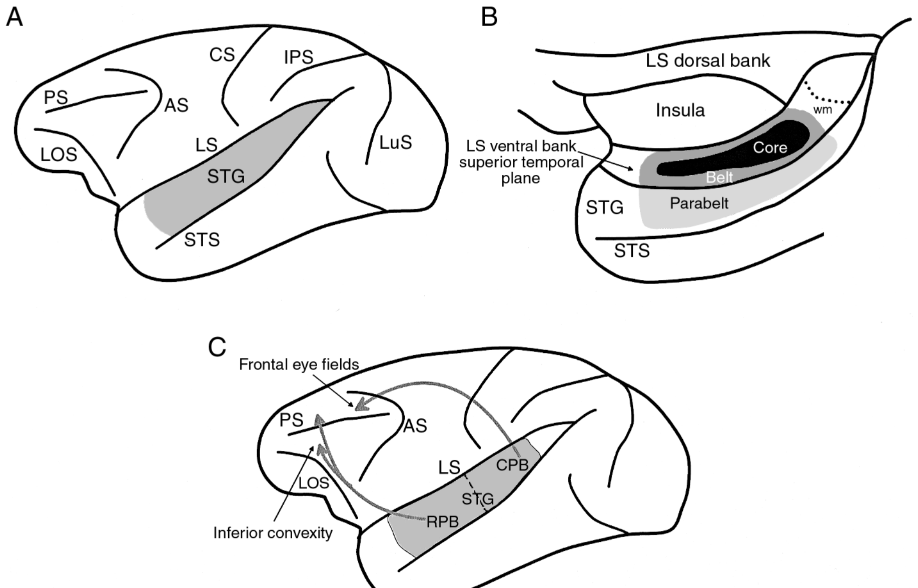
Fig. 2. Functional referents and acoustic similarity. (A) Spectrograms of the calls used by rhesus monkeys that have discovered food. The 'warble' and the 'harmonic arch' are given by individuals that have found rare, high-quality foods. The 'grunt' is given by individuals who have found a common food of lower quality. **(B–C)** Within-referent habituation experiments: (B) subjects were habituated to 'harmonic arches' and then tested with a 'warble'; (C) subjects were habituated to 'warbles' and then tested with a 'harmonic arch'. **(D–E)** Between-referent habituation experiments: (D) subjects were habituated to 'grunts' and then tested with either a 'warble' or a 'harmonic arch'; (E) subjects were habituated to either 'warbles' or 'harmonic arches' and then tested with a 'grunt'. The results show that, after habituation, monkeys respond only to changes in referential features (between-referent conditions) of subsequent calls, and not to changes in acoustic features alone (within-referent conditions). Data represent the mean time individuals spent looking in the direction of the speaker (error bars represent ±SD). All dishabituation effects were statistically significant. (Data from Ref. 12.)

Rhesus monkeys produce two call types ('harmonic arches' and 'warbles') when they find high quality/rare food, and produce another call type ('grunts') when they find low quality/common food[12] (Fig. 2A). To determine whether rhesus classify these calls as a function of their acoustic or referential similarities, an habituation–dishabituation procedure was used. If rhesus monkeys attend to acoustic features alone, then having been habituated to multiple exemplars of one call type, they should respond to a test playback involving either of the other two call types. In contrast, if they attend to referential features, then having been habituated to one call type they should respond to a call type from a different class or category, but not respond to a call type from the same class. Results provide strong support for the referential hypothesis. In particular, when rhesus monkeys were habituated to harmonic arches, they failed to respond to warbles (Fig. 2B). Similarly, when they were habituated to warbles, they failed to respond to harmonic arches (Fig. 2C). However, when they were habituated to either warbles or harmonic arches, they responded to grunts. Interestingly, when they were habituated to grunts, they also responded to harmonic arches and warbles, but the magnitude of the response was substantially greater than in the opposite habituation–dishabituation order (Fig. 2D,E). This asymmetry in the pattern of response suggests that rhesus attend to the putative reference of the call when classifying stimuli. These general findings have been obtained for two other species (vervet and Diana monkeys) and three other contexts (social affiliation, aggressive inter-group encounters, and predator alarm)[32,38].

