Salience of Caller Identity in Rhesus Monkey (*Macaca mulatta*) Coos and Screams: Perceptual Experiments With Human (*Homo sapiens*) Listeners

Michael J. Owren
Cornell University

Drew Rendall
University of Lethbridge

Recent evidence from acoustic analysis and playback experiments indicates that adult female rhesus monkey (*Macaca mulatta*) coos are individually distinctive but their screams are not. In this study, the authors compared discrimination of individual identity in these sounds by naive human listeners who judged whether 2 sounds had been produced by the same monkey or 2 monkeys. Each of 3 experiments using this same–different design showed significantly better discrimination of vocalizer identity from coos than from screams. Experiment 1 demonstrated the basic finding, Experiment 2 also tested the effect of non-identity-related scream variation, and Experiment 3 added a comparison with human vowel sounds. Outcomes suggest that acoustic structural differences in coos and screams influence salience of caller-identity cues, with significant implications for understanding the functions of these calls.

A prominent theme of recent work in primatology has been the importance of kinship and interindividual relationships in shaping the social behavior of monkeys and apes (reviewed in Cheney & Seyfarth, 1990; Cheney, Seyfarth, & Smuts, 1986; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987), which can be described as being both individualistic and nepotistic. Many species are marked by stable dominance relationships among group members, with numerous components of social behavior being strongly influenced by the identities of the animals involved as well as by their kin relationships. Such complex interaction patterns ultimately require that social primates be able to discriminate among other group members, or more likely, to explicitly recognize one another. Consistent with these observations, studies of nonhuman primate vocal communication have identified a variety of calls with acoustic structures that are potentially individually distinctive (reviewed in Snowdon, 1986).

In many cases, the evidence of individual distinctiveness involves sounds produced through stable, synchronized vocal-fold action producing a relatively low-frequency source-energy vibration (fundamental frequency; F_0) that is subsequently shaped by vocal-tract resonances (formants) above the larynx (see, e.g., Owren & Rendall, 1997, 2001). In human speech production these are the voiced sounds including vowels as well as voiced consonants like /l/, /r/, /m/, and /n/. Voice quality is prominent in these sounds, which provides acoustic cues to talker characteristics such as sex, individual identity, emotional state, and language background. Similar sounds are also common among nonhuman primates, including macaque coos (e.g., S. Green, 1975; see Figure 1A of the current article), baboon grunts (e.g., Owren, Seyfarth, & Cheney, 1997), and tonal calls in a host of other species (Fitch & Hauser, 1995). Evidence from a number of studies further shows that these animals can often discriminate among the voices of conspecific vocalizers on the basis of call acoustics alone (e.g., Rendall, Rodman, & Emond, 1996; Rendall, Seyfarth, Cheney, & Owren, 1999). Rendall et al. (1996, Rendall, Owren, & Rodman, 1998) found strong evidence of individual distinctiveness in the case of rhesus monkey (*Macaca mulatta*) coos in particular, both statistically in acoustic features of the sounds and in the responses shown by these monkeys when hearing playbacks of coos.

However, there is also evidence that not all nonhuman primate calls are equally well suited to providing identity cues. It is not a given, for instance, that caller identity can be heard in vocalizations that either have very high F_0s or are produced through unstable or desynchronized vocal-fold vibration. Both aspects are characteristic of nonhuman primate screaming; for example, S. Gouzoules, Gouzoules, and Marler (1984) reported that screams of juvenile rhesus monkeys variously consist of very high-frequency tonal components and high-amplitude broadband noise (see Figure 1B). Subsequent analyses have shown that the acoustic features of these sounds are unstable, often changing from moment to moment and showing a variety of nonlinear phenomena like subharmonics, biphonation, and deterministic chaos (e.g., Riede, Wilden, & Tembrock, 1997; Tokuda, Riede, Neubauer, Owren, & Herzel, 2002; reviewed by Wilden, Herzel, Peters, & Tembrock, 1998, and Fitch,
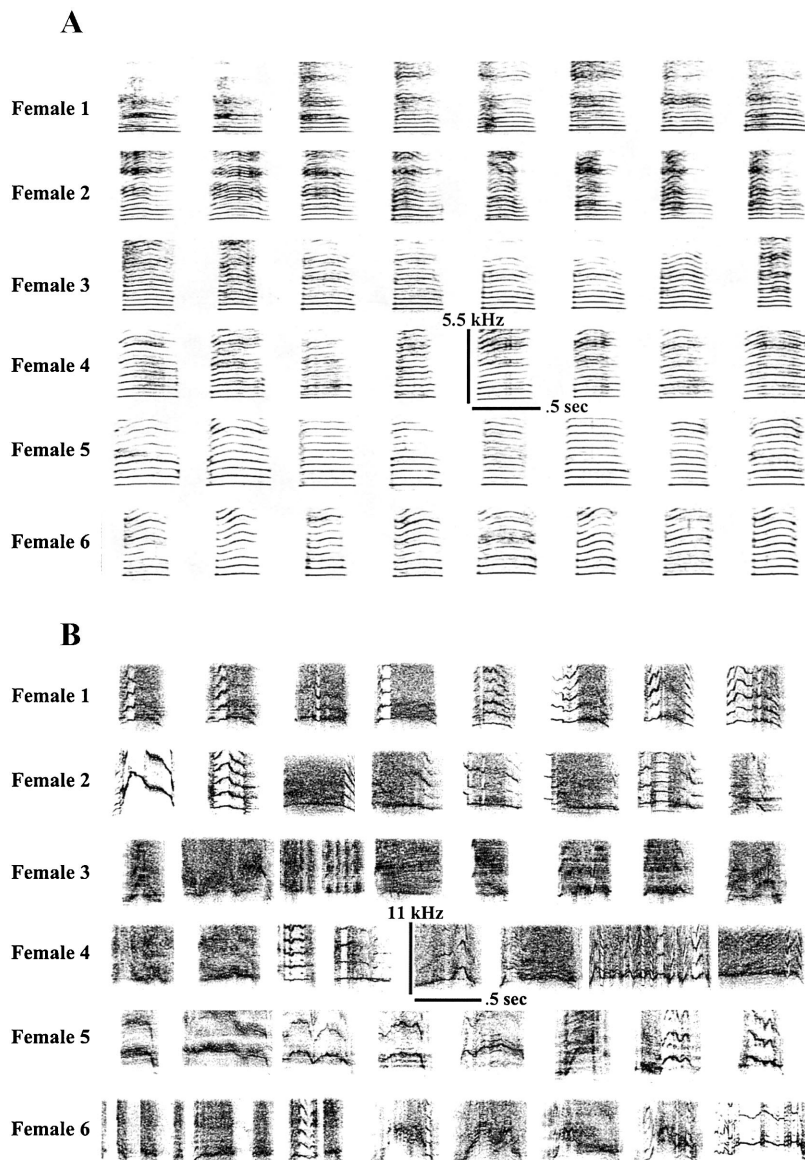
Figure 1. Eight coos (A) and eight screams (B) from each of the same six adult female rhesus macaques are shown in Fourier transform-based narrowband spectrograms (0.029-s Gaussian analysis window). Coos were downsampled to 11.025 kHz to produce these illustrations. sec = seconds.

