Orienting asymmetries in rhesus monkeys: the effect of time-domain changes on acoustic perception

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ABSTRACT

Humans exhibit left-hemisphere dominance for processing spoken language, a species-specific acoustic signal characterized by a suite of spectro-temporal parameters. Some nonhuman primates (genus *Macaca*) also exhibit left-hemisphere dominance for processing their species-specific vocalizations, as evidenced by right-ear biases in orienting and reaction-time studies, and more damaging effects from left- than right-hemisphere lesions. Little, however, is known about the acoustic features underlying such biases. We conducted field playback experiments on adult rhesus monkeys, *Macaca mulatta*, to determine whether asymmetries in perception (measured as an orienting bias) are sensitive to changes in the temporal characteristics of their calls. If the observed right-ear bias for perceiving conspecific calls (**Hauser & Andersson** 1994, *Proceedings of the National Academy of Sciences, U.S.A.*, **91,** 3946–3948) depends upon particular acoustic parameters, then experimental manipulations beyond the species-typical range of signal variation will cause a change in perceptual asymmetry, either reversing the pattern (i.e. right to left ear) or wiping it out (i.e. no asymmetry). We presented manipulated and unmanipulated exemplars of three pulsatile call types within the rhesus repertoire: an affiliative signal 'grunt', an alarm signal 'shrill bark', and a mating signal 'copulation scream'. Signal manipulations involved either (1) a reduction of the interpulse interval to zero or the population minimum or (2) an expansion of the interpulse interval to the population maximum, or two times the maximum. For the grunt and shrill bark, manipulations of interpulse interval outside the range of natural variation either eliminated the orienting bias or caused a shift from right- to left-ear bias. For the copulation scream, however, a right-ear bias was observed in response to all stimuli, manipulated and unmanipulated. Results show that for some call types within the repertoire, temporal properties such as interpulse interval provide significant information to listeners about whether the signal is from a conspecific or not. We interpret the orienting bias as evidence that hemispheric asymmetries underly this perceptual effect.

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Studies of brain-damaged patients, and of normals using neuroimaging techniques, indicate that the left-hemisphere of the human brain is dominant in language processing, both spoken and signed (Bellugi et al. 1990; Hellige 1993; Kimura 1993; Posner & Raichle 1994). From a comparative perspective (Corballis 1991; Bradshaw & Rogers 1993; Hiscock & Kinsbourne 1995), the human

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brain's asymmetry for language may have evolved from a relatively ancient mammalian ancestor given that rats (O'Connor et al. 1993), mice (Ehret 1987), bats (Kanwal, in press) and macaques (Dewson et al. 1975; Dewson 1977; Petersen et al. 1978; Heffner & Heffner 1984; Hauser & Andersson 1994) all show a left-hemisphere bias in auditory processing tasks, and for mice and macaques, the bias in discrimination is for species-typical vocalizations. Although these communicative systems cannot be equated with human language, neither in terms of their formal structure (i.e. syntax) nor in terms of their meaning (i.e. semantics), they are all species-specific signals. Consequently, one can ask a more general evolutionary question about functional asymmetries in the brain. Is

the left hemisphere of the mammalian brain specially designed for processing conspecific auditory signals? To address this question, we present results from experiments on semi-free-ranging rhesus monkeys, *Macaca mulatta*, living on the island of Cayo Santiago, Puerto Rico.

Three factors guided our selection of species and population. First, neuroanatomical and neurophysiological studies reveal that the cytoarchitecture of rhesus auditory cortex is similar to that in humans, and has been considered homologous by many authors (e.g. Brugge & Merzenich 1973; Merzenich & Brugge 1973; Pandya & Sanides 1973; Pandya et al. 1988; Morel et al. 1993; Hashikawa et al. 1995; Jones et al. 1995; Rauschecker et al. 1995; Tramo et al. 1996). Second, a great deal of information has been collected on the acoustic morphology of the rhesus monkey's vocal repertoire and the perceptual salience of particular acoustic features (Gouzoules et al. 1984; Hauser 1991, 1992, 1998; Hauser & Fowler 1992; Hauser & Marler 1993; Hauser et al. 1993; Rendall et al. 1996). Third, orienting studies provide some evidence for a left-hemisphere bias in perception of conspecific vocalizations, but a right-hemisphere bias for nonconspecific acoustic signals (Hauser & Andersson 1994). All of these communication studies have been conducted on the Cayo Santiago population.

