Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons

Drew Rendall[a)]
Department of Psychology, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada

Hugh Notman[b)]
Department of Anthropology, Athabasca University, 1 University Drive, Athabasca, Alberta T9S 3A3, Canada

Michael J. Owren[c)]
Department of Psychology, Georgia State University, P.O. Box 5010, Atlanta, Georgia 30302-5010

A key component of nonhuman primate vocal communication is the production and recognition of clear cues to social identity that function in the management of these species' individualistic social relationships. However, it remains unclear how ubiquitous such identity cues are across call types and age-sex classes and what the underlying vocal production mechanisms responsible might be. This study focused on two structurally distinct call types produced by infant baboons in contexts that place a similar functional premium on communicating clear cues to caller identity: (1) contact calls produced when physically separated from, and attempting to relocate, mothers and (2) distress screams produced when aggressively attacked by other group members. Acoustic analyses and field experiments were conducted to examine individual differentiation in single vocalizations of each type and to test mothers' ability to recognize infant calls. Both call types showed statistically significant individual differentiation, but the magnitude of the differentiation was substantially higher in contact calls. Mothers readily discriminated own-offspring contact calls from those of familiar but unrelated infants, but did not do so when it came to distress screams. Several possible explanations for these asymmetries in call differentiation and recognition are considered.
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I. INTRODUCTION

A central and continuing theme in research on nonhuman primates concerns the importance of kinship and individual identity in structuring species' social behavior (reviewed in Chapais and Berman, 2004). Many species are noted for strongly differentiated social relationships which suggest a capacity for discriminating among, and perhaps explicitly recognizing, individual conspecifics and biological kin (reviewed in Rendall, 2004; Widdig, 2007). They are also noted for the variety of vocalizations they produce to mediate social behavior in different contexts, in some of which their individualized social relationships are literally called into play. That is, the structure of some call types has been shown to be differentiated according to the kinship and individual identity of callers (e.g., Marler and Hobbett, 1975; Macedonia, 1986; Gouzoules and Gouzoules, 1990; Hauser, 1991; Rendall *et al.*, 1998; Fischer *et al.*, 2001), and, in some cases, field and laboratory experiments have also confirmed the perceptual salience and behavioral significance of these identity cues to listening animals (Hansen, 1976; Waser, 1977; Kaplan *et al.*, 1978; Cheney and Seyfarth, 1980; Snowdon and Cleveland, 1980; Symmes and Biben, 1985; Pereira, 1986; Rendall *et al.*, 1996; Hammerschmidt and Fischer, 1998; Jovanic *et al.*, 2000; Nunn, 2000; Fischer, 2004). Thus, the animals appear to recognize and respond to the vocalizations of different callers in ways that are functionally commensurate with their kinship or individual relationship to them. Taken together, these patterns suggest that the organization of primate vocal repertoires might be determined in part by the social networks they function to support and, in turn, that flexible management of social networks is to some extent affected by the structural differentiation of vocalizations along lines of social identity.

It is not yet clear, however, whether all calls in a species' repertoire are sufficiently distinctive to allow ready recognition of callers, or whether this is true only for certain call types for which there has been a selective premium on identity signaling and recognition. It is also often unclear exactly what vocal production mechanisms are responsible for generating distinctive voice cues and whether they might create identity cues that are common across call types (Ghazanfar and Santos, 2004; Ghazanfar *et al.*, 2007). For example, although the calls of different individuals could differ in a range of acoustic features, Rendall *et al.* (1998) proposed that patterns of vocal tract resonance might be a

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a)Electronic mail: d.rendall@uleth.ca
b)Electronic mail: hughn@athabascau.ca
c)Electronic mail: owren@gsu.edu

particularly common and productive source of identity cues in primates. Such cues might arise inevitably, and also largely incidentally, as a product of idiosyncrasies in individual vocal tract development. They might also impart a characteristically distinctive voice pattern across most or all of the calls produced by a given individual because, regardless of their source characteristics, all calls must ultimately be radiated through, and thus be structurally shaped by, the supralaryngeal airways. At the same time, primates have long been suspected to have only limited ability to modify the resonances of these airways through dynamic vocal-tract articulations during vocal production (Lieberman *et al.*, 1969). Together, these effects might yield characteristically distinctive voice resonance patterns in each individual (Rendall *et al.*, 1998; Ghazanfar *et al.*, 2007). However, any one of these assumptions might be faulty, or at least too simplistic: vocal tract development might not always be sufficiently different between individuals to yield perceptually distinctive voice resonance patterns; some laryngeal sources (e.g., those with very high fundamental frequency, F_0) might not highlight the supralaryngeal resonances very well, and primates might have a greater capacity for vocal tract modulation than previously suspected (Hauser, 1992; Riede and Zuberbühler, 2003).