Neubauer, & Herzel, 2002). In marked contrast to outcomes for coos, analysis of adult female rhesus monkey screams have shown few acoustic correlates of individual identity (Rendall et al., 1998). Although H. Gouzoules, Gouzoules, and Marler (1986) argued from playback-experiment evidence that adult female rhesus monkeys can recognize caller identity from juvenile screams, Rendall et al.'s (1998) later tests with the same monkey groups found no evidence of kin- or individual-based discrimination.

The current work was designed to further explore the issue of individual-identity cuing in rhesus monkey coos and screams by testing human listeners. Ultimately, the question of interest is whether rhesus monkeys themselves can hear caller identity from these sounds. Nonetheless, it is potentially informative to also test

humans because human auditory perception shows critical similarities to that of many nonhuman primates—specifically including rhesus monkeys and other macaque species. These similarities include basic sensitivity across the audible frequency range (e.g., Owren, Hopp, Sinnott, & Petersen, 1988) and both duration and amplitude discrimination (Moody, 1994; Sinnott, Owren, & Petersen, 1987a, 1987b; Sinnott, Petersen, & Hopp, 1985). Although monkeys are typically found to be significantly worse than humans in discriminating frequencies of pure-tone stimuli, evidence from Japanese macaques (*Macaca fuscata*) has shown these animals to be virtually identical to humans in sensitivity to the filtering effects associated with vocal-tract resonances (Sommers, Moody, & Prosen, 1992). Subsequent psychophysical testing has confirmed

that Japanese macaques are specifically sensitive to the amplitude profile of synthetic sounds, whether the harmonic structures involved are modeled on human vowels (Le Prell, Niemiec, & Moody, 2001) or coo calls (Le Prell & Moody, 2002). Sinnott (1994; Sinnott & Kreiter, 1991) requisitely concluded that although monkeys and humans sometimes perform differently when tested with pure tones, they respond similarly with more complex, naturalistic stimuli. It has therefore been fruitful to test monkeys like macaques and baboons with human speech sounds, with the expectation that they will show critical commonalities in auditory perception (reviewed by Sinnott, 1994).

The converse approach of using humans in experiments with monkey sounds can thus provide a natural complement to both laboratory- and field-based data from the animals; for instance, it allows more thorough examination of the interaction of acoustics and auditory response. Because humans perform well in a variety of perceptual tasks, the particular procedure used is much less constrained than is the case with nonhumans. For example, with monkeys it can be difficult to compare results from one setting or with a particular kind of sound with outcomes from another setting or a different kind of sound. One of the best ways to make such comparisons is to convert response data to the common metric of d' values derived from signal-detection theory (Fine & Jacobs, 2002). The general approach is to take multiple aspects of performance into account, thereby being able to separate an individual's sensitivity to the perceptual dimension being tested from subject biases that shape response probabilities independently of detection or discrimination capabilities. This approach has been fruitfully applied in after-the-fact analyses of nonhuman performance both in the laboratory (e.g., Hienz & Brady, 1988; Le Prell, Hauser, & Moody, 2002) and in the field (e.g., Rodriguez-Gironez & Lotem, 1999), albeit relatively rarely.

Even better, of course, is to explicitly use signal detection as the basis of experimental procedures from the beginning, using a common testing strategy no matter what stimuli are involved. In the approach used here, two sounds are presented on each trial and the participant's task is to decide if they are the same or different on the dimension of interest. Results are tabulated as hits (correctly responding "same"), misses (incorrectly responding "different"), false alarms (incorrectly responding "same"), and correct rejections (correctly responding "different"). If the stimulus includes an equal number of same and different trials, unbiased sensitivity is indexed by d' values by comparing the relative proportion of observed hits and false alarms to underlying statistical distributions of these values (D. M. Green & Swets, 1974; Macmillan & Creelman, 1991). In practice, this method has been found to be both reliable and robust to violations of underlying assumptions, likely because of its grounding in normally distributed sampling outcomes and the central-limit theorem (Fine & Jacobs, 2002).

Although some nonhuman primates can eventually master the sort of two-alternative forced choice involved in an explicit same–different paradigm, training can be quite arduous (e.g., Owren, 1990; although see Sinnott & Saporita, 2000). Humans, in contrast, grasp the task immediately from verbal instructions, and in our study, participants were readily able to perform a vocalizer-discrimination task using rhesus–macaque coos and screams as well as human vowel sounds. The listeners did not receive feedback at any time during the task and were simply asked to judge whether the two sounds heard on each trial were both from the

same monkey or had been produced by different vocalizers. In Experiment 1, a balanced sample of eight coos and eight screams from each of six adult female rhesus monkeys was used. In Experiment 2, a subset of these calls was presented, with the screams sorted into two acoustic classes and selectively paired to disentangle sensitivity to vocalizer-identity cues from possible confounding effects of unrelated acoustic variation. Finally, in Experiment 3 we compared discrimination performance using the monkey calls with outcomes for human sounds by including brief, naturally recorded vowel segments in the stimulus set. This last experiment was designed to provide a measure of the relative salience of vocalizer identity in the coo calls in particular.