Psychophysical experiments indicate that Japanese macaques, *Macaca fuscata*, but not closely related species, exhibit a right-ear/left-hemisphere bias for discriminating between two types of affiliative 'coo' vocalizations from their repertoire (Petersen et al. 1978); the primary difference between the two call types lies in the relative temporal position of the fundamental frequency peak (May et al. 1988, 1989). Lesioning the left auditory cortex of Japanese macaques causes a significant decrement in discrimination accuracy, whereas lesioning the right auditory cortex does not (Heffner & Heffner 1984). In closely related rhesus macaques, field playback experiments reveal that adults, but not infants (4–12 months), exhibit a strong right-ear bias for orienting to conspecific calls (all call types within the repertoire), but a left-ear bias for orienting to one call type from a familiar seabird, the ruddy turnstone, *Arenaria interpres* (Hauser & Andersson 1994). The orienting bias of the right ear has been interpreted as evidence that the left hemisphere is dominant for processing species-specific vocalizations (see Kinsbourne 1975 for a discussion of possible mechanisms). Although the procedure used with rhesus differs from those classically used to study laterality (e.g. dichotic listening), a head orienting task on humans provided comparable results (e.g. Yazgan et al. 1995). Based on the research summarized, our experiments were designed to test the prediction that changes in the acoustic morphology of a signal beyond the range of species-typical variation will either reverse the pattern of perceptual asymmetry (e.g. a shift from right- to left-ear bias) or eliminate it altogether.

Acoustic signals can be dissected into spectral and temporal features. Only perceptual experiments, however, can determine which features are most important in terms of classifying exemplars into meaningful classes. In the experiments presented here, we focus on temporal features of the call. Two factors guided our decision to restrict the initial experiments to the time domain, leaving spectral manipulations for future experiments. First, results from Japanese macaques, discussed above, indicated that temporal parameters were important in classifying exemplars as conspecific as opposed to nonconspecific. That is, the relative location of the peak frequency was a diagnostic feature for Japanese macaques, but not other species. Second, several call types within the rhesus repertoire can be distinguished, morphologically, by characteristic temporal parameters such as interpulse duration, overall call duration, and so forth. Digitally manipulating these features is relatively simple compared with spectral changes which require more sophisticated sound synthesis techniques. Third, recent work on language impairments in humans has revealed that during the acquisition phase, many children experience delays due to an inability to decode the appropriate temporal features of critical phonemic distinctions (Merzenich et al. 1996; Tallal et al. 1996). Although such children fail to show a left-hemisphere bias for language processing, asymmetry can be instantiated by means of explicit training procedures.

METHODS

We observed and tested semi-free-ranging rhesus monkey adults living on the island of Cayo Santiago, Puerto Rico (for a description of the island, population demography and study subject, see Rawlins & Kessler 1987). Experiments focused on three call types within the vocal repertoire of adult rhesus that are each associated with different socioecological contexts: 'grunts' (affiliation), 'shrill barks' (alarm) and 'copulation screams' (mating). All three call types are characterized by distinctive pulses of energy separated by gaps of silence (i.e. a string of pulses equals one call; Figs 1a, 2a and 3a). Each pulse is an intermittent vocalization, not a glottal pulse.

To set up the playback stimuli properly, we first analysed a large sample of calls from adult males and females in the population; a description of recording techniques and acoustical analyses is provided elsewhere (Hauser 1991, 1992; Hauser & Fowler 1992; Hauser & Marler 1993; Hauser et al. 1993) In brief, we recorded calls under field conditions (Sennheiser MKH816 with K3U power module, Sony TCD-5M stereo cassette recorder), from known individuals and in unambiguous social contexts; although acoustic conditions varied (wind, surf noise), subject–microphone distances were typically less than 5 m. We recorded calls digitally on a computer 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 rhesus vocalizations extends from a minimum of 90 Hz to a maximum of 18 kHz. We then performed acoustic analyses of the time–amplitude waveform and spectrogram using the SIGNAL sound analysis system (Beeman 1996). This allowed us to extract spectro-temporal measures for descriptive statistics.