It is thus important that we continue to test the production and recognition of identity cues in different vocalizations to more fully understand the ubiquity and underlying vocal production mechanics of identity signaling in primates and thus also how vocal communication patterns in these species integrate with the functional demands of their individualistic social lives. In this paper, we report acoustic analyses examining individual distinctiveness in two distinct call types produced by infant baboons and then follow-up field experiments testing maternal recognition of infants' calls.

We focus specifically on baboons because they are among the best-studied primate species, yielding a comparatively solid understanding of their social life (Altmann, 1980; Smuts, 1985; Strum, 1987; Cheney and Seyfarth, 2007). There has also been considerable recent research on their vocal communication, including studies related to identity cueing and vocal recognition of group members which point to individually distinctive and recognizable calls in at least some kinds of vocalizations produced by adults (e.g., Cheney *et al.*, 1996; Owren *et al.*, 1997; Cheney and Seyfarth, 1999; Rendall *et al.*, 1999, 2004; Semple, 2001; Fischer *et al.*, 2001, 2002; Engh *et al.*, 2006). We focus the current work on infants then because, by comparison to adults, there has been relatively little systematic research on infant vocal repertoires, either in baboons or in other primate taxa. At the same time, infants are, by definition, the most vulnerable members of primate groups, subject to high risks of predation and, in some species including baboons, also infanticide from adult males (Palombit *et al.*, 1997, 2000). As a result, infants are the individuals that most often need social support, and most often solicit it. Finally, we focused also on the responses of mothers to their infants' calls because they are the most natural source of social support in primates. Thus, of all possible social relationships, that between infants and their mothers
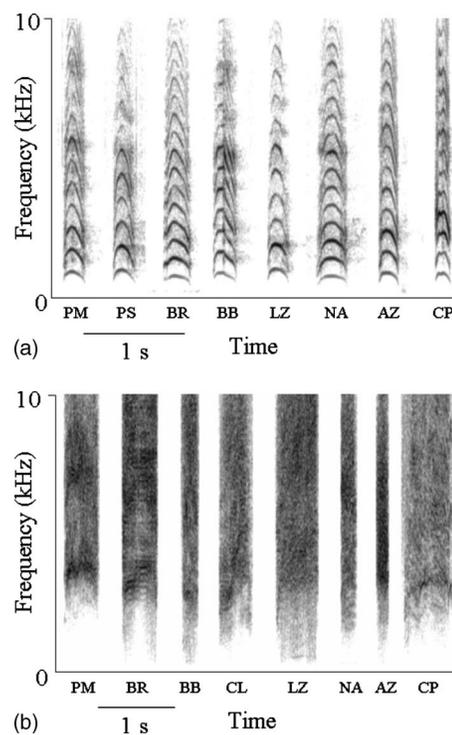

FIG. 1. Examples of contact calls (a) and distress screams (b) produced by infant baboons used in this study. Spectrograms were generated using a 1000-point FFT and a Gaussian window with 95% frame overlap.

was deemed the most likely to manifest unambiguous cues to identity in vocalizations and acute sensitivity to such cues.

The two contexts of vocalization chosen for study are common ones for baboons and most other social primates. The first involves situations in which individuals get physically separated from one another or the group at large. Such separation happens daily when the group is moving and foraging and group members invariably become widely dispersed, sometimes in dense habitats that preclude visual contact. For infants, it can also occur during group rest periods because infants often remain active playing with age mates. Sometimes they wander a considerable distance from their mothers and end up out of sight. In either situation, infants can become visibly agitated when they register the separation. They begin to scan their surroundings rapidly and repeatedly, sometimes climbing to an elevated position in a tree. Ultimately, they produce loud harmonically structured vocalizations in an attempt to relocate their mother [see Fig. 1(a)]. Adults produce calls of exactly analogous structure when they get separated from the group or from particular social companions (Cheney *et al.*, 1996). These adult calls appear to be individually distinctive and recognized by others, which are characteristics that would facilitate their presumed function of promoting contact and reunion with the group at large or with specific group members (Cheney *et al.*, 1996; Fischer *et al.*, 2001, 2002).

The second focal context involves aggressive conflicts, or fights, which occur commonly in the stratified social groups of baboons and other primates. For infants, such aggression occurs when play bouts escalate into more serious fights and when conflicts with peers or adults arise over access to food, water, or other valued resources. Especially dire

