

The Role of Temporal Cues in Rhesus Monkey Vocal Recognition: Orienting Asymmetries to Reversed Calls

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Key Words

Temporal coding · Hemispheric asymmetry · Vocalization · Primate · Vocal communication · Call recognition · Mammal

Abstract

An understanding of the acoustic cues that animals use to categorize their vocalizations has important implications for the way we design neuroethological investigations of auditory function. Compared to other species, we know relatively little about the kinds of acoustic features used by nonhuman primates to recognize and categorize vocalizations. To further our understanding, this study explores the role of temporal features in recognition of conspecific vocalizations by rhesus macaques (*Macaca mulatta*). Experiments were designed to extend an earlier set of findings showing that adult rhesus macaques selectively turn with the right ear leading when a conspecific vocalization is played 180° behind them, but turn left or not at all when a non-conspecific signal is played. Two call types were used as stimuli: shrill barks (alarm call) and harmonic arches (food call). We found that for normal calls, rhesus macaques turned to the right – supporting earlier findings – but for time-

reversed shrill barks and harmonic arches, subjects oriented to the left. These results suggest that for at least a subset of calls, rhesus macaques use temporal cues to recognize conspecific vocal signals. The asymmetry of the behavioral response, and the corresponding asymmetry in the time-amplitude waveform, may have important implications for studies of temporal coding in the primate auditory system.

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Introduction

Each animal has evolved to detect and process a very specific set of stimuli in its environment. Studies of an animal's ecology can help us to identify these critical stimuli as well as the natural behavioral responses that these stimuli evoke and control. Because we cannot verbally test an animal as we do a human subject, scientists must rely on an animal's natural responses in order to examine which components of a stimulus are relevant and why. Ultimately, understanding these critical stimulus components will allow neuroscientists to formulate specific hypotheses about the design and function of brains.

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To understand the design of animal vocal communication, one needs to examine the range of acoustic variation within and between signal types, as well as the perceptual mechanisms that allow for adaptive behavioral responses to these signals. This information can then be used to decipher the acoustic cues used by a species to distinguish among conspecific and non-conspecific sounds, as well as how they discriminate vocal signals within their own repertoire. In birds, amphibians and insects, numerous studies of vocal signaling have successfully uncovered the distinctive acoustic features that characterize species-specific calls, how they may be used to guide call and species recognition, and how they relate to brain design [for reviews see Becker, 1982; Doherty and Hoy, 1985; Gerhardt, 1988]. In all three of these taxa, temporal cues often play a decisive role in conspecific call recognition [birds: Emlen, 1972; Searcy and Marler, 1981; amphibians: Gerhardt, 1981; insects: Pollack and Hoy, 1981].

Our knowledge of the acoustic features that encode the unique identities of communication sounds within a primate species' repertoire is limited at best. Nevertheless, there is a growing body of work that suggests that temporal cues are important for call classification in primates. Psychophysical experiments with Japanese macaques (*Macaca fuscata*) revealed that this species can use multiple temporal cues to discriminate between two different 'coo' call types. The temporal position of the peak of the fundamental frequency inflection [May et al., 1988], the overall upward versus downward frequency sweeps [May et al., 1989], and/or the temporal features of harmonics [Le Prell and Moody, 1997] can all be used by this species to discriminate their coo calls. In rhesus macaques (*Macaca mulatta*), the duration of the inter-pulse interval is important for categorizing a subset of pulsatile calls in this species' repertoire [Hauser et al., 1998]. In a New World primate, the cotton-top tamarin (*Saguinus oedipus*), temporal cues such as the amplitude envelope and the inter-syllable interval play a critical role in eliciting antiphonal calling responses [Ghazanfar et al., 2001a, b].

There are several reasons why the rhesus macaque is an attractive model for understanding the perceptual and neurobiological mechanisms of acoustic signal processing in primates. First, a great deal is known regarding the acoustic structure and perceptual salience of many different calls in the rhesus macaque vocal repertoire [Gouzoules et al., 1984; Hauser, 1991, 1998; Hauser and Fowler, 1992; Hauser and Marler, 1993; Rendall et al., 1998]. Second, previous studies have provided behavioral evidence for a right ear/left hemisphere bias in the perception of conspecific calls [Hauser and Andersson, 1994;

Le Prell et al., 2001], one that is sensitive to temporal parameters [Hauser et al., 1998]. Third, extensive neuro-anatomical studies of this species have identified homologies with human auditory cortical structures [Galaburda and Sanides, 1980; Hackett et al., 1998a] and have mapped the projections of auditory cortical areas to and from 'higher' cognitive areas such as the prefrontal cortex [Hackett et al., 1998b; Romanski et al., 1998, 1999; Barbab et al., 1999]. Finally, neurophysiological experiments have begun to investigate how conspecific vocalizations are represented in the auditory cortex [Rauschecker et al., 1995; Tian et al., 2001].