Together, these studies provide considerable support for the notion that, like humans, primates can use their vocalizations to refer functionally to objects or events in the external environment. Several primates respond to the call's referent rather than to its acoustic morphology alone, suggesting that they have a representation of the external referent and not a simple conditioned response to the acoustic signal. Monkeys also store a representation of caller identity and use this information to guide their responses. The neural bases for these representations and decision processes have yet to be explored, but with the behavioral data in hand, such primates are ideally suited for neurobiological exploration.

The neurobiology of primate vocal communication: a brief review and prospectus

The wealth of data on the vocal behavior of primates provides an unprecedented foundation for investigating the neurobiological mechanisms underlying auditory processing. As illustrated by the neuroethological studies of birdsong, bat echolocation and face processing in primates, research on the neurobiology of primate auditory function might profit from using the animal's species-specific vocalizations to explore the brain's design features.



trends in Cognitive Sciences

Fig. 3. Organization of the auditory cortex. (A) Lateral view of the left hemisphere of the rhesus monkey cerebral cortex. Shaded region corresponds to the approximate location of the auditory-related areas on the exposed surface of the superior temporal gyrus. **(B)** View of the superior temporal plane, which contains the 'core' and 'belt' areas of auditory cortex. In this representation, the overlying dorsal bank of the lateral sulcus is graphically reflected upwards to reveal the ventral bank. **(C)** Lateral view of the rhesus brain indicating some of the major connections between the rostral and caudal parabelt regions with subdivisions of the prefrontal cortex. (Abbreviations: AS, arcuate sulcus; CS, central sulcus; CPB, caudal parabelt; IPS, intraparietal sulcus; LS, lateral sulcus; LOS, lateral orbital sulcus; LuS, lunate sulcus; PS, principal sulcus, RPB, rostral parabelt; STG, superior temporal gyrus; STS, superior temporal sulcus; wm, white matter.) (Adapted from Ref. 66.)

Homologous substrates for homologous behaviors

The region of neocortex that responds most robustly to auditory stimuli lies in and around the superior temporal plane and superior temporal gyrus of the temporal lobe (Fig. 3A,B). This region has been broadly subdivided into three areas each representing a different level of cortical processing: the core, belt and parabelt[39] (Fig. 3B). Neurons in the core area respond best to simple acoustic stimuli such as tones, while belt and parabelt neurons respond best to more complex stimuli. Our anatomical knowledge of these areas derives mainly from data collected on species of the Old World monkey genus, *Macaca*. However, based on tonotopic organization and intracortical connections, several New World monkey species[40–43] appear to have at least a subset of core auditory cortical areas that are homologous to those found in macaques.

In comparison with the human temporal lobe, there is cytoarchitectonic evidence that macaques and humans share a number of auditory cortical areas[44]. More recently, the use of multiple staining techniques to delineate and compare directly the architecture of auditory cortex in macaques, chimpanzees and humans has revealed similarities both in the architecture and shape of auditory areas in these primates. These data suggest that at least some stages of auditory cortical processing might be similar[45]. While these comparative neuroanatomical data are first approximations at best, they provide a convincing rationale for the application of knowledge from primate auditory behavioral and neurobiological studies to humans.

Neural processing of spectro-temporally-manipulated vocal signals

To date, the squirrel monkey represents the most extensively studied mammalian model system for the auditory processing of species-specific vocalizations. Recordings of single-unit activity in the superior temporal gyrus of the awake squirrel monkey revealed that more than 80–90% of the neurons in this region responded differentially to species-specific vocalizations used as stimuli[46]. Although the relative lack of information regarding squirrel monkey cortical architectonic boundaries in these studies limits what one can say about the functional organization of auditory cortex, they nevertheless provided substantial evidence that auditory neurons were tuned to species-specific vocalizations. More recent experiments in identified subdivisions of auditory cortex of anesthetized rhesus and marmoset monkeys largely support the results from squirrel monkeys, demonstrating that cortical neurons selectively respond to conspecific vocalizations with complex temporal patterns of firing[47–49].