Experiments 1–3

General Method

Participants

Except where noted, participants were Cornell University undergraduates working for course credit and recruited through a departmental, Internet-based sign-up system. Each person provided informed consent and completed a personal-history questionnaire before the session, and each was debriefed immediately after the session. Personal-history items included whether the participant had been diagnosed with any speech- or hearing-related impairments.

Materials

Apparatus. Participants were tested in a small room containing five listening booths equipped with Beyerdynamic DT831 headphones (Farmingdale, NY) and four-button Tucker–Davis Technologies response boxes (TDT; Gainesville, FL). Each station was connected to TDT control modules in an adjacent room, operated by computer with custom-written software (Tice & Carrell, 2002). The system provided 1-ms resolution in recording response latencies. Participants were observed from the control room via a two-way mirror throughout testing, allowing the experimenter to monitor hand and body position, finger placement on the buttons, and evident attention to the task. The experimenter noted in the laboratory log book if a participant failed to respond in the manner instructed or showed evidence of inattention, such as fidgeting or wandering gaze. In either case, that participant's results were excluded from the experiment prior to data tabulation. Statistical analyses were conducted with NCSS 2000 (Hintze, 1999).

Stimuli. The sounds used were drawn from recordings made from provisioned, free-ranging rhesus monkeys on Cayo Santiago island in Puerto Rico in 1993–1994. Local conditions, recording equipment, and the acoustics of these vocalizations have been described in detail by Rendall et al. (1996, 1998). A balanced sample of eight coos and eight screams from each of six adult females were selected for use in the experiments, with the only selection criteria being that the sounds came from identified individuals vocalizing under known circumstances and that they represented the best recording quality available within the data set (i.e., absence of background noise or overlap with other callers). The calls had originally been digitized as 16-bit, 22.05 kHz files with 10-kHz lowpass filtering using Canary 1.1 bioacoustics software (Charif, Mitchell, & Clark, 1995). Human vowel stimuli were /ɛ/ sounds (from the word *test*) drawn from a large set described in detail by Bachorowski and Owren (1995, 1999). These sounds were originally digitized as 12-bit, 50-kHz files with 5-kHz lowpass filtering using CSRE version 4.0 software (AVAAZ Innovations, 1993). Both rhesus and human sounds were prepared as experimental stimuli using ESPS/waves+ version 5.3 acoustics software (Entropic, 1998). They were individually normalized to a mean RMS amplitude of 76.0 dB with a

22.05 kHz sampling rate. Stimuli were constructed by pairing sounds so that the second one always began at the 1,400-ms point in the file, with a 600-ms silent gap between the two. Files also began and ended with at least 100-ms silence, thereby preventing audible onset and offset transients during presentation. Lowpass filtering was set to 10 kHz throughout testing.

Procedure. Participants were tested in groups of up to 5, after first hearing introductory information and instructions read aloud. Listeners thus knew in advance that the stimuli would be rhesus monkey calls and in some cases human vowels, that there would be two sounds occurring on each trial, that it was important to respond as quickly as possible, and that they would not receive any performance feedback. The task was to use one of two buttons labeled *Same* and *Different* to indicate whether the same vocalizer had produced both sounds occurring on the trial or alternatively that the sounds were from different vocalizers. Label position was reversed at the beginning of each testing day for counterbalancing purposes. Participants responded using their index fingers, resting them lightly on the two response buttons at all times. Before beginning the experiment, participants completed 16 practice trials with coos, screams, or vowels from vocalizers that were not represented in the experimental trials. No feedback was given on these trials either.

Stimulus sets always included same and different trials in equal numbers. Individual vocalizers were equally represented within a (same-species) set, with each call appearing an equal number of times in first or second position within a stimulus pair. Order of stimulus presentation was randomized in each testing session and trial parameters included an alerting cue-light flash occurring 750 ms before each trial, a maximum response window of 5 s, and a 2-s intertrial interval. Response latencies were measured from the onset of the second sound in each stimulus pair, and sessions lasted 30–40 min.

Statistical analysis. Dependent measures used were d' and median response latency, with mean values of each calculated separately for individual participants. d' values were derived from the number of hits and false alarms recorded from each participant based on the differencing model (Macmillan & Creelman, 1991). In signal-detection analysis, chance performance with balanced stimulus sets produces an expected d' score of 0, and d' values form an exponential scale composed of standard deviation units rather than being a linear, equal-interval scale. In practice, d' values of 1.0 to 1.5 have been suggested as empirical thresholds, meaning criterion scores at which reliable discrimination performance is occurring (Macmillan & Creelman, 1991). Data from trials with reaction times of less than 200 ms were excluded as being anticipatory rather than representing responses to the trial stimuli, and most statistical testing was based on repeated measures analyses of variance (ANOVAs).

Experiment 1

The first experiment tested listeners with all 48 coos and 48 screams from the rhesus monkey vocalizers. On the basis of the markedly different results reported for field playback tests of kin- and individual-discrimination with coos versus screams (cf. Rendall et al., 1996, and Rendall et al., 1998), we predicted that human participants would be significantly better in hearing vocalizer identity from the coos than from the screams.

Method

Participants

Participants were 16 women, 11 of whom were recruited and tested as described in the *General Method* section and 5 of whom were clerical staff at Cornell University. All of the participants were naive to the goals of the study, and their ages ranged from 19 to 43 years. Data from 2 other participants were excluded from analysis, in one case because of experimenter error in testing, and in the other because of evident inattention during the session.

Materials

Apparatus and procedure. The apparatus and procedure were as described in the *General Method* section.

Stimuli. The stimuli were eight coos and eight screams from each of six different adult female rhesus monkeys, as described earlier and shown in Figure 1. Pairs were always composed of two coos or two screams, with 192 experimental trials in the counterbalanced form outlined above. Practice trials were based on two coos and two screams each from four other adult female rhesus monkeys.