One way to test the general importance of temporal cues in the structure of vocal signals is to conduct playback experiments of time-reversed versions of the calls. The advantage of using time-reversed calls is that such signals have identical long-term frequency profiles as forward versions. Time-reversed stimuli have been used in human and non-human primate psychophysical experiments designed to investigate temporal processing [Akeroyd and Patterson, 1997; Le Prell and Moody, 2000], field playback experiments on behavioral selectivity in birds and anurans [Gerhardt, 1981; Whaling et al., 1997], and in numerous neurophysiological studies investigating the selectivity of auditory neurons to conspecific vocalizations [Margoliash, 1983; Wang et al., 1995; Esser et al., 1997; Gehr et al., 2000; Wang and Kadia, in press].

Using field playback techniques, involving the placement of an audio speaker 180° behind a subject, Hauser and colleagues [Hauser and Andersson, 1994; Hauser et al., 1998] showed that semi-free-ranging rhesus macaques exhibit a right ear orienting bias when conspecific calls are played back and a left-ear orienting bias when the alarm call of a sympatric avian species (i.e., heterospecific) is played back. Hauser and colleagues interpreted these orienting biases as further evidence for hemispheric asymmetries in processing acoustic signals by macaques, with a left hemisphere/right ear bias for conspecific calls and a right hemisphere/left ear bias for heterospecific or non-conspecific signals. The results of these experiments suggest that the orienting bias can be exploited as a behavioral assay for assessing whether rhesus macaques perceive a sound as conspecific or not [Hauser et al., 1998]. Here, we used this assay to determine whether asymmetries in perception [measured as orienting biases; Hauser and Andersson, 1994; Hauser et al., 1998] are sensitive to time-reversed versions of two calls from the rhesus macaque vocal repertoire.

Table 1. Temporal analysis of shrill barks and harmonic arches

Call type	Call or pulse duration, ms mean (\pm SD)	Duration to peak amplitude, ms mean (\pm SD)	Ratio (duration to peak amp/call or pulse duration)
Shrill barks*	29.7 \pm 18.9	6.6 \pm 7.7	0.22
Harmonic arches	363.5 \pm 143.3	118.1 \pm 91.4	0.33

* Shrill barks are pulsatile calls. Accordingly, measurements were taken from the time amplitude waveform of individual pulses not the whole call.

Sample sizes (number of calls/pulses): shrill barks, 9/35; harmonic arches, 10/na.

Materials and Methods

Subjects

The subjects for our experiments were semi-free ranging adult rhesus macaques (*M. mulatta*) living on the island of Cayo Santiago, Puerto Rico. Detailed descriptions of the island and demographic information can be found elsewhere [Rawlins and Kessler, 1987; Bercovitch and Berard, 1993]. This research adheres to the guidelines for the use and care of animals as required by the Caribbean Primate Research Center, National Institutes of Health, and Harvard University.

Stimuli

Experiments focused on two call types within the vocal repertoire of adult rhesus macaques: 'shrill barks', and 'harmonic arches'. Each call type is associated with a distinctive socioecological context. Shrill barks are associated with alarm, and harmonic arches are given upon the discovery of high-quality foods [Hauser and Marler, 1993; Bercovitch et al., 1995]. Shrill barks are broadband pulsatile calls, but have a rapid amplitude onset when compared to the end of the call [Rowell and Hinde, 1962; Hauser and Marler, 1993; Bercovitch et al., 1995; Hauser et al., 1998]. Harmonic arches are tonal calls with an asymmetrical amplitude envelope and a rapid frequency-modulated sweep that rises to a peak frequency no earlier than the middle of the call [Hauser and Marler 1993; Hauser, 1998]. The different call types can be characterized by the asymmetry of their amplitude envelopes (table 1).

Playback stimuli were selected from a large sample of adult male and female calls from the study population. Detailed descriptions of recording techniques and acoustic analyses can be found elsewhere [Hauser, 1991; Hauser and Marler, 1993]. Briefly, calls were recorded under field conditions (Sennheiser MKH816 microphone with K3U power unit; Sony TCD-5M stereo cassette recorder) from known individuals and in unambiguous socioecological contexts. Although acoustic conditions varied (wind, surf noise, etc.), subject-microphone distances were typically less than 5 m. Recorded calls were then digitized using a 16-bit A/D board (50 kHz maximum sample rate) and an anti-aliasing filter. Sample rates varied from 25 to 50 kHz depending upon the call type acquired. The bandwidth of the rhesus macaque vocal repertoire extends from \sim 90 Hz to 18 kHz. Acquisition of calls and acoustic analyses of the time-amplitude waveform and spectrogram were performed using the SIGNAL sound analysis system (Engineering Design, Belmont, Mass.) [Beeman, 1996].