Given that auditory cortical neurons can be call-selective, how is selectivity built up by neural circuits? One approach to answering these questions involves presenting acoustically manipulated vocal stimuli. With the advent of sophisticated digital-signal technology for bioacousticians[50], it is possible to alter systematically specific features of a call and then use such perturbed signals to determine how components of the call affect neural response patterns. In rhesus macaques, filtering certain frequencies of a call results in less robust responses from call-selective neurons when compared with responses to normal, intact vocalizations[47]. Similarly, in the temporal domain, it has been shown that editing out parts of, or reversing, vocalizations used as stimuli results in a drop in neuronal responsiveness for call-selective neurons in squirrel monkeys[46], marmosets[49], and rhesus monkeys[51]. Together, these data suggest that neurons in the auditory cortex of primates are 'combination-sensitive' (i.e. they respond nonlinearly) to conspecific vocalizations in the same way that neurons in the songbird forebrain and bat auditory cortex are combination-sensitive to their own vocalizations[4,6].

Several questions remain concerning the behavioral relevance of the combination-selectivity of primate auditory neurons. For example, how do spectro-temporal manipulations that affect responses at the neural level affect responses at the perceptual level, and vice versa. Does removing or extending particular portions of vocalizations affect how subjects respond to them? And how are the temporal manipulations of vocalizations that influence behavior[16] processed by call-selective neurons? A final point to consider here is that the relative importance of the temporal as opposed to the spectral domain might differ depending on call type or the information to be extracted, a possibility that can be explored both at the neural and behavioral levels.

Neural correlates of behavioral asymmetries

The behavioral asymmetries discussed earlier are supported by both neuroanatomical and experimental lesion studies. For human subjects that show functional left-hemispheric biases for language processing, it has been shown that the Sylvian fissure (bordering auditory cortex) is significantly longer in the left hemisphere than in the right[52]. It is assumed that the length of the fissure corresponds to the size of auditory cortex. Using this measurement, potential anatomical asymmetries have similarly been measured in several species of primates. Left Sylvian-fissure length was found to be significantly greater than in the right hemisphere in apes (*Pan*, *Gorilla*, and *Pongo*)[53], Old World macaques (*M. fascicularis* and *M. mulatta*), and New World Callichtrids (cotton-top tamarins and marmosets)[54]. These cerebral asymmetries might represent the 'specialized' neural circuitry that mediates the behavioral asymmetries to conspecific vocalizations[14,15].

Further evidence of specialization comes from experiments on Japanese macaques. Following lesions of the left auditory cortex, subjects exhibited a selective impairment for discriminating species-specific vocalizations but not other types of auditory stimuli[55]. In particular, subjects' performance on discriminating SE ('smooth early high') and SL ('smooth late high') coos was greatly impaired following lesions of the left superior temporal gyrus, but was unimpaired by similar lesions in the right hemisphere. Thus, the left auditory cortex of Japanese macaques appears to be specialized for processing communicative signals. Similar experiments on rhesus macaques, which also show a left-hemisphere bias to conspecific vocalizations, would be beneficial. For example, pharmacological inactivation of specific subdivisions of the auditory cortex (e.g. injections of muscimol) could be combined with playback experiments (e.g. monaural presentation or head-orienting task) to investigate which particular cortical areas are specialized for communication signals.

Auditory–prefrontal cortical interactions

When a non-human primate hears a call from a conspecific, its response will depend upon the identity of the caller, his distance, the current context, and the message conveyed.

As in human interactions, there are times when it is appropriate for a primate to respond to a call and there are times when it must withhold a response. The prefrontal cortex has been implicated in such 'response inhibition'[56]. In the auditory domain, rhesus monkeys can be trained to reach into a box for a food pellet after hearing one (positive) tone, or to withhold this response upon hearing a different (negative) tone. However, lesions of the inferior frontal convexity (see Fig. 3C), the region lying between the principal and lateral orbital sulci, result in perseverative interference in the performance of this auditory go/no-go task (i.e. they were unable to withhold their responses to the negative tone)[57]. The rostral 'belt' and 'parabelt' regions of macaque auditory cortex project to this region of the prefrontal cortex[39] (Fig. 3C), and it seems likely that this auditory–prefrontal circuitry plays a pivotal role in controlling responses to behaviorally relevant signals. Indeed, recent neurophysiological experiments have shown that neurons in the inferior convexity are selective to faces[58] and species-specific vocalizations[59].