Results and Discussion

Mean durations of the sounds used in this experiment were different, as shown in Figure 2A. Repeated measures ANOVAs with vocalizer identity entered as the subject variable revealed that call durations did not vary by individual, $F(4, 84) = 1.42$, *ns*, but that screams were significantly longer than coos, $F(1, 84) = 11.9$, $p < .05$. There was no interaction between these factors, $F(5, 84) = 1.84$, *ns*. Participant response data were analyzed using repeated measures ANOVAs with listener identity as the subject
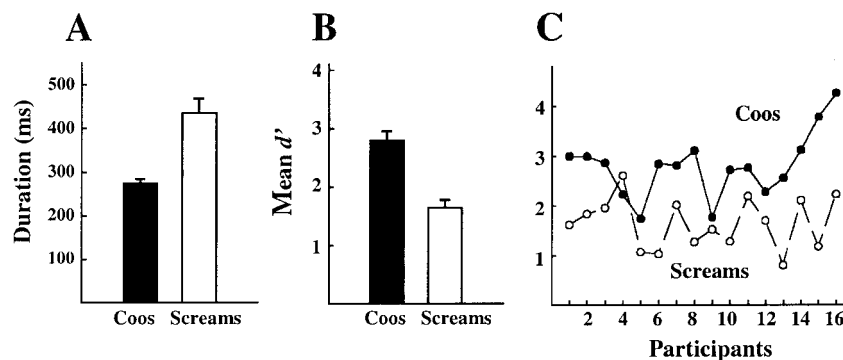

Figure 2. Coos used in Experiment 1 showed shorter mean durations than screams (A), but listeners hearing the coos produced significantly higher mean d' scores in discriminating vocalizer identity than when hearing screams (B). The advantage for coos was shown by 15 of 16 participants tested (C). Error bars represent standard errors.

variable and call type as the within-subject factor. As shown in Figure 2B, listeners showed significantly higher mean d' values when discriminating caller identity for coos ($M = 2.80$, $SE = 0.16$) than for screams ($M = 1.65$, $SE = 0.52$), $F(1, 31) = 37.2$, $p < .01$. These results reflected mean proportions of .79 hits and .32 false alarms for coos, as opposed to .68 hits and .44 false alarms for screams. In other words, d' results reflected both a lower hit rate and higher false-alarm rate for screams than for coos. The performance difference involved is large, given the exponential nature of d' scaling. Outcomes for response latencies corroborated this difference, with reaction times on trials with correct responses (hits) being significantly faster for coos ($M = 795.1$ ms, $SE = 215.6$) than for screams ($M = 962.8$ ms, $SE = 206.0$), $F(1, 31) = 34.2$, $p < .01$.

Taken together, the results indicate that these human listeners were much better able to hear vocalizer identity from the coos than from the screams. However, d' outcomes for screams were also not inconsequential and were significantly greater than a discrimination threshold value of 1.0, $t(15) = 5.05$, $p < .01$. This finding suggests that participants were also able to discriminate among vocalizers to some degree when hearing their screams. The next experiment examined the acoustic basis of this discrimination more closely.

Experiment 2

As shown in Figure 1B, the screams used in Experiment 1 exhibited a diversity of acoustic features. For example, sounds from Female 3 were quite noisy, whereas screams from Female 5 were much more tonal. Other individuals were represented by screams in which either noise or tonality might be considered predominant. As a result, participant judgments of vocalizer identity in Experiment 1 may have been influenced by differences in scream type in addition to caller characteristics per se. That point is important in that individual rhesus monkeys routinely produce screams that are noisy or tonal (S. Gouzoules et al., 1984; Rendall et al., 1998) or a mix of the two (Kitko, Gesser, & Owren, 1999; Owren & Nederhouser, 2000), with no indication that the degree of noisiness or tonality is specific to that particular caller. In contrast, heterogeneous F_0-related and formant-related features (both of which can be detected in Figure 1A) have been found to provide potential identity cues (Hauser, 1991; Owren, Dieter, Seyfarth, & Cheney, 1992; Rendall et al., 1998) but not to be correlated with behavioral context (Hauser, 1991). We therefore surmised that the heterogeneity of scream acoustics across the vocalizers represented in Experiment 1 may have artificially inflated d' results. In other words, because relative noisiness and tonality did in fact covary with individual caller in this stimulus set, listeners may have been responding to this aspect of each scream, thereby increasing response accuracy on the basis of cues that would not be reliable with a larger stimulus set or under natural conditions. To examine this possibility, we tested a new group of listeners using a subset of the calls, with noisy and tonal screams balanced more evenly across the individual vocalizers involved.

Method

Participants

Participants were 14 females, recruited and tested as described in the *General Method* section. Data from 2 other females were excluded from

the analysis, in one case because of the participant's failure to consistently respond using both index fingers and in another because of evident inattention during the session.

Materials

Apparatus. The apparatus was as described in the *General Method* section.

Stimuli. Stimuli were selected on the basis of first subjectively rating the noisiness and tonality of the screams from the spectrographic representations shown in Figure 1. Initial ratings were based on a 4-point scale of *very tonal* (1), *somewhat tonal* (2), *somewhat noisy* (3), and *very noisy* (4); representative sounds from each level are shown in Figure 3. Distinguishing between Categories 2 and 3 could be difficult, with the criterion being that more than 50% of the duration of the call be predominantly tonal or predominantly noisy. For final stimulus selection, calls scored as 1 or 2 were considered tonal, and those scored as 3 or 4 were considered noisy. The subset of 20 screams included balanced representation of noisy and tonal sounds across vocalizers, with 3 noisy and 3 tonal screams from both Females 1 and 2, and 2 noisy and 2 tonal screams from both Females 4 and 5. A corresponding set of coos was then selected for each individual on the basis of the generic stimulus label that had been arbitrarily assigned to each sound at the beginning of testing. In other words, the coos used were those from the same vocalizers that happened to have received the same letter designations (a–h) as the screams that had been selected. The final stimulus set thus included 40 sounds, with an equal number of coos and screams.