For both call types, four unique exemplars were selected, each produced by a different individual. The calls were temporally reversed across amplitude as well as frequency domain in SIGNAL, altering the temporal domain while preserving the spectral content.

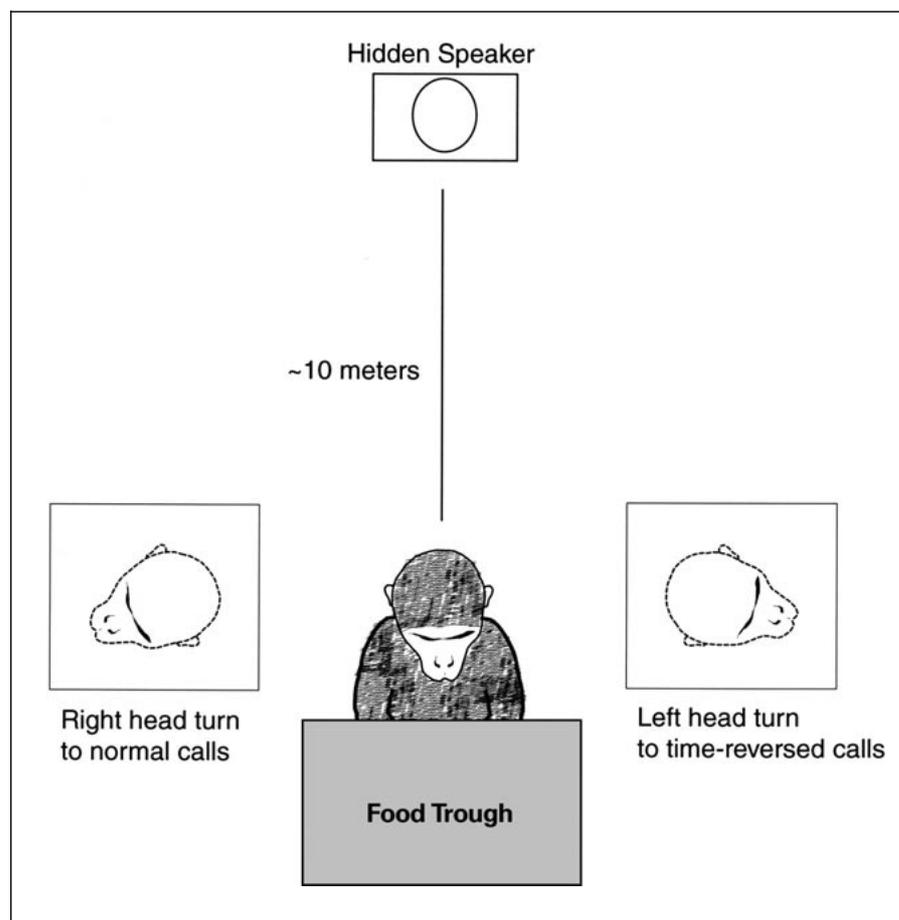
Playback Procedure

Playbacks of normal and reversed calls were conducted from August, 1998 to October, 1999 using a portable computer (Apple Powerbook G3) with 16-bit signal output through an Anchor Audio (AN-256) speaker. A Hypercard program was used to randomize and play back the stimulus set, and for online scoring of responses. The frequency range of the speaker was flat from 70 Hz to 18 kHz, thereby providing an accurate representation of the calls played back. This equipment has been used in previous playback studies [Hauser, 1998; Hauser et al., 1998].