aggression can also occur when immigrant adult males try to injure or kill infants when left unprotected by their mothers (Palombit *et al.*, 2000). When attacked, the victims of aggression produce loud distress screams. These calls are among the most ubiquitous in primates, occurring in every species for which vocalizations have been described and, within species, in animals of every age and sex class (reviewed in Andrew, 1963; Gautier and Gautier, 1977; Marler and Tenaza, 1977; Oppenheimer, 1977). Screams can vary substantially in form, even within single bouts of calling, and can include broad-band noisy variants, pure-tone frequency-modulated variants, and various intermediate forms (Gouzoules and Gouzoules, 2000). However, the most common are the broad-band noisy variants [see Fig. 1(b)], which are also often the first and loudest screams produced when attacked. Research on species closely related to baboons suggests that noisy screams occur more commonly when aggression is most severe with the greatest risk of injury (Gouzoules *et al.*, 1984, 1986; Fugate *et al.*, 2008). These distress screams are proposed to function in recruiting intervention and support from mothers, collateral kin, or other social allies who might be out of sight but not earshot. This recruitment function is again thought to be facilitated by individually distinctive call structures which allow listeners to readily identify the caller and then to intervene or not based on their relationship to it (Gouzoules *et al.*, 1986; Gouzoules and Gouzoules, 1990; Fugate *et al.*, 2008).

Together, infant contact calls and distress screams constitute a productive comparison. Although they vary considerably in their detailed acoustic structure and mediate very different behavioral contexts, they are nevertheless structurally and functionally similar in being loud conspicuous calls that transmit considerable distances seemingly in the service of similar functional goals, namely, to capture the attention and recruit the support of mothers or other caregivers. Hence, both calling contexts place a selective premium on individually distinctive call structures that permit ready recognition and responding by mothers and potentially others. In the first part of this paper, we report acoustic analyses quantifying the degree of individual distinctiveness in these two call types. In the second part of this paper, we test maternal recognition of both call types.

II. INDIVIDUAL DISTINCTIVENESS IN INFANT CONTACT CALLS AND DISTRESS SCREAMS

A. Methods

1. Study site, subjects, and calling contexts

Research was conducted on free-ranging chacma baboons (*Papio hamadryas ursinus*) in the Moremi Game Reserve in northern Botswana, which lies within the Okavango Delta. The habitat is a mosaic of open grassy floodplains and wooded islands that rise a few meters above the floodplains. The subjects of research were the adult females and their immature offspring, from the main study group at this site (group C). At the time of research (February 1996–March 1997), this group contained approximately 75 individuals and had been studied continuously since 1977 (Cheney and Seyfarth, 2007). As a result, the animals were fully habitu-

ated to human observers and the social and genealogical history of natal animals was known.

For this project, research focused on immature baboons between the ages of 6–15 months. Baboons in this age range are socially immature and rely heavily on their mothers for social support and physical comforting. However, they are also motorically independent and thus often stray considerable distances from, and end up out of sight of, their mothers. It is during such absences from their mothers that young baboons are especially vulnerable to predators, and to aggression from others, including infanticidal attack. As a result, this context of visual separation between infants and their mothers defines a situation in which infants should be maximally motivated to provide unambiguous cues to identity in their contact calls or distress screams, and mothers in turn should be strongly motivated to detect and act on such cues. Our analyses were therefore limited to contact calls and distress screams produced in such contexts. For distress screams, we further limited our analyses to calls produced during aggressive attacks (from immature peers or adults) that involved direct physical contact that could potentially result in injury. These attacks are more serious than ones involving only threats and chases, and therefore they represent the aggressive context for which immature animals would benefit the most from agonistic support and to which mothers should be the most motivated to respond. During this study, no instances of infanticidal attacks were captured in vocal recordings or direct behavioral data collection. Hence, this most dire context of infant screaming is not included in analyses.

2. Vocalization recording

Infant contact calls and distress screams were recorded during the course of an ongoing regimen of behavioral sampling of mothers and their infants. Behavioral sampling involved collecting a continuous record of a focal animals' general activity state (e.g., resting, moving, and foraging), social behavior, and proximity to other group members. A variety of other spatial and ecological data were collected at the same time (for additional details, see Rendall *et al.*, 2000). In addition, a continuous record was made of all vocalizations produced and the ecological and social contexts associated with calling. Where possible, audio recordings were made of these vocalizations. Recordings were made using a Sony TC-D5M cassette tape recorder, a Sennheiser ME88 directional microphone with K3U powering module, and type-IV Sony metal cassette tapes. Because the baboons had been observed for decades and had been tape recorded by numerous previous investigators, the animals were accustomed to human observers and recording equipment. As a result, high-quality recordings could therefore be made at close range ($<$5 m).

3. The vocalization sample

To provide the most comparable and direct tests of individual differentiation in contact calls and distress screams, we attempted to create a completely balanced sample of the two call types as produced by the same set of individual

TABLE I. Summary of the vocalization sample.