Field observations and playback experiments have shown that when a call is heard, primates will almost invariably (unless habituated) look towards the source of the signal and/or its referent (e.g. a predator). Higher-order auditory areas of the *caudal* 'belt' and 'parabelt' regions, which are responsive to vocalizations[47] and sound source location[60], send projections to the periarcuate region of the prefrontal cortex[39]. This circuit might be involved in the decision process and the control of eye movements to auditory targets, such as a group member or a predator. Neurons in this area are involved in selective attention, are responsive to auditory stimuli, and have been shown to encode the association of visual and auditory stimuli (see, for example, Ref. 61). The frontal eye field (FEF) lies within this area and plays an important role in the selection and control of eye movements to particular targets in the environment[62].

Outstanding questions

- Like adult humans, some species of adult non-human primates exhibit a right-ear bias for processing conspecific vocalizations. These asymmetries are matched by neuroanatomical asymmetries in the temporal lobe. Similar behavioral biases are absent in some children with specific language impairments as well as in some primate infants. A primate model, such as the rhesus monkey, might allow us to explore the development of these hemispheric biases at both the behavioral and neuronal level. With the advent of better staining techniques, the size of different auditory areas can be measured and a more detailed analysis of which particular areas are related to the developmental onset of orienting asymmetries carried out. This circuitry can also be explored with multi-electrode recording techniques, and recent advances in functional imaging techniques.
- As in speech, primate calls are multidimensional: one call can represent many things at the same time, including a specific object or event (i.e. the call's referent), the caller's identity (e.g. sex, species), and the caller's emotional state (e.g. aggressive, fearful). There is a need to investigate how the acoustic morphology of calls relates to these information channels. Using digital sound synthesis and manipulation, different acoustic features can be manipulated and then used to test behavioral responses. For example, an aggressive call from a large dominant male could be made to sound as if it were produced by a smaller individual by shifting formant frequencies. These manipulated calls could then be tested both in the field and the lab to measure the perceptual and neural correlates, respectively. With the current technology, such neuroethological experiments are quite feasible.
- The functional organization of the primate auditory cortex has not been determined beyond the tonotopical mapping of the core areas. In the bat auditory cortex, neurons that are sensitive to distinct features carried in the biosonar signal are clustered together. An understanding of the information-bearing parameters of primate calls might lead to similar insights into the organization of primate auditory cortex. For example, what is the organization of neural responses to atonal versus tonal vocalizations in higher-order auditory cortical areas? Do the different categories of vocalizations, such as food calls versus alarm calls, map to different auditory cortical areas? For example, do food calls map to auditory cortical areas that project to the orbitofrontal cortex given this region's apparent association with the reward system?

Moreover, it has been demonstrated that FEF neurons are active during eye movements to both aurally and visually guided eye movements[63]. It is likely that this neural circuitry underlies the eye movement responses of primates to the source of vocalizations and other relevant sounds.

Future directions: the neurobiology of call meaning

Field experiments on several species of monkeys have provided evidence that individuals often appear to ignore large acoustic differences between two calls, focusing primarily on the call's referent[12,32,38]. It might be possible to simulate the habituation–dishabituation paradigm used in the field to explore the underlying neurophysiology of the representation of call meaning in the laboratory – in other words, to measure the habituation–dishabituation of neural, as opposed to behavioral, responses to vocalizations. It remains unclear how auditory neurons will habituate to ethologically relevant stimuli such as vocalizations, and whether this varies according to the level of cortical processing. In this paradigm, neurons habituated to one vocalization might be dishabituated by another vocalization that differs with respect to acoustic features alone, or acoustic features and meaning. The hypothetical neurons that encode the call's referent should not be dishabituated by a functionally similar call despite its different acoustic morphology. Such neurons are not likely to exist in lower-order core areas, such as primary auditory cortex, but might be present in higher-order areas. Alternatively, it is conceivable that the correlates of call-meaning might only be discerned by observing the collective action of many neurons.