The experimental procedure used was identical to that used in previous studies [Hauser and Andersson, 1994; Hauser et al., 1998] (fig. 1). In brief, playback experiments were conducted in close proximity to one of two food dispensers on the island. Each food dispenser was physically, visually, and acoustically separated from the others. Playbacks conducted from one dispenser could not be heard by individuals located at the other dispenser. Prior to testing, the speaker was hidden in dense vegetation, approximately 10 m from the dispenser; the sound pressure level ranged between 65 to 75 dB (measured with a Radio Shack sound level meter, C-weighting). Appropriate care was taken to line up the speaker with the center of the dispenser to ensure that the broadcast was aimed directly at the subject's back. Playbacks were conducted only when an individual sat and faced the food dispenser straight on. The response assay was to record whether, during or immediately following the playback, subjects turned with their right or left ear toward the speaker. This response was unambiguous. Although both ears, and thus both hemispheres, receive auditory input under these conditions, turning to one side to listen causes a relative increase in the intensity of the signal at that ear (if the signal continues or another is forthcoming), thereby creating an auditory input bias to the contralateral hemisphere. Given prior results [Hauser and Andersson, 1994; Hauser et al., 1998], we expected right-ear orientations to calls classified as species-typical, or conspecific, and either a left-ear bias or no bias for signals classified as species-atypical, heterospecific or non-conspecific; our present assay does not allow us to distinguish between these categories.

Subjects were selected as follows. The observers responsible for scoring the subject's response positioned themselves in line with the

Fig. 1. Schematic illustration of playback setup. Playback experiments were conducted in close proximity to one of the three food dispensers on the island. At a dispenser, a playback station was set up by concealing the speaker in dense vegetation 180° behind the dispenser and ~10 m away from it. Playback experiments were conducted only when an individual sat and faced the food dispenser straight on. The response assay was to record whether following playback the subject turned the right or left ear toward the speaker.



speaker and dispenser in order to mimic the potential subject's position, but displaced ~10 m behind. Observations commenced when an individual arrived at the dispenser and sat with his or her back to the observer. Once the individual was parallel with the front panel of the dispenser, one observer raised a hand to signal playback initiation. Because our main concern was the subject's position relative to the speaker, we did not control for the number or identity of individuals nearby, nor the amount of time spent feeding at the dispenser prior to playback. Only single calls were played back. The selection of the call to be played back (both call type and whether the exemplar was normal or reversed) was random and neither experimenter knew which call was going to be played at the time just prior to the playback. Following a playback, a minimum of 10 min was allowed to expire before another playback was conducted provided that a different subject was in the proper position relative to the feeder and speaker. The sex and in most cases the identity of the animal was noted. All trials were videotaped.

Analysis

Two observers scored orienting responses at the time of playback. To count as an acceptable trial, both observers had to agree on the subject's response. In addition, one observer was naïve regarding the sound of rhesus macaque vocalizations and could not tell if a forward

or reversed call was played back. Trials were eliminated if the orienting response was ambiguous due to subject movement or possible distraction by other activities (e.g., fights, new groups moving into the area) occurring around the time of playback.

The direction of orienting responses to playbacks was almost always unambiguous and could be scored 'online' with ease – there was never a disagreement between the two observers regarding the direction of an orienting response. In a previous study that used identical methods as reported here, twenty trials were videotaped and subsequently analyzed blind with regard to the playback sound and the response given [Hauser et al., 1998]. In that study, there was 100% agreement between response measures taken in the field and those analyzed from videotape. In the current study, 8% of the trials were recorded in the field as slightly ambiguous and only these trials were subsequently re-analyzed using the video recordings. In all cases, the videotape readily resolved the nature of the response.

Statistical tests were carried out using binomial tests, contrasting the number of individuals orienting right versus left, and χ^2 tests, contrasting the distributions of responses to normal versus reversed calls. The χ^2 is justified because individuals were only tested once. Statistical significance was set at an α level of $p < 0.05$ for a two-tailed test.