Individual	Sex	Mother's rank[a]	Matriline[b]	Contact calls	Screams
Palm	F	1	1	26	21
Persephone	F	2	1	18	
Bart	M	4	2	59	19
Bilbo	M	5	2	16	34
Cleopatra	F	7	4		16
Lizzy	F	12	5	29	36
Nat	M	17	6	59	26
Amazon	F	21	7	17	20
CP	F	23	8	35	10
Total				259	182

[a]Total number of ranked adult females in group C=23.
[b]Total number of matrilines in group C=9.

infants. However, given the exigencies of fieldwork and inevitable variation in the number of recordings we had for different individuals, this was not entirely possible. Ultimately, we had a sufficient number of high-quality recordings of contact calls to permit statistical analysis for eight infants. For seven of these same infants, we had sufficient scream recordings as well. To avoid an unbalanced number of individuals in statistical tests of individual distinctiveness in the two call types, we therefore added to the scream sample an additional infant of similar age for which we also had sufficient recordings. The sample thus constituted consisted of 259 contact calls recorded from 91 different episodes of calling from eight infants, and 182 distress screams recorded from 40 different episodes of calling from eight infants, seven of which were identical to those in the contact call sample (see Table I). These infants provided broad sampling of mothers of varying social rank and representing several different martilines. They also included both male and female infants and included some variation in the age of individuals within the 6–15 month bracket. In this range, age and sex differences in call structure are probably minimal. Nevertheless, they represent additional potential sources for variation in call structure that, in the strictest sense, might not be attributable to individual identity *per se*. At the same time, they are additional relevant dimensions of callers in naturally constituted groups that, in practical terms, should help to facilitate their identification and recognition by others. Hence, we make no further attempt to control for or eliminate their effects, but instead fold them into the naturalistic problem of vocal identification and recognition.

4. Acoustic analysis

Vocal recordings were digitized at 44.1 kHz with 16 bit accuracy after lowpass filtering at 20.0 kHz, and acoustic analyses were performed using PRAAT 4.6 (Boersma, 2001). Analysis focused on acoustic features that could be measured from single vocalizations. Both contact calls and distress screams often occur in bouts in which single vocalizations are concatenated into longer series, and it is possible that additional identity cues might be carried in the more protracted temporal organization of call sequences. However, most previous analyses of these and similar call types in primates have omitted this more complex level of organization and focused instead on the structure of single vocalizations; hence, we chose to follow this precedent to improve the comparability of our results to previous work. Furthermore, it seemed reasonable to predict, *a priori*, that if conveying cues to identity to distant listeners were an important function of these two call types then a system in which those cues are carried within each of many repeated single vocalizations would be far more functional, efficient, and redundant than one in which identity cues emerge only if and after listeners can hear a complete sequence of calls.

Acoustic analysis of contact calls and distress screams involved three broad classes of variables addressing their temporal, spectral, and intensity characteristics. For both call types, we measured the duration of each call and the relative timing of the intensity peak within the call. Although contact calls and distress screams both had broad-band spectral structures, contact calls characteristically involved a relatively stable F_0 with multiple harmonic partials, while distress screams were predominantly harsh and noisy. Therefore, different variables were required to characterize the detailed spectral structure of each call type.

For contact calls, we made multiple measurements of the F_0 contour which often contained an appreciable chevron-shaped modulation over the course of a single call. We used PRAAT to extract the F_0 ("pitch") contour for each call and from this F_0 contour we retained as variables, its beginning frequency, ending frequency, maximum frequency, and mean frequency. We also measured the relative time of the maximum F_0 within the call and used this variable to derive measures of the beginning and ending slope of the F_0 contour. We characterized potential instabilities in the voicing associated with the F_0 of each call using a measure of vocal jitter that corrects for longer-term F_0 modulation (the PPQ5 algorithm in PRAAT) and using the harmonic-to-noise ratio (HNR). Finally, to characterize the broader spectral envelope of contact calls as described by their harmonic partials, we measured the amplitude of each harmonic (up to 6) from a single 2048–point (50 ms) fast-Fourier transform (FFT) straddling the midpoint of each call. Because all calls were recorded at close range (<5 m), these amplitude measurements were unlikely to be affected by variable spectral

transmission effects or variation in ambient environmental conditions. Nevertheless, as an additional precaution, we converted our absolute measurements into relative amplitude (RelAmp) values by subtracting the amplitude of each harmonic from the mean amplitude of all harmonics (including the focal harmonic) within a given call. The resulting Rel Amp values thus express the strength of a particular harmonic relative to the other harmonics in the same call.

Because screams lacked a stable F_0, we could not make the same F_0 and harmonic measurements for these calls. It was also the case that the patterning of diffuse noisy energy within screams could vary appreciably over the course of a single call which further complicated spectral analysis of these calls. Nevertheless, to try to capture the global spectral patterning of screams, we divided the frequency spectrum into a series of nonoverlapping 500 Hz frequency bins (up to 12 kHz) and measured the amplitude of the signal spectrum within each bin. We then converted these values to RelAmp values for each bin using the same procedure that was used to generate Rel Amp values for the contact calls and for the same precautionary reasons. The resulting relative amplitude values for screams thus express the strength of the vocal signal in a particular frequency bin relative to the other frequency bins in the same call. For screams, this procedure was conducted using a single long-term average spectrum computed for each call and resulted in a set of 24 Rel Amp values characterizing the global distribution of energy in these calls over the frequency range spanning $0-12$ kHz.