Procedure. The stimuli were paired and counterbalanced as before. The final total of 160 trials included 80 with paired coos and 80 with paired screams. Twenty of the latter trials were with noisy screams, 20 were with tonal screams, and 40 presented one of each type. Practice trials used the same stimuli as in Experiment 1.

Results and Discussion

As shown in Figure 4, mean duration of the coos was again significantly shorter than that of the screams, $t(39) = -2.20$, $p < .05$. Listener discrimination of vocalizer identity based on d' scores was nonetheless again significantly higher for coos ($M = 2.69$, $SE = 0.15$) than for screams ($M = 1.12$, $SE = 0.11$), $F(1,$
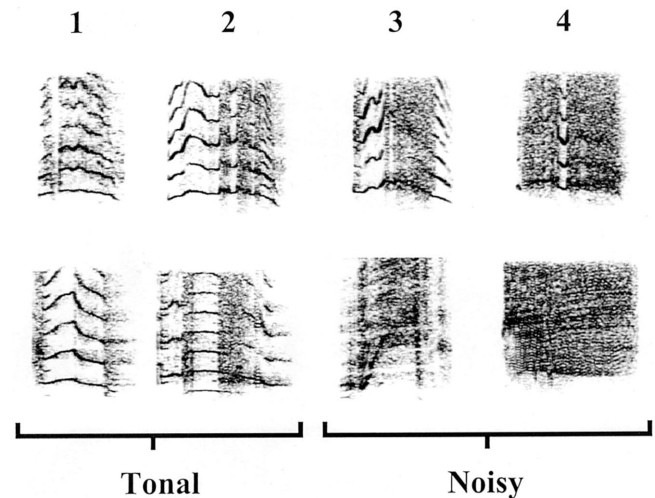

Figure 3. Wideband spectrograms of eight of the screams shown in Figure 1 illustrate scoring of relative tonality and noisiness in the screams on a scale of 1 (*very tonal*) to 4 (*very noisy*).
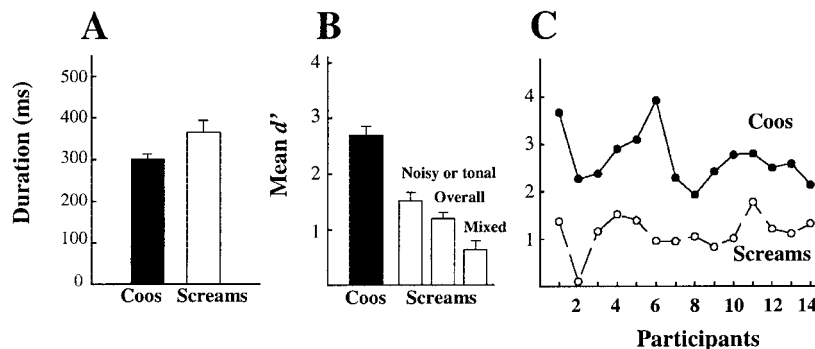
Figure 4. Coos in Experiment 2 showed shorter mean durations than screams (A), with listeners producing significantly higher mean *d'* scores with the former than the latter (B). The advantage shown with coos was evident for all 14 participants tested (C). Error bars represent standard errors.

27) = 96.9, *p* < .01. Here, overall mean *d'* values for screams were not significantly greater than an empirical threshold of 1.0, *t*(13) = 1.08, *ns*. However, outcomes for homogeneous scream pairs were significantly higher (*M* = 1.46, *SE* = 0.15) than when the pairing was heterogeneous (*M* = 0.69, *SE* = 0.15), *F*(1, 27) = 13.8, *p* < .01. There was no difference between hit latencies for coos (*M* = 842.6 ms, *SE* = 52.8) versus screams (*M* = 893.5 ms, *SE* = 40.9), *F*(1, 27) = 3.19, *ns*, or between the different scream-pairing conditions.

These results indicate that incidental acoustic differences among the screams were increasing apparent listener sensitivity to vocalizer identity, but that some vocalizer cuing is nonetheless present in these sounds. The occurrence of incidental cuing is underscored by noting that although classification of coos was no different than in Experiment 1, *t*(28) = 0.5, *ns*, outcomes for screams were clearly dependent on how the sounds were paired. These sounds showed a significant decline across experiments when pairings included a balanced mix of noisy and tonal combinations, *t*(28) = 3.03, *p* < .01. In other words, the observed decline in *d'* results for screams indicates that listeners in Experiment 1 were in fact attending to circumstantial differences in tonality and noisiness in a given pair of screams when judging vocalizer identity. Classification accuracy dropped most precipitously on trials in which the sounds were a mix of noisy and tonal screams. Scores also fell when listeners heard "side-by-side" comparisons of either noisy or tonal screams, although remaining significantly above a *d'* value of 1.0, *t*(13) = 3.03, *p* < .01. This aspect of the results suggests a second basic finding, that there are some acoustic correlates of vocalizer identity in screams as well.

Taken together, these outcomes with human listeners are consistent with both acoustic analysis results and playback experiments with free-ranging rhesus monkeys reported by Rendall et al. (1996, 1998). Rendall et al.'s (1998) work with 507 coo calls produced in a variety of contexts by 17 adult female rhesus monkeys is the most extensive acoustic analysis of these sounds conducted to date, and it showed that both F_0-related and formant-related features contributed to statistical classification by caller identity. In this case, discriminant-function analyses correctly assigned 91% of the calls to the individual who produced them (90% error reduction). Statistical classification of screams was much less effective, with only 30% of the 115 screams of 9 adult females

(20% error reduction) being sorted correctly. Classification of screams achieved statistical significance but was obviously far below that shown for the coos. Rhesus monkeys tested in the field similarly showed strong evidence of hearing vocalizer identity from coos (Rendall et al., 1996), whereas no evidence of identity cuing could be detected for screams under these conditions (Rendall et al., 1998).