With the advent of functional magnetic resonance imaging (fMRI) technology suitable for smaller animals, experiments using both anesthetized and alert primates are now feasible[64]. Experiments such as the one just described could provide an excellent opportunity to explore the large-scale neural circuitry involved in the processing of vocalizations. At a basic level, it could assist in the localization of areas responsible for higher-level vocal processing to guide subsequent multi-area, multi-electrode neurophysiological experiments[65]. At a cognitive level, if fMRI responses to vocalizations are lateralized, then experiments parallel to those done in the field[16] could be conducted during imaging to determine whether or not activity shifts to different cortical areas and/or cerebral hemispheres when acoustic features of vocalizations are manipulated within and beyond the species-typical range. Ultimately, both neurophysiology and neuroimaging experiments will shed light on the common neural circuitry underlying vocal behavior between primates and humans, and will pave the way for a deeper understanding of the evolution of human speech.

Acknowledgements

We thank Troy Hackett, Jon Kaas, Don Katz and Cory Miller for their helpful comments on this manuscript.

References

1 Cheney, D.L. and Seyfarth, R.M. (1990) *How Monkeys See the World*, University of Chicago Press
2 Hauser, M.D. (1996) *The Evolution of Communication*, MIT Press
3 Deacon, T.W. (1997) *The Symbolic Species: The Co-Evolution of Language and the Brain*, W.W. Norton
4 Suga, N. *et al*. (1987) The personalized auditory cortex of the mustached bat: adaptation for echolocation *J. Neurophysiol.* 58, 643–654
5 Marler, P. (1970) Birdsong and speech development: could there be parallels? *Am. Sci.* 58, 669–673
6 Margoliash, D. and Fortune, E.S. (1992) Temporal and harmonic combination-sensitive neurons in the zebra finch's HVc *J. Neurosci.* 12, 4309–4326
7 Nottebohm, F. (1989) From bird song to neurogenesis *Sci. Am.* 260, 74–79
8 Ryan, M.J., Perrill, S.A. and Wilczynksi, W. (1992) Auditory tuning and call frequency predict population-based mating preferences in the cricket frog, *Acris crepitans Am. Nat.* 139, 1370–1383
9 Perrett, D.I. *et al*. (1988) Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies *Behav. Brain Res.* 29, 245–258
10 Worden, F.G. and Galambos, R. (1972) Auditory processing of biologically significant sounds *Neurosci. Res. Prog. Bull.* 10, 1–119
11 Seyfarth, R.M., Cheney, D.L. and Marler, P. (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate *Anim. Behav.* 28, 1070–1094
12 Hauser, M.D. (1998) Functional referents and acoustic similarity: field playback experiments with rhesus monkeys *Anim. Behav.* 55, 1647–1658
13 Marler, P., Evans, C.S. and Hauser, M.D. (1992) Animal signals?: reference, motivation, or both?, in *Nonverbal Vocal Communication: Comparative and Developmental Approaches* (Papoucek, H., Jurgens, U. and Papoucek, M., eds), pp. 66–86, Cambridge University Press
14 Hauser, M.D. and Andersson, K. (1994) Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: field experiments *Proc. Natl. Acad. Sci. U. S. A.* 91, 3946–3948
15 Petersen, M.R. *et al*. (1984) Neural lateralization of vocalizations by Japanese macaques: communicative significance is more important than acoustic structure *Behav. Neurosci.* 98, 779–790
16 Hauser, M.D., Agnetta, B. and Perez, C. (1998) Orienting asymmetries in rhesus monkeys: effect of time-domain changes on acoustic perception *Anim. Behav.* 56, 41–47
17 May, B., Moody, D.B. and Stebbins, W.C. (1988) The significant features of Japanese macaque coo sounds: a psychophysical study *Anim. Behav.* 36, 1432–1444
18 Cheney, D.L. and Seyfarth, R.M. (1997) Some general features of vocal development in nonhuman primates, in *Social Influences on Vocal Development* (Snowdon, C.T. and Hausberger, M., eds), pp. 249–273, Cambridge University Press
19 Harnad, S. (1987) *Categorical Perception: The Groundwork of Cognition,* Cambridge University Press
20 Liberman, A.M. *et al*. (1967) Perception of the speech code *Psychol. Rev.* 74, 431–461
21 Fitch, R.H., Miller, S. and Tallal, P. (1997) Neurobiology of speech perception *Annu. Rev. Neurosci.* 20, 331–353
22 Green, S. (1975) Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study, in *Primate Behavior* (Rosenblum, L.A., ed.), pp. 1–102, Academic Press
23 Beecher, M.D. *et al*. (1979) Perception of conspecific vocalizations by Japanese macaques *Brain Behav. Evol.* 16, 443–460
24 Zoloth, S.R. *et al*. (1979) Species-specific perceptual processing of vocal sounds by monkeys *Science* 204, 870–873
25 Kimura, D. (1993) *Neuromotor Mechanisms in Human Communication*, Oxford University Press
26 Schwartz, J. and Tallal, P. (1980) Rate of acoustic change may underlie hemispheric specialization for speech perception *Science* 207, 1380–1381
27 Jurgens, U. (1979) Vocalizations as an emotional indicator: a neuroethological study in the squirrel monkey *Behaviour* 69, 88–117
28 Smith, W.J. (1977) *The Behavior of Communicating*, Harvard University Press
29 Struhsaker, T.T. (1967) Auditory communication among vervet monkeys (*Cercopithecus aethiops*), in *Social Communication Among Primates* (Altmann, S.A., ed.), pp. 281–324, University of Chicago Press
30 Macedonia, J.M. (1991) What is communicated in the antipredator calls of lemurs?: evidence from playback experiments with ring-tailed and ruffed lemurs *Ethology* 93, 177–197
31 Gouzoules, S., Gouzoules, H. and Marler, P. (1984) Rhesus monkey (*Macaca mulatta*) screams: representation signalling in the recruitment of agonistic aid *Anim. Behav.* 32, 182–193