(a)

(b)
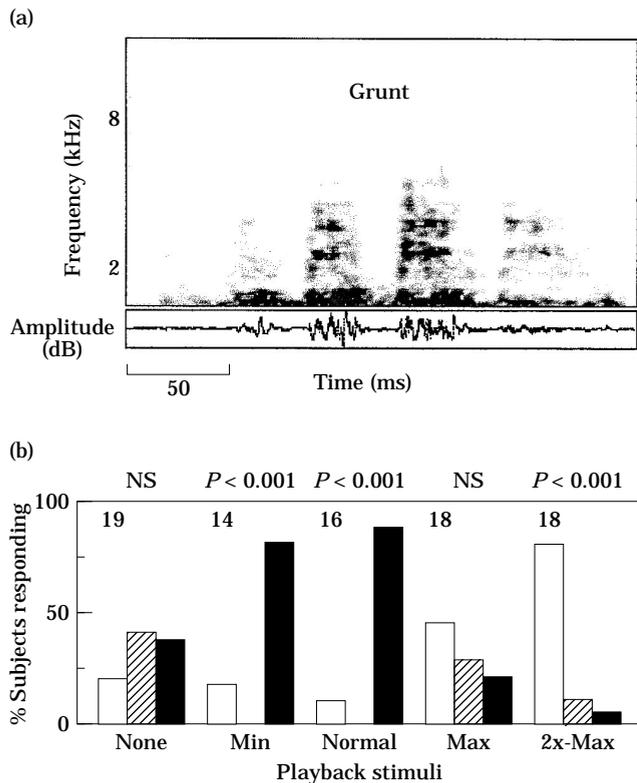
Figure 1. (a) Spectrogram (above) and time–amplitude waveform (below) of a 'grunt' vocalization. (b) Proportion of subjects turning the right ear (■), left ear (□) or failing to orient (▨) in response to grunts; sample sizes are shown in the upper left-hand corner. A binomial test was used to test for differences in the number of individuals turning to the right or left.

(a)

(b)

Figure 2. (a) Spectrogram (above) and time–amplitude waveform (below) of a 'shrill bark' vocalization. (b) Stimuli as described in Fig. 1.

For each call type, we selected three unique exemplars, each produced by a different individual. In terms of temporal features, each of these exemplars fell within one standard deviation of the mean for pulse and interpulse duration (IPI). For each call type, IPIs were: (1) eliminated, (2) reduced to the minimum observed in the population, (3) stretched to the maximum observed in the population, or (4) stretched to twice the maximum observed in the population. We conducted playbacks from a portable computer, with signals output (16 bit) from an Anchor Audio (AN-256) speaker; the frequency range was flat from 70 Hz to 18 kHz, thereby providing an accurate representation of the calls played back.

Our experimental playback procedure was identical to one used previously (Hauser & Andersson 1994). In brief, we placed a speaker 180° behind an individual sitting approximately 10–15 m away, facing a food dispenser. We then played back calls that had been digitized onto a computer at a distance of 10 m; the sound pressure level (measured with a Radio Shack sound level meter, C-weighting) ranged between 65 and 75 dB.

Upon hearing the call, subjects could orient by turning with either their right or left ear leading. 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 forth-

coming), thereby creating an auditory-input bias to the contralateral hemisphere. Given prior results, we expected right-ear orientation to calls classified as species-typical, or conspecific, and either a left-ear bias or no bias to signals classified as species-atypical, or nonconspecific.

Subjects were selected as follows. The observers responsible for scoring and/or filming (see below) the subject's response lined up with the speaker and dispenser; the observers' position was meant to mimic the subject's position, but displaced 5–10 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. Our main concern, therefore, was the subject's position relative to the speaker. Consequently, 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.

Three observers scored orienting responses at the time of playback. To count as an acceptable trial, two of the three observers had to agree on the subject's response. Trials were eliminated from the data set if the call was played back as the test subject was moving, if the orienting response was ambiguous, or if the subject might have been distracted by activities (e.g. fights, new groups moving into the area) occurring around the time of playback.