The last experiment was designed primarily to follow up the results obtained with coos. Here the goal was to provide some comparative perspective on how well listeners were discriminating vocalizer identity in these sounds. To that end, we added human vowels to the study, expecting that listeners would readily discriminate vocalizer identity in these sounds and thereby provide an external point of comparison for their performance with coos.

Experiment 3

Macaque coos and human vowel sounds are fundamentally similar, both in the underlying production involved and in their resulting acoustic characteristics (cf. Figure 5 and Figure 1). In both cases, the sounds consist of harmonically structured source energy produced through regular vocal-fold vibration, which is then shaped by resonance characteristics of the supralaryngeal vocal tract. Viewed as a combination of source energy and subsequent filtering, the sounds are understandably rich in potential cues to vocalizer identity. For example, individual idiosyncrasies in vocal-fold morphology might give rise to characteristically distinctive features in the source waveform. Similarly, because of inevitable individual variation in the sizes, shapes, and damping properties of cavities and tissues above the larynx, every vocalizer can be expected to show a uniquely patterned supralaryngeal filter function. Spectrally rich harmonic sounds with low F_0s are particularly well suited to showing these effects, and the two factors taken together suggest that macaque coos and human vowel sounds should both be excellent vehicles for listener perception of vocalizer identity.

However, the same factors also suggest that individual voice quality could be more evident in the human versions of these sounds. For example, there are two reasons to suspect that potential idiosyncrasies in source energy will be more audible in human vowels than in macaque coos. First, human vocal folds are phys-
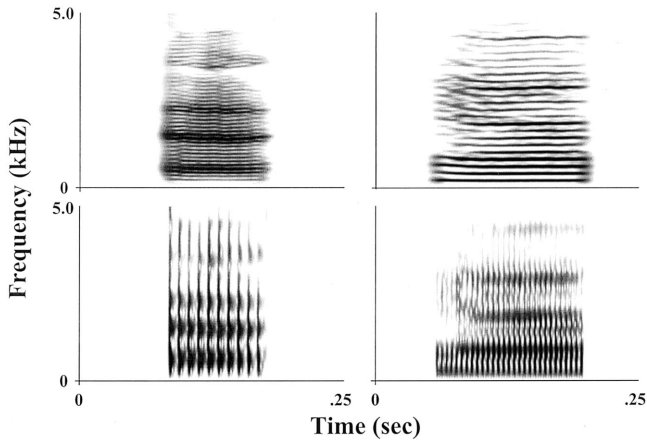
Figure 5. Representative /ɛ/ sounds shown in both narrowband (top) and wideband (bottom) representations for a male (left) and female (right) human talker saying the word *test.* Both density of harmonics and resolution of vocal-tract resonances are significantly greater in the male, as illustrated in the narrowband and wideband spectrograms, respectively.

ically longer and thicker than are corresponding tissues in macaques (e.g., Schon Ybarra, 1995; Titze, 1994), a size difference that should produce a greater range of variation among individuals and more opportunity for idiosyncratic differences to emerge during the course of development. Second, whereas F_0s in adult female rhesus coo calls are approximately 400 Hz (Rendall et al., 1998), corresponding values are almost one half and one quarter that value in adult female and adult male humans, respectively (Baken, 1987). In other words, the number of harmonics occurring in a given spectral range in a human vowel sound is typically 2–4 times greater than that in a macaque coo. The imprint left by supralaryngeal resonances on harmonic-amplitude patterning is requisitely better defined when more harmonics are present, thereby making individual variation in detailed aspects of the resonance pattern more salient.

Because humans have longer supralaryngeal vocal tracts than do rhesus macaques (Fant, 1960; Fitch, 1997; Fitch & Giedd, 1999), they also exhibit requisitely lower frequency resonances (Fant, 1960), with more of these formants occurring in the spectral range of highest amplitude harmonics. The imprint of the supralaryngeal filter was therefore expected to be richer in human sounds for this reason as well, again leading to better expected vocalizer discrimination with vowels than with coos. However, we hypothesized that performance with each of these vocalizations should still be clearly better than with screams.

Method

Participants

Participants were 14 females, recruited and tested as described in the *General Method.* Data from 1 other female were excluded from the analysis because the participant did not respond using the index fingers of both hands.

Materials

Apparatus and procedure. The apparatus and testing procedure were as described in the *General Method* section.

Stimuli. Stimuli included five different /ɛ/ sounds from each of six adult male and 6 adult female humans (see Figure 5), which were added to a subset of the calls used in Experiment 1. That set consisted of five coos and five screams from each of the six rhesus females. There were 192 trials, with pairs of male vowels, female vowels, coos, and screams each presented on 48 trials. Screams were paired as in Experiment 1, without regard to their acoustic features. Practice trials included eight pairings of two /ɛ/ sounds from each of two human adult males and two human adult females as well as eight trials based on two coos and two screams from each of three adult female rhesus monkeys.

Results and Discussion

Results from this experiment are illustrated in Figure 6. Mean duration of the vowel sounds used was 131.1 ms (*SE* = 4.2), which reflected significantly shorter segments from male talkers (*M* = 108.2 ms, *SE* = 4.7) than from female talkers (*M* = 154.0 ms, *SE* = 3.5), *t*(58) = 7.75, *p* < .01. General linear model ANOVAs showed mean durations of coos, screams, male vowels, and females vowels to be significantly different overall, *F*(3, 120) = 75.3, *p* < .01, with Newman-Keuls post hoc comparisons further showing that all four sound types were significantly different from one another. Repeated measures ANOVAs revealed significant differences among mean *d'* values for vowels (*M* = 3.5, *SE* = 0.22), coos (*M* = 2.3, *SE* = 0.16), and screams (*M* = 1.7, *SE* = 0.19), *F*(1, 41) = 34.0, *p* < .01. Post hoc Newman-Keuls comparisons revealed that mean *d'* results were significantly different among all three stimulus types. Response times were also significantly different for vowels (*M* = 740.8 ms, *SE* = 43.5), coos (*M* = 964.6 ms, *SE* = 65.8), and screams (*M* = 1,078.6 ms, *SE* = 46.7), *F*(1, 41) = 50.1, *p* < .01. Here again, post hoc comparisons showed all three outcomes to be different from one another.