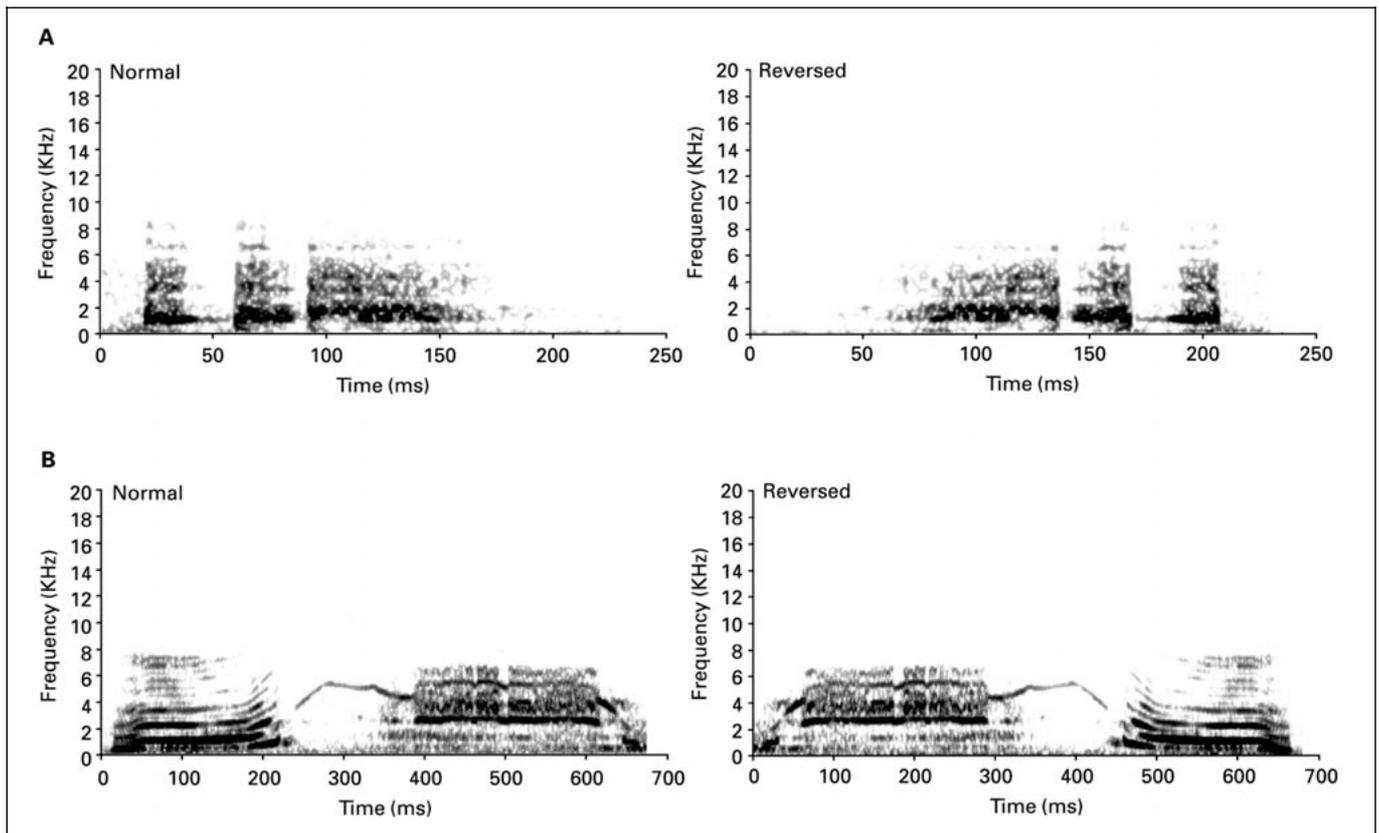


Fig. 2. Sound spectrogram exemplars of the stimuli and their temporally-reversed counterparts used in field playback experiments with rhesus monkeys. **A** ‘Shrill bark’, an alarm call. **B** ‘Harmonic arch’, produced by individuals that have discovered a rare, high-quality food. Spectrograms were generated from a 256-pt Fast Fourier Transform (Hanning window applied). x-Axis represents time (ms); y-axis represents frequency (kHz). Note that both exemplars represent single calls, not bouts.

Results

Figures 2 and 3 show spectrograms and time-amplitude waveforms of representative exemplars used in our study. A comparison of the amplitude envelopes of normal versus reversed calls (fig. 3; table 1) reveals that the asymmetrical amplitude envelopes of the shrill bark and harmonic arches might provide a temporal cue for the recognition of these conspecific calls by rhesus macaques. The ratio between the duration to the peak amplitude and overall call (or pulse) duration is less than 0.5 for shrill barks and harmonic arches. The FM sweep in the middle of harmonic arches could also be used as a temporal cue (fig. 2B); specifically, the peak frequency of the fundamental frequency never occurs at the beginning of the call, but rather occurs between the middle and end of the call [Hauser and Marler, 1993].

For both call types, subjects consistently oriented to the right in response to playbacks of unmanipulated exemplars (shrill barks, $n = 20$, $p < 0.005$; harmonic arches, $n = 10$, $p < 0.05$) (fig. 4), replicating earlier findings [Hauser and Andersson, 1994; Hauser et al., 1998]. Playbacks of reversed calls resulted in a different pattern (fig. 5). Rhesus macaques responded with a left-ear orienting bias for playbacks of reversed shrill barks ($n = 19$, $p < 0.001$) and harmonic arches ($n = 20$, $p < 0.05$). A comparison of the distributions of responses to normal versus reversed calls confirmed these results by demonstrating significant differences for shrill barks ($\chi^2 = 24.63$, $p < 0.000001$) and harmonic arches ($\chi^2 = 11.31$, $p < 0.001$).