5. Statistical Analysis

We used multivariate discriminant analysis to evaluate individual differentiation in the structure of contact calls and screams. Because the results of such analyses can be dramatically influenced by the number of predictor variables used, we first conducted a principal components analysis (PCA) on the acoustic features measured for each call type. This preliminary step allowed us to examine natural covariation among the original acoustic features according to their associations within and between PCA factors. It also effectively reduced the number of predictor variables to be used in discriminant analysis to a small set of orthogonal multivariate dimensions that retained most of the variation in the entire set of original acoustic features. We then used the multivariate factors identified from PCA as variables in discriminant analysis of each call type. In evaluating successful call classification from discriminant analysis we followed a conservative split-sample approach (Klecka, 1980). For each call type, the sample was randomly divided in half. One-half of the cases was used as the reference sample to generate discriminant functions which were then applied to the other half of cases, the test sample. All statistics were conducted using NCSS version 5.1 (Hintze, 1999).

B. Results and discussion

1. Acoustic features of calls and possible production mechanisms

a. Contact calls. Summary statistics for the acoustic features of each call type are given in Table II. Contact calls were shorter, on average, than distress screams and were

TABLE II. Descriptive statistics for acoustic features of contact calls (a) and distress screams (b). The association of acoustic features with PCA factors and the significance (*) ($p < 0.001$) of those factors in discriminant analysis tests of individual differentiation are shown.

(a) Contact calls			
Variable	M	CV	PCA factors[a]
Duration (ms)	259	0.201	1
Intensity peak (as % duration)	46.3	0.305	2*, 3*
F_0-begin (Hz)	499	0.192	5*
F_0-end (Hz)	465	0.166	
F_0-maximum (Hz)	756	0.076	1
F_0-mean (Hz)	653	0.080	1
F_0-slope-begin (Hz/s)	2780	0.361	5*
F_0-slope-end (Hz/s)	1820	0.048	1
F_0-maximum (as % duration)	0.383	0.261	2*
Jitter (%)	0.034	0.179	
HNR (dB)	12.35	0.244	4*
H1 RelAmp (dB)	−8.85	0.118	1
H2 RelAmp (dB)	8.43	0.156	7*
H3 RelAmp (dB)	5.64	0.169	
H4 RelAmp (dB)	−1.03	0.141	
H5 RelAmp (dB)	−2.67	0.103	6*
H6 RelAmp (dB)	−1.52	0.108	4*
Overall mean		0.171	

(b) Distress screams			
Acoustic feature	M	CV	PCA factors[b]
Duration (ms)	351	0.810	4
Intensity peak (as % duration)	0.464	0.488	4
Percent voiced (%)	0.154	0.064	7
RelAmp 0–500 Hz (dB)	−11.25	0.561	2*
RelAmp 500–1000 Hz (dB)	−12.29	0.831	2*
RelAmp 1000–1500 Hz (dB)	−9.37	0.532	1, 2*
RelAmp 1500–2000 Hz (dB)	−4.61	0.322	1
RelAmp 2000–2500 Hz (dB)	1.35	0.232	1
RelAmp 2500–3000 Hz (dB)	8.22	0.193	1
RelAmp 3000–3500 Hz (dB)	9.38	0.197	1
RelAmp 3500–4000 Hz (dB)	7.32	0.173	1
RelAmp 4000–4500 Hz (dB)	5.85	0.184	1
RelAmp 4500–5000 Hz (dB)	5.91	0.182	1
RelAmp 5000–5500 Hz (dB)	6.13	0.172	1
RelAmp 5500–6000 Hz (dB)	6.28	0.162	1
RelAmp 6000–6500 Hz (dB)	6.05	0.156	2*, 3*
RelAmp 6500–7000 Hz (dB)	5.65	0.157	2*
RelAmp 7000–7500 Hz (dB)	4.74	0.172	2*
RelAmp 7500–8000 Hz (dB)	3.71	0.179	1, 2*
RelAmp 8000–8500 Hz (dB)	2.43	0.193	1
RelAmp 8500–9000 Hz (dB)	0.71	0.222	1
RelAmp 9000–9500 Hz (dB)	−1.72	0.265	1
RelAmp 9500–10 000 Hz (dB)	−4.06	0.321	1
RelAmp 10 000–10 500 Hz (dB)	−5.80	0.363	1
RelAmp 10 500–11 000 Hz (dB)	−7.06	0.369	1
RelAmp 11 000–11 500 Hz (dB)	−8.18	0.385	1
RelAmp 11 500–12 000 Hz (dB)	−9.40	0.423	1
Overall mean		0.308	