Results for human male versus human female sounds were also tested separately, on the basis of the same rationale leading to better expected performance for vowels versus coos, namely that human males have larger vocal folds, lower F_0s, and longer vocal tracts than do human females (Titze, 1994). As we expected, listener performance was significantly higher for vowels from human males (*M* = 3.81, *SE* = 0.24) than for vowels from human females (*M* = 3.30, *SE* = 0.31), *F*(1, 27) = 4.88, *p* < .05. However, there was no difference in hit latencies for trials involv-
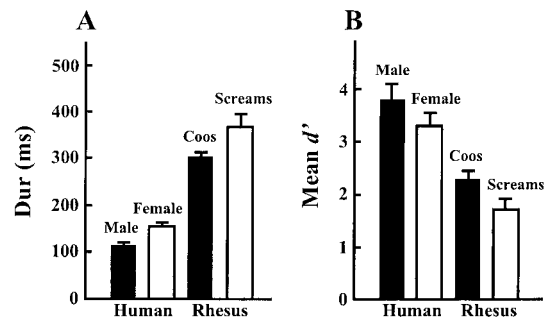

Figure 6. Human /ɛ/ segments used in Experiment 3 were significantly shorter than either coos or screams (A), with male sounds in turn being significantly shorter than female sounds. Listeners nonetheless showed significantly different mean *d'* scores for all four sets of sounds, in inverse order of sound duration (B). Error bars represent standard errors. Dur = duration.

ing vowels from human males ($M = 757.7$, $SE = 57.6$) versus vowels from human females ($M = 737.0$, $SE = 40.5$), $F(1, 27) = 0.44$, *ns*.

Overall, the results showed the expected performance pattern for vowels, coos, and screams. Mean d' results for screams were virtually identical to those of Experiment 1, whereas values for coos were somewhat lower than in the previous experiment, $t(28) = 2.19$, $p < .05$. The rationale of expecting size differences in vocal folds and vocal tracts to be reflected in vocalizer discriminability was confirmed both in the case of human vowel sounds versus macaque coos and for human male versus human female sounds.

General Discussion

Taken together, these three experiments provide two main conclusions concerning vocalizer-identity cuing in rhesus macaque coos and screams. First, each experiment showed a substantial advantage in discrimination performance when listeners heard coos compared with when they heard screams. In Experiment 2, restricting scream presentation to a subset that better controlled for orthogonal acoustic variation lowered performance with these sounds even further. Second, performance with the screams was nonetheless above chance in each study, hovering within the range of values that have been suggested as an empirical threshold of discrimination. In other words, the acoustics of these sounds are correlated with individual identity in some way that is perceptible to humans, whereas Rendall et al.'s (1998) playback experiments with rhesus monkey listeners were unable to demonstrate any effect under naturalistic conditions.

Another noteworthy aspect of the results is that the salience of vocalizer identity followed acoustically based expectations concerning the effects of significant differences in size and likely morphological details of vocal-tract anatomy. Specifically, listeners were better able to discriminate individual identity in vowels from human males than from human females, both of which showed more evident cuing than did the coo calls. An alternative interpretation is that these human listeners were either innately bettered attuned to, or simply more familiar with, voice quality in human sounds than in comparable vocalizations from nonhumans. However, F_0s and resonances are also characteristic of immature humans, meaning that sounds with coo-like acoustic parameters are not entirely foreign to human listeners. Two alternative predictions follow. If the acoustically grounded explanation is correct, it predicts that rhesus–macaque listeners tested for maximal sensitivity under laboratory conditions will show their best performance in identity discrimination with human vowels rather than species-typical sounds. If human performance in the current experiments instead reflected species-specific sensitivities, rhesus listeners should perform better with coos than with human vowels.

It is arguably counterintuitive to predict that any animal would be less sensitive to individual-identity cues in sounds from conspecifics than from vocalizers of some other species. However, the prediction does in fact follow, at least to the extent that formant effects are both salient to macaque listeners and play a significant role in identity cuing. The perceptual salience of spectral-peak patterning to nonhuman primates and other mammals has in fact been confirmed by a variety of researchers (e.g., Le Prell et al., 2001; Sinnott & Kreiter, 1991; Sommers et al., 1992; see Le Prell

& Moody, 2002, for a recent review) as has the occurrence of spectral peaks that reflect formant effects in naturally occurring calls of both rhesus macaques (Fitch, 1997; Hauser, Evans, & Marler, 1993; Rendall et al., 1998) and other monkeys (reviewed by Owren et al., 1997).

Evidence from psychophysical testing of Japanese macaques with synthetic vowel sounds suggests that the first counterintuitive prediction would be supported (Le Prell et al., 2001). In this work, five adult male Japanese macaques were tested in their ability to discriminate changes in the spectral shape of harmonic complexes modeled on human /ae/ sounds. The monkeys resembled human listeners from other studies in showing greatest sensitivity to amplitude changes in harmonics at simulated formant locations rather than regions of the spectrum in which harmonic amplitudes were low. More important for acoustically grounded expectations about rhesus identity discrimination in vowels and coos, Le Prell et al. (2002) tested the animals both with a 20-component stimulus based on a 120-Hz F_0 (resembling typical human male values) and with a 5-component stimulus based on a 480-Hz F_0 (resembling typical female macaque values). By design, both sounds thus included a 480-Hz component, allowing direct comparison of sensitivity to the amplitude of this harmonic. As with human participants tested in other studies (reviewed by Le Prell et al., 2002), the monkeys showed lower sensitivity to amplitude changes in the high-F_0 version than in the low-F_0 version. In other words, these experiments showed that in simulating formant-filtering effects on a harmonic component, the amplitude change was more salient to monkeys when hearing a richer, human-like stimulus than when hearing a sound modeled on their own species-typical coo calls.