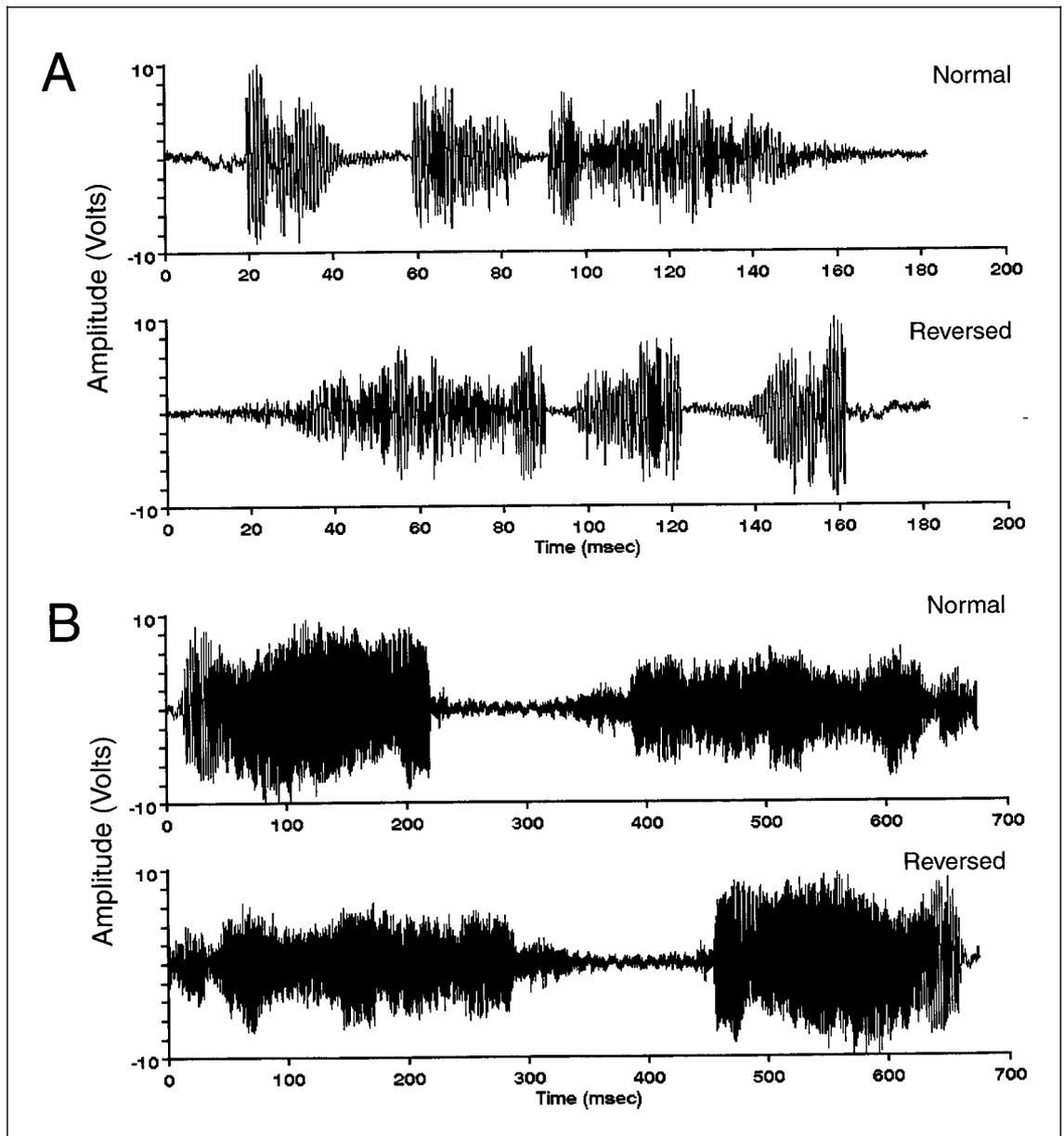


Fig. 3. Normal and reversed time-amplitude waveforms of stimuli depicted in figure 2. **A** Shrill bark, and **B** harmonic arch. x-Axis represents time (ms); y-axis represents amplitude (volts).

Discussion

Our experimental results reveal that reversing the temporal structure of shrill barks and harmonic arches cause rhesus macaques to shift from a right-ear orienting bias to a left-ear orienting bias. These orienting biases are consistent with the idea that rhesus macaques can use temporal cues to distinguish between conspecific and time-reversed

conspecific signals. For broadband shrill barks, the amplitude envelope is the only temporal cue that explains the orienting asymmetry because the spectral contour is flat for the entire duration of the call. For harmonic arches, both the amplitude envelope and the FM sweep near the middle of the call could be used as temporal cues.