32 Cheney, D.L. and Seyfarth, R.M. (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys *Anim. Behav.* 36, 477–486

33 Zuberbuhler, K., Noe, R. and Seyfarth, R.M. (1997) Diana monkey long-distance calls: messages for conspecifics and predators *Anim. Behav.* 53, 589–604

34 Rendall, D. *et al*. (1999) The meaning and function of grunt variants in baboons *Anim. Behav.* 57, 583–592

35 Gouzoules, H. and Gouzoules, S. (1989) Design features and developmental modifications of pigtail macaque (*Macaca nemestrina*) agonistic screams *Anim. Behav.* 37, 383–401

36 Dittus, W. (1984) Toque macaque food calls: semantic communication concerning food distribution in the environment *Anim. Behav.* 32, 470–477

37 Hauser, M.D. and Marler, P. (1993) Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors *Behav. Ecol.* 4, 194–205

38 Zuberbuhler, K., Cheney, D.L. and Seyfarth, R.M. (1999) Conceptual semantics in a nonhuman primate *J. Comp. Psychol.* 113, 33–42

39 Kaas, J.H., Hackett, T.A. and Tramo, M.J. (1999) Auditory processing in primate cerebral cortex *Curr. Opin. Neurobiol.* 9, 164–170

40 Morel, A. and Kaas, J.H. (1992) Subdivisions and connections of auditory cortex in owl monkeys *J. Comp. Neurol.* 318, 27–63

41 Bieser, A. and Muller-Preuss, P. (1996) Auditory responsive cortex in the squirrel monkey: neural responses to amplitude-modulated sounds *Exp. Brain Res.* 108, 273–284

42 Luethke, L.E., Krubitzer, L.A. and Kaas, J.H. (1989) Connections of primary auditory cortex in the New World monkey, *Saguinus J. Comp. Neurol.* 285, 487–513

43 Aitkin, L.M., Kudo, M. and Irvine, D.R.F. (1988) Connections of the primary auditory cortex in the common marmoset, *Callithrix jacchus jacchus J. Comp. Neurol.* 269, 235–248

44 Galaburda, A. and Sanides, F. (1980) Cytoarchitectonic organization of the human auditory cortex *J. Comp. Neurol.* 190, 597–610