[a]PCA factor 8 was not associated with any single specific acoustic feature.
[b]PCA factors 5, 6, and 8 were not associated with any single specific acoustic features.

characterized by a relatively stable F_0 with relatively low jitter values and a very high mean HNR (12.35 dB) which represents an average HNR of 18:1. The F_0 contour of con-

tact calls showed a consistent rising and falling pattern with an average frequency excursion of approximately 150 Hz, starting from approximately 500 Hz and finishing slightly lower in frequency. Contact calls also showed a consistent pattern of harmonic emphasis in which the second and third harmonics were stronger than either the first harmonic (the F_0) or higher harmonics (H4–H6). This pattern of differential harmonic emphasis might be inherent to the laryngeal source spectrum. Alternatively, it might reflect some degree of supralaryngeal vocal-tract filtering.

Vocal-tract filtering effects have been shown to account for spectral patterning in similar harmonically rich grunt vocalizations produced by adult baboons (Owren *et al.*, 1997; Rendall, 2003) as well as in harmonically rich contact calls produced by closely related rhesus monkeys (Rendall *et al.*, 1998; Ghazanfar *et al.*, 2007). For baboons, the F_0 of adult grunts ranges between 50 and 120 Hz (for males and females, respectively: Owren *et al.*, 1997; Rendall *et al.*, 2004) and thus affords excellent harmonic sampling of vocal tract resonances which are prominent in the spectral structure of these calls. By comparison, the F_0 of infant baboon contact calls is quite high (500 Hz) and the consequently wide spacing of harmonics inherently affords much sparser sampling of vocal tract resonances, which might then argue against vocal-tract filtering effects accounting for differential harmonic emphasis in these calls. At the same time, infant baboons also have a relatively short vocal-tract compared to adults. Hence, it is possible that the second harmonic is emphasized in infant contact calls, relative to the F_0, because it coincides with the first resonance of their immature vocal tract.

We are not aware of any systematic data on vocal-tract length (VTL), and thus resonant frequency locations, in infant baboons that could be used to evaluate this possibility more directly. However, we can attempt some preliminary indirect assessment by evaluating the plausibility of the estimated (VTL) that would result from a first resonance peak coincident with the observed H2 harmonic emphasis. VTL can be estimated from resonance frequencies using the following equation: $VTL = (2k+1)c/4F$, where F is the formant (or resonant) frequency, k is the formant number minus 1, and c is the speed of sound in air (34 400 cm/s). We can then use H2 frequency values of 1000 and 1300 Hz to bracket the possible range of the putative first resonance based on values from Table II. The resulting estimates of VTL for this sample of infant baboons would be 6.6–8.6 cm. These values are approximately 1/3 to $\frac{1}{2}$ of VTL estimates for adult baboons (17–19 cm; see Owren *et al.*, 1997). Given the marked difference in overall body and head size between adults and infants in this age range, our estimated VTL for infants appears reasonable. However, without more systematic VTL measurements for both age classes, it remains speculative.

b. Distress screams. By comparison to contact calls, distress screams were approximately 40% longer in duration and were characterized by a predominantly aperiodic source with detectable voicing occurring in only 15% of analysis frames. The resulting noisy spectrum of screams was extremely broadband, with detectable energy extending up to and beyond 12 kHz. However, at this frequency and beyond, signal strength had fallen off appreciably. Within the range from 0 to 12 kHz, distress screams displayed some additional substructuring across individuals. Most calls showed relatively discrete attenuation of low-frequency components (0–2500 Hz) in addition to the inherent gradual attenuation of signal strength at higher frequencies (8500–12 000 Hz), which left a broadly emphasized region of the spectrum between 2500 and 8500 Hz. The bandwidth of emphasized frequencies within this broad region could vary somewhat between calls, and, on average, the region of greatest emphasis was between 2500 and 4000 Hz. However, in general, within the broader region between 2500 and 8500 Hz there was little obvious subpatterning.

It is difficult to evaluate the likely production mechanisms responsible for these patterns in screams. One possibility is that the excess attenuation of low-frequency components in distress screams reflects some vocal-tract filtering (antiresonances) of the aperiodic laryngeal source spectrum. However, if this were true, we would also expect to see some obvious peaks in the broader spectrum between 2500 and 8500 Hz reflecting vocal-tract resonances in that region that should have been well sampled by the strong aperiodic source. The alternative is that the relatively unstructured noisy spectrum of distress screams stems primarily from the laryngeal source and reflects extremely high-amplitude driving of the vocal folds inducing chaotic (or nearly chaotic) vocal-fold activity which has been shown in closely related species (Fitch *et al.*, 2002; Riede *et al.*, 2004, 2007; Tokuda *et al.*, 2002). The absence of low-frequency components in the source spectrum could then be a by-product of the extreme amplitude of the source which would naturally drive the vocal folds at higher frequencies. This effect, combined with the relatively short vocal folds of immature baboons which naturally limit low-frequency vibratory modes to begin with, could effectively eliminate most low-frequency energy in the calls.