(a)

Copulation screams

(b)

$P < 0.032$ $P < 0.032$ $P < 0.016$ $P < 0.016$ $P < 0.032$
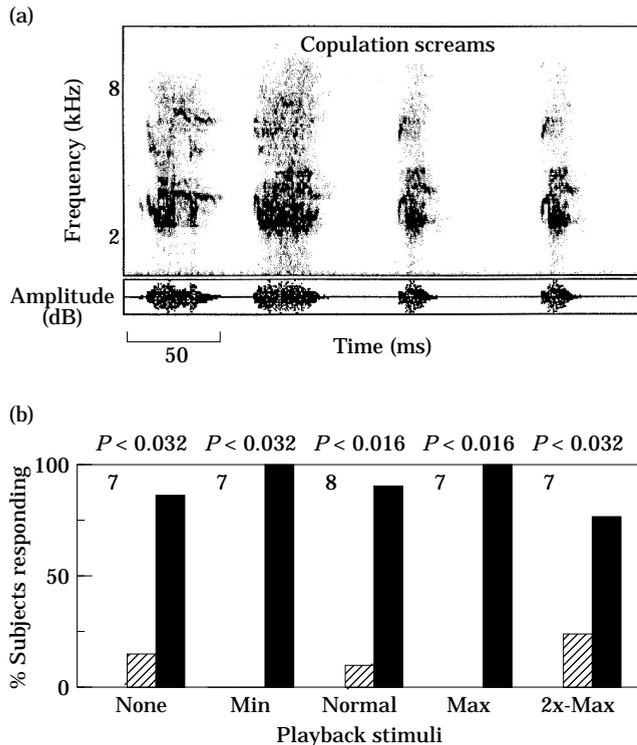
Figure 3. (a) Spectrogram (above) and time–amplitude waveform (below) of a 'copulation scream' vocalization. (b) Stimuli as described in Fig. 1.

In addition to our field records, we videotaped 20 trials which were digitized with a Radius VideoVision board (30 frames/s), and subsequently analysed blind with regard to the auditory stimulus played and the response given. The Adobe Premiere software we used to quantify orienting responses from field footage allowed us to view digitized video records without the sound track. It was still possible, however, to determine stimulus onset by referring to the time–amplitude waveform, which appears in a separate window beneath the sequence of video frames; we used this window to flag the frame associated with sound onset, but turned it off when scoring the subject' orienting response. There was complete agreement between our response measures in the field and in the laboratory.

Statistical tests were carried out using a binomial test, contrasting the number of individuals orienting right versus left; statistical significance was set at $P<0.05$.

RESULTS

Mean IPIs were comparable for all three call types (Table 1). For grunts and shrill barks, the number of pulses per call ranged from 2 to 5 (mode=3), whereas the range for copulation screams was 1–8 (mode=2). Variation between call types was primarily due to differences in the maximum IPI, with grunts and shrill barks showing comparable values, but copulations screams showing a much broader range. In contrast to shrill barks and copulation screams, grunts were softer and had a narrower frequency range. Shrill barks and copulation screams were comparable in intensity and generally covered the same spectral range, although shrill barks had a lower dominant frequency component.

For all three call types with unmanipulated IPIs, subjects consistently ($P<0.016$–0.001) turned to the right when orienting (Figs 1b, 2b and 3b), replicating earlier findings (Hauser & Andersson 1994). When minimum IPIs were presented, subjects oriented to the right for all three call types ($P<0.032$–0.001). However, when IPIs were eliminated, there was no significant orienting bias for grunts and shrill barks, but a statistically significant right-ear bias was preserved for copulation screams ($P<0.032$). Increases in IPI to the population maximum resulted in no significant orienting bias for grunts and shrill barks, but there was a significant right-ear bias for copulation screams ($P<0.016$). Lastly, when IPIs were

Table 1. Acoustic analyses of grunts, shrill barks and copulation screams

Feature	Statistic	Grunts	Shrill barks	Copulation screams
Temporal measures				
Interpulse interval	$\bar{X}$	17.9	16.4	23.9
(ms)	SD	9.7	7.2	28.3
	Min–Max*	5.4–48.7	4.5–59.3	4.8–235.0
Pulse duration	$\bar{X}$	43.8	47.6	116.4
(ms)	SD	12.9	21.3	104.1
	Min–Max*	14.2–68.7	7.0–140.2	7.0–311.5
Number of pulses	Mode	3	3	2
	Min–Max*	2–5	25	1–8
Spectral measures				
Lowest/highest dominant	$\bar{X}$	287/4534	885/9166	2079/11 334
frequency (Hz)†	SD	207/1776	310/12 432	988/3070