45 Hackett, T.A., Preuss, T.M. and Kaas, J.H. (1998) Architectonic identification of core and belt auditory cortex in macaque monkeys, chimpanzees, and humans *Soc. Neurosci. Abstr.* 24, 1880

46 Wollberg, Z. and Newman, J.D. (1972) Auditory cortex of squirrel monkeys: response properties of single cells to species-specific vocalizations *Science* 175, 212–214

47 Rauschecker, J.P., Tian, B. and Hauser, M. (1995) Processing of complex sounds in the macaque nonprimary auditory cortex *Science* 268, 111–114

48 Tramo, M.J., Bellew, B.F. and Hauser, M.D. (1996) Discharge patterns of auditory cortical neurons evoked by species-specific vocalizations and synthetic complex signals in alert *Macaca mulatta Soc. Neurosci. Abstr.* 22, 1623

49 Wang, X. *et al*. (1995) Representation of a species-specific vocalization in the primary auditory cortex of the common marmoset: temporal and spectral characteristics *J. Neurophysiol.* 74, 2685–2706

50 Beeman, K. (1998) Digital signal analysis, editing and synthesis, in *Animal Acoustic Communication* (Hopp, S.L., Owren, M.J. and Evans, C.S., eds), pp. 59–104, Springer-Verlag

51 Rauschecker, J.P. (1998) Parallel processing in the auditory cortex of primates *Audiol. Neuro-otol.* 3, 86–103

52 Geschwind, N. and Levitsky, W. (1968) Human brain: left–right asymmetries in temporal speech region *Science* 161, 186–187

53 LeMay, M. and Geschwind, N. (1975) Hemispheric differences in the brains of great apes *Brain Behav. Evol.* 11, 48–52

54 Heilbroner, P.L. and Holloway, R.L. (1988) Anatomical brain asymmetries in New World and Old World monkeys: stages of temporal lobe development in primate evolution *Am. J. Phys. Anthropol.* 16, 38–48

55 Heffner, H.E. and Heffner, R.S. (1984) Temporal lobe lesions and perception of species-specific vocalizations by macaques *Science* 226, 75–76

56 Hauser, M.D. (1999) Perseveration, inhibition and the prefrontal cortex: a new look *Curr. Opin. Neurobiol.* 9, 214–222

57 Iversen, S.D. and Mishkin, M. (1970) Perseverative interference in monkeys following selective lesions of the inferior prefrontal convexity *Exp. Brain Res.* 11, 376–386

58 Scalaidhe, S.P.O., Wilson, F.A.W. and Goldman-Rakic, P.S. (1997) Areal segregation of face-processing neurons in prefrontal cortex *Science* 278, 1135–1138

59 Romanski, L. and Goldman-Rakic, P.S. Physiological identification of an auditory domain in the prefrontal cortex of an awake behaving monkey *Soc. Neurosci. Abstr.* 25 (in press)

60 Leinonen, L., Hyvarinen, J. and Sovijarvi, A.R.A. (1980) Functional properties of neurons in the temporo-parietal association cortex of awake monkey *Exp. Brain Res.* 38, 203–215

61 Watanabe, M. (1992) Frontal units of the monkey coding the associative significance of visual and auditory stimuli *Exp. Brain Res.* 89, 233–247

62 Schall, J.D. and Thompson, K.G. (1999) Neural selection and control of visually guided eye movements *Annu. Rev. Neurosci.* 22, 241–259

63 Russo, G.S. and Bruce, C.J. (1994) Frontal eye field activity preceding aurally-guided saccades *J. Neurophysiol.* 71, 1250–1253

64 Logothetis, N.K. *et al*. (1999) Functional imaging of the monkey brain *Nat. Neurosci.* 2, 555–562

65 Nicolelis, M.A.L. *et al*. (1998) Simultaneous encoding of tactile information by three primate cortical areas *Nat. Neurosci.* 1, 621–630

66 Kaas, J.H. and Hackett, T.A. (1998) Subdivisions of auditory cortex and levels of processing in primates *Audiol. Neuro-otol.* 3, 73–85