Although the exact role that vocal-tract filtering may play in the observed spectral patterning of either call type remains uncertain, there was little indication that it acted within individuals to impart a common resonance pattern across the two call types (see Rendall *et al.*, 1998).

2. Individual variation in calls

Coefficients of variation (CVs) were calculated for each acoustic feature and for each individual, and grand means for these values are provided in Table II. These CVs quantify the relative stability of specific acoustic features within individuals and, as a result, are often taken as a preliminary metric of the potential for reliable identity signaling. The manifest variability in these CVs for both call types suggests that some features might prove better than others in this respect. Overall, CVs for the acoustic features of contact calls were lower and less variable than were those for distress screams (contact calls: mean CV=0.171, range=0.048–0.361; distress screams: mean CV=0.308, range=0.064–0.831), perhaps suggesting greater potential for reliable identity signaling in contact calls compared to screams.

a. Contact calls. PCA on the acoustic features of contact calls identified a set of eight orthogonal factors with eigenvalues greater than 1. Together, these factors accounted for 80.81% of the variation in contact calls encompassed by the original set of 17 acoustic features. For seven of the eight factors, one or more of the original acoustic features had a factor loading of 0.5 or higher and thus could be explanatorily linked to it (see Table II).

Discriminant analysis using PCA scores for these eight factors produced an overall Wilk's lambda of 0.063, which is very close to the lower limit of 0.0 for this test statistic (which would indicate perfect discrimination among groups) and represents a statistically significant degree of differentiation in call structure between individuals ($F = 15.8$, $P < 0.0001$). This analysis identified five statistically significant dimensions of discrimination among individuals which involved all but one of the PCA factors and encompassed a mix of original acoustic features related to intensity, the F_0 contour, and harmonic amplitudes (see Table II). Notably, these acoustic features were not necessarily those with the lowest CVs. Some acoustic features with low CVs (e.g., H2-RelAmp, H5-RelAmp, and H6-RelAmp) did help to differentiate individuals but some others with low CVs did not (e.g., F_0-mean, F_0-max). At the same time, some features with relatively high CVs nevertheless contributed to differentiating individuals (e.g., intensity peak, F_0-slope-begin). These outcomes indicate that, despite their regular reporting in this kind of research, CVs are a quite imperfect metric of individual differentiation probably because the relative stability of features within individuals says little about the potential variability in these features between individuals.

It is also noteworthy that the only PCA factor that did not contribute to individual differentiation in contact calls was the first factor, which accounted for more variation in contact calls (23.8%) than any other single factor from PCA and more than 25% of the variation in the calls that was explained by the entire set of eight factors. This outcome indicates that a considerable amount of the measured variability in contact calls is unrelated to individual identity. Nevertheless, discriminant functions successfully classified the majority of calls to the infant that produced them. Classification success for the full sample of 259 calls was 73.3% (range: 62.5%–86.2% for different individuals). Using the more conservative split-sample approach, classification success dropped marginally to 70.5% (range: 44.4%–86.0%), which represents a 66.0% reduction in the error that would accompany random classification of the calls. Figure 2 plots each call in a bivariate space captured by the first two canonical variates from discriminant analysis and illustrates the degree of multidimensional overlap and separation of individuals' calls.

b. Distress screams. PCA on the acoustic features of screams identified only five factors with eigenvalues greater than 1. Together, these factors accounted for 80.4% of the variation in these calls encompassed by the original set of 27 acoustic features. Compared to contact calls then, the measured variation in screams was packaged into fewer significant orthogonal dimensions. To maintain comparability in our analyses of the two call types, we nevertheless retained the first eight PCA factors for screams for use in discriminant analysis tests of individual differentiation in these calls. Together, this set of eight factors accounted for 89.1% of the measured variation in screams, which actually represented approximately 10% more of the variation in these calls than was used to test individual differentiation in contact calls. Once again, for several of these factors, one or more of the original acoustic features could be explanatorily linked to it (see Table II).