Taken together, these perceptual results and findings from acoustic analysis of rhesus monkey coos (Hauser, 1991; Owren et al., 1992; Rendall et al., 1998) suggest that both F_0 and formant variation may provide cues that conspecific animals attend to in identifying callers. However, it is not yet known whether either sort of cue is significantly more salient than the other. Statistically, formant variation has allowed significantly better discriminant-function classification of vocalizers than has F_0-related cuing, both in coos by adult female rhesus (Rendall et al., 1998) and in vowel segments by adult male and adult female humans (Bachorowski & Owren, 1999). Both sources do provide substantial error reduction when considered separately, and combining them increases classification accuracy significantly in comparison with either used alone. It remains an open question as to whether perceptual responses in rhesus monkeys and humans mirror these acoustical outcomes, an issue that it would be useful to address in future work.

Functional Implications of Acoustic Structure

The relative durations of coos, screams, and vowels fell in reverse order of vocalizer-discriminability outcomes. This result underscores the point that identity cues are determined primarily by differences in vocal-production mode rather than the length of the sounds per se. We have argued that generally stable vocal-fold vibration that reveals filtering effects of supralaryngeal vocal-tract resonance characteristics is the critical feature. In this case, noisiness resulting from a limited degree of irregularity in vocal-fold action may then increase individual distinctiveness if it shows even

more details of resonance filtering (Fitch et al., 2002). In contrast, vocal-fold vibration in screams is highly unstable (Owren & Nederhouser, 2000; Tokuda et al., 2002), and these sounds fail to reveal supralaryngeal resonances (Rendall et al., 1998). The important observation is simply that acoustic cues to individual identity are much more prominent in coos than in screams, not that the latter show no individual distinctiveness whatsoever. On the contrary, responses by our human participants suggest that under optimal "side-by-side" comparison conditions, listeners can respond to individual differences reflected in scream acoustics to some degree—they were just much less reliable than with coos.

Scream Acoustics Are Poorly Suited to Referential Signaling

S. Gouzoules et al. (1984) argued that rhesus monkeys show five acoustically discrete scream types, each of which conveys different referential information to listeners concerning detailed aspects of the agonistic situation. The proposed function of calling is to recruit help from among potential allies that hear the calls and were not previously aware of what was happening. If so, the calls must have two critical attributes, namely stable acoustic features that are unambiguously correlated with each behavioral situation and vocalizer-identity cues that are salient to kin and other potential social allies. Although interpretations of playback studies by S. Gouzoules et al. (1984) and H. Gouzoules et al. (1986) favor both a referential function and individual distinctiveness of scream vocalizations, other analyses indicate that these sounds have unstable acoustic features (Owren & Nederhouser, 2000), are produced through chaotic vocal-fold vibration (Fitch et al., 2002; Tokuda et al., 2002), and show little evidence of individual distinctiveness (Rendall et al., 1998). The acoustic structure of screams thus makes them very poorly suited either to conveying semantic information about the agonistic event or for recruiting allies who are out of sight. Corroborating perceptual evidence is also now available on both counts (Le Prell et al., 2002).

An alternative argument is that rhesus screams are used as a kind of acoustic bludgeon wielded at short range by a caller who although generally powerless against its opponent can still attempt to make itself a less inviting target by producing noxious sounds (Owren & Rendall, 1997, 2001; Rendall & Owren, 2002). In this view, the target of screaming is the antagonist rather than third-party listeners. If the function of screaming is to be more aversive to an opponent close at hand, screams are expected to be extremely loud, to have piercing auditory properties, and to show on-going acoustic variability that helps reduce perceptual and affective habituation by the target. The latter properties, although adding to the aversive quality of screams, are antithetical to the proposed referential and recruitment functions of the calls. It is nonetheless likely that third-party listeners are able to draw important inferences concerning ongoing agonistic events when hearing screams, on the basis of both their first- and second-hand experience of screaming and aggressive encounters. However, we suggest that this aspect is a secondary outcome, as indicated by the fact that screams are extremely salient although only very modestly distinctive by caller.

Consistency of Identity Cuing Across the Vocal Repertoire

Unlike chaotic screams, harmonically based calls like coos are not jarring to listeners. Their features are strongly correlated with vocalizer identity, with a definite, perceptible, and distinctive voice quality. Although our human participants received no special instruction and had no known previous experience with monkey calls, they were immediately able to discriminate among individual vocalizers—showing discrimination results that were largely consistent with playback outcomes with the rhesus monkeys themselves (Rendall et al., 1996; Rendall et al., 1998). Rendall (1996) argued that supralaryngeal vocal-tract filtering is an especially good vehicle for identity cues in nonhuman primate calls because monkeys and apes generally show few articulatory gestures that modify the resonances involved. That fact, combined with individual variation in vocal-tract cavities, means that supralaryngeal resonance characteristics are likely to be consistent among the various calls an individual makes. As long as the source energy of a call provides a clear imprint of the supralaryngeal filter, the sound will bear the caller's distinctive resonance signature.

That proposal is supported by the current results with screams, sounds that have been found to reveal very little about supralaryngeal filtering (Rendall et al., 1998). Discrimination performance in Experiment 2 declined markedly when orthogonal variation in noisiness and tonality was removed as a confounding cue to vocalizer identity and many of the trials required comparing identity across noisy and tonal screams. Under these conditions, listeners were notably less able to hear whether the sounds were from one or two callers, indicating that whatever individually distinctive cues may be present in these screams, they are not consistent across noisy and tonal scream types.

Conclusions

As many have noted, coming to grips with communication requires an understanding of signaling at a variety of levels, including underlying production processes, signal form, the behavioral and environmental contexts in which signaling occurs, and receiver psychological responses. We suggest that the challenges involved make it important to address foundational, mechanistic issues like individual distinctiveness as a prerequisite to taking on larger questions like the function and evolutionary history of vocalizing. In the case of rhesus calls, identity cuing results for coos and screams underscore that there can be crucial diversity within a vocal repertoire on even the most basic signal dimensions. Ultimately then, the most fruitful strategy for understanding the origins and functions of any given signal will be a comparative one that takes both its similarities to and its differences from other communicative events into account.

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