Using the identical methods as reported here, Hauser et al. [1998] focused on one temporal feature, the inter-

Fig. 4. Number of subjects orienting either left or right in response to normal calls. x-Axis, black bars represent left head turns, gray bars represent right head turns; y-axis, number of subjects.

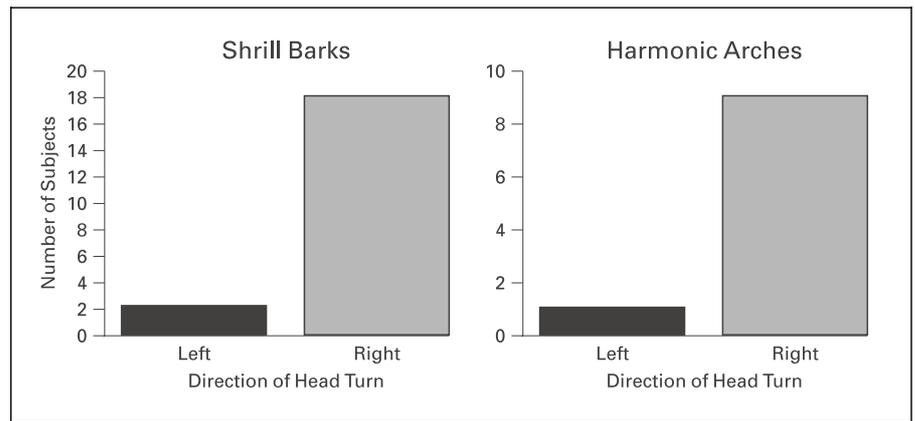
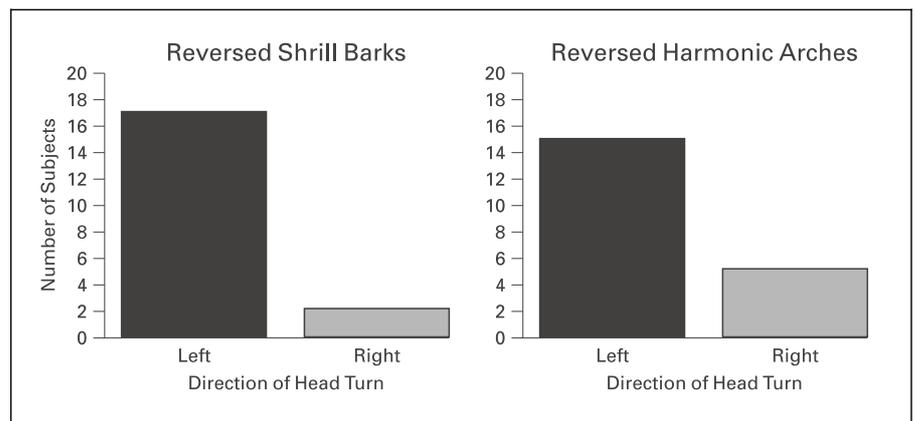


Fig. 5. Number of subjects orienting either left or right in response to reversed calls. x-Axis, black bars represent left head turns, gray bars represent right head turns; y-axis, number of subjects.



syllable interval, embedded in a subset of calls within the rhesus macaque vocal repertoire. Some rhesus call types are ‘pulsatile’ – they are composed of short, repeated bursts of acoustic energy separated by brief periods of silence. Playback experiments of temporally-manipulated exemplars of a subset of these calls (shrill barks, grunts, and copulation screams) demonstrated that increasing or decreasing the inter-pulse interval beyond the species-typical range eliminated the right-ear orienting bias normally seen for shrill barks and grunts, but did not eliminate the right-ear bias seen for copulation screams [Hauser et al., 1998].

Together with the present results, these experiments underscore the importance of temporal cues in rhesus macaque vocalization recognition. Overall, temporal manipulations such as these elicit a different response than normal versions of rhesus calls, but it is unclear whether the subjects perceive manipulated calls as ‘non-conspecific’ sounds. Furthermore, the degree of complexity in natural sounds makes it difficult to establish whether the behavioral selectivity is a highly specialized feature of the

auditory system for processing conspecific calls, or if it is partially a consequence of a more general temporal processing mechanism such as the sensitivity to temporal asymmetry [Belin et al., 1998].