Sample sizes (number of calls/number of subjects) for each call type are: grunts: 265/31; shrill barks: 198/26; copulation screams: 433/29.
*The minimum and maximum values were derived from a large sample of recordings of naturally produced vocalizations by rhesus monkeys on Cayo Santiago.
†The lowest and highest dominant frequencies were obtained from power spectra using a smoothed (75 Hz window) 128 point fast Fourier transform.

increased to twice the population maximum, subjects consistently turned left for grunts ($P<0.001$) and shrill barks ($P<0.006$), but maintained a right-ear bias for copulation screams ($P<0.032$). Although samples sizes were insufficient to test statistically for sex differences in response, inspection of the data suggest that males and females showed comparable patterns of response across stimulus conditions.

DISCUSSION

These results reveal that eliminating IPIs or expanding them beyond the maximum exhibited by this group of rhesus macaques caused a shift from a right-ear orienting bias to either no asymmetry or to a left-ear bias in response to grunts and shrill barks, but not copulation screams. For copulation screams, the temporal manipulations had no significant effect on the orienting bias. The observed pattern may arise from asymmetries in perceptual processes within the central auditory system, from cognitive processes mediating the integration of auditory information with stored representations of vocalizations (e.g. in the course of deriving their meaning), or from a combination of auditory, multimodal and supramodal (e.g. attentional) processing (Kinsbourne 1975; Davidson & Hugdahl 1995). For example, Kinsbourne (1975, personal communication) has suggested that if the left hemisphere is preferentially activated while processing a meaningful auditory signal , such activational bias could interact with the left frontal eye fields causing a visually mediated orienting bias. Work at the single-unit level, together with additional behavioural experiments, will help resolve these alternative accounts (Rauschecker et al. 1995; Tramo et al. 1996).

The pattern observed for grunts and shrill barks may represent a continuum, rather than a discrete set of responses. Specifically, the right-ear bias for normal calls was preserved when IPI was reduced to the population minimum, but when IPI was eliminated, there was no significant orienting bias. Increasing IPI to the maximum caused a noticeable decrease in right-ear responses and an increase in left-ear responses. This reversal was not statistically significant, however, until IPI was increased to twice the population maximum. Future experiments will use stimuli with finer incremental changes in IPI (e.g. smaller temporal steps from the minimum IPI to zero), thereby providing a more precise characterization of the psychophysical function underlying this perceptual response pattern.

These data have important implications for two areas of research. First, they provide a window into the relevant units of analysis in nonhuman animal communicative signals, a topic that is of considerable interest in understanding how the nervous system both generates and perceives salient features (Ehret 1987; Gerhardt 1987, 1988, 1992; Ryan et al. 1992; O'Connor et al. 1993; Ryan & Rand 1993; Hauser 1996). Thus, in the case of grunts and shrill barks, it appears that once subjects have heard the first pulse of the signal, they use the duration of the silent gap that follows as a key feature in call classification. If the IPI exceeds or undershoots the natural range

of variation, it is classified as falling outside the range of conspecific variation. In contrast, such temporal manipulations appear to be irrelevant for classifying copulation screams. This makes sense given the fact that copulation screams can be produced with a single pulse. Thus, the temporal patterning of energy that follows is unimportant in call type classification although it may be relevant in other contextual domains, such as during mate choice (Hauser 1993).

Second, and as demonstrated for human speech (Merzenich et al. 1996; Tallal et al. 1996) and the communicative signals of a wide variety of nonhuman animals (Ehret 1987; Capranica 1992; Ryan & Rand 1993), some rhesus vocalizations are associated with a characteristic temporal pattern, or a 'call-specific signature', for which the left hemisphere appears to play a dominant role in processing (Petersen et al. 1978; Heffner & Heffner 1984; Hauser & Andersson 1994). Importantly, however, temporal features are only critical for processing some macaque calls, not all. If our hypothesis is correct, that is, that particular acoustic features are diagnostic for classifying signals as conspecific or not, and that the left hemisphere plays a dominant role in this processing task, then the path is open for future research to probe the salience of both additional temporal parameters, as well as spectral features. Such field studies are important on their own, but can also inform researchers interested in the neurophysiological mechanisms underlying cortical processing of acoustic signals (e.g. Rauschecker et al. 1995; Tramo et al. 1996) and in the origins of language processing asymmetries.

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