Behavioral Responses to Time-Reversed Vocal Signals

Playback experiments of time-reversed vocal signals are a straightforward way of testing whether temporal cues are important in call recognition. For example, in a study of two frog species, *Hyla cinerea* and *H. gratiosa*, female responsiveness to different acoustic features of male advertisement calls were measured [Gerhardt, 1981]. In order to determine whether the shape of the amplitude envelope influenced female responsiveness, females were presented with a choice between forward and reversed exemplars of their conspecific calls. Females of *H. gratiosa* never responded to conspecific calls played backwards, whereas females of *H. cinerea* showed no preference for either normal or reversed conspecific calls. Thus, the amplitude envelope plays an important role in call recognition for *H. gratiosa* females, but not *H. cinerea*

females, even though both have asymmetrical amplitude envelope features. In another frog species, *Physalaemus pustulosus*, neither males nor females recognize reversed versions of the male advertisement call [Ryan, 1983; Zelick et al., 1991].

In primates, Le Prell and Moody [2000] have shown that for coo calls with asymmetrical spectral contours, Japanese macaques show little or no differences in their behavioral performance discriminating two different types of forward versus time-reversed coo vocalizations. It should be noted, however, that there was very little amplitude variation in the coo calls. Thus, for the changes in spectral contours between forward and reversed coo exemplars to be detected, more amplitude variation may be required [Le Prell, 1998]. Along similar lines, experiments conducted on a New World primate, the cotton-top tamarin, reveal that individuals of this species are equally responsive (in terms of antiphonal calls) to playbacks of reversed 'long' calls, even though reversal of the signal disrupts the direction of FM sweeps and syllable order [Ghazanfar et al., 2001b]. Both Japanese macaques and cotton-top tamarins are able to use different cues to recognize their calls. Thus, the mere presence of certain temporal cues does not obligate a receiver to use it as a call recognition cue, nor is it likely that a species uses only one cue to distinguish among call types or between conspecific versus non-conspecific sounds [Doherty, 1985]. Nevertheless, our data support the notion that for shrill barks and harmonic arches, rhesus monkeys might use temporal cues to recognize these calls.

The Putative Significance of the Orienting Bias

The present data, as well as data from previous field studies [Hauser and Andersson, 1994; Hauser et al., 1998], suggest that rhesus macaques have a left hemisphere bias for processing conspecific signals. This phenomenon has extensive support from psychophysical experiments and neurobiological studies. Perceptual experiments on rhesus and Japanese macaques have revealed a right-ear advantage when discriminating conspecific calls [Petersen et al., 1984; Le Prell et al., 2001]. Most recently, rhesus macaques trained to discriminate between two different classes of scream vocalizations ['arched' and 'tonal' screams; Gouzoules et al., 1984] perform better when these calls are presented to the right ear as opposed to the left ear [Le Prell et al., 2001].

Neurobiologically, the perceptual asymmetries for vocal perception are supported by both neuroanatomical and experimental lesion studies in macaques. For instance, as in humans, left Sylvian fissure length was found

to be significantly greater than the right in macaques (*M. fascicularis* and *M. mulatta*) [Falk et al., 1986; Heilbronner and Holloway, 1988]. Volumetric measurements of the temporoparietal area (cytoarchitectonic area Tpt) in macaques, which is the equivalent of the planum temporale in humans and pongids, also indicate that the left area Tpt is significantly larger than the right [Gannon et al., 1999]. Functionally, unilateral lesions of the left (but not right) auditory cortex in Japanese macaques result in a selective, but transient, impairment at discriminating species-specific vocalizations but not other types of auditory stimuli [Heffner and Heffner, 1984, 1986]. Our data extend these findings by demonstrating a link between the temporal features of a subset of macaque vocalizations and neural lateralization, as has been demonstrated for auditory/speech processing in humans [Schwarz and Tallal, 1980; Belin et al., 1998; see Ghazanfar and Hauser, 1999 for review].

Conclusions

Time-reversed vocal signals are often used as stimuli in neurophysiological experiments in vertebrates [Margoliash, 1983; Wang et al., 1995; Esser et al., 1997; Gehr et al., 2000; Wang and Kadia, in press]. Responses to such signals are compared with responses to normal calls in order to ascertain the 'selectivity' of neurons to the normal calls. Unfortunately, the behavioral consequences of time-reversing calls are rarely tested and we therefore know little about how differences seen in neural activity patterns relate to behavioral responses. As primates become increasingly popular models for neuroethological approaches to auditory function [Ghazanfar and Hauser, 2001], it will be necessary to bridge this behavioral-neural gap. In light of the present results, we predict that there would be greater activation of the left auditory cortical region, and greater selectivity of neurons therein, to normal shrill barks and harmonic arches than to time-reversed versions.

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