Discriminant analysis using PCA scores for these eight factors produced an overall Wilk's lambda of 0.195, which is higher than that obtained for contact calls and thus suggests less individual differentiation in the calls, but this
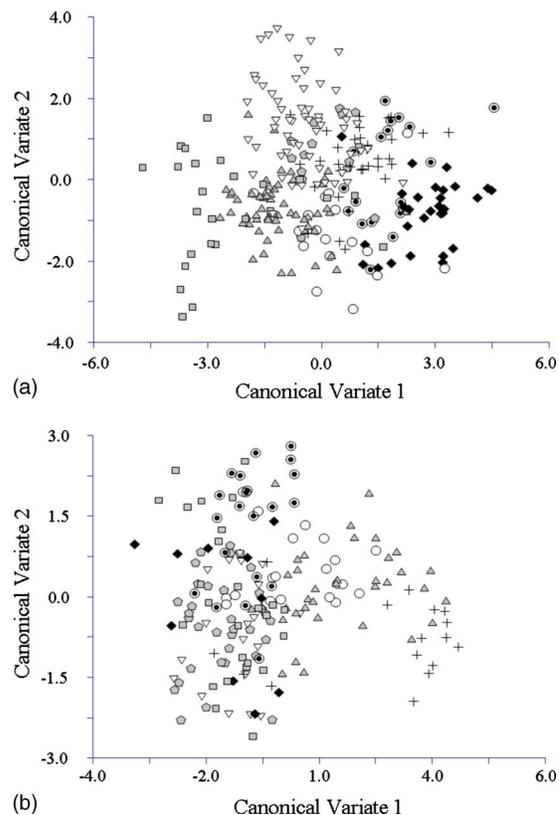

FIG. 2. (Color online) Scatterplots depicting each infant's contact calls (a) and distress screams (b) in the multidimensional space captured by the first two canonical variates from discriminant analysis tests of individual differentiation. Each individual is represented by a different symbol. The relative distinctiveness of individuals' calls is manifested in the degree of symbol separation and overlap.

value was nevertheless statistically significant ($F = 5.7$, $P < 0.0001$). Analysis of screams identified four statistically significant dimensions of discrimination among individuals which involved only five of the eight PCA factors and encompassed seven of the original acoustic features (see Table II). The original acoustic features contributing to individual differentiation in screams pertained only to the attenuated low-frequency spectral bins (0–1500 Hz) and a set of mid-frequency spectral bins (6000–8000 Hz). Once again, these acoustic features were characterized by some of the lowest CVs but also some of the highest CVs.

For screams it was also true that the first PCA factor did not contribute to individual differentiation in screams despite accounting for a substantial proportion of the measured variation in these calls (48.7%) and more than 50% of that encompassed by the entire set of eight PCA factors used for discriminant analysis. Three additional PCA factors (4, 5, and 7), accounting for an additional 12% of the measured variation in these calls, did not contribute to individual differentiation. Overall then, the majority of measured variation in distress screams is unrelated to individual identity. Despite this fact, discriminant functions applied to the full sample of 182 screams classified 45.1% to the infant that produced them (range: 30.0%–68.8%), and classification success using the more conservative split-sample approach was similar at 46.2% (range: 0.0%–75%). The latter classification success represents a 38.5% reduction in the error that would accompany random classification of the calls. These classification rates are substantially lower than those obtained for contact
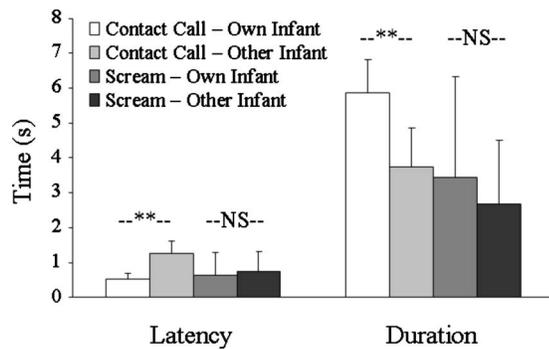
FIG. 3. Results of playback trials testing mothers' ability to discriminate the contact calls and distress screams of their own infant from those of a familiar but unrelated infant matched for age and sex. The data plotted represent the mean (+SEM) latency and duration of orienting responses by female baboons in the different experimental conditions. Females responded significantly faster and longer to contact calls in own than in other infant trials ($**P < 0.01$). Their responses to distress screams in own and other infant trials did not differ significantly (NS, $P > 0.05$). See text for test statistics.

calls, and this can be seen graphically in Fig. 3 where multidimensional overlap in individuals' calls is greater for screams than for contact calls. Nevertheless, the level of successful classification for screams was also appreciably above the simple theoretical chance threshold for this sample (12.5%).

Taken together, acoustic results suggest a potential for individual identity signaling in both call types consistent with the hypothesis that the functions of both call types include capturing the attention and soliciting support of some kind from specific other group members, in this case most likely from their mothers. The evidence suggests somewhat greater potential for this in contact calls than screams, but no firm conclusion can be drawn. Ultimately, how distinctive or not either call type is depends on the ability of others actually to discriminate among callers. And, here, it is quite possible that the differences identified in our acoustic analyses are not actually perceptible to mothers. It is also possible that there exist differences in one or both call types that are not captured by our acoustic analysis but that nevertheless facilitate recognition. Therefore, it is also critical to test maternal recognition of both call types.

III. MATERNAL RECOGNITION OF INFANT CONTACT CALLS AND DISTRESS SCREAMS

To test maternal recognition of infant contact calls and distress screams we undertook a naturalistic field playback experiment. The experiment involved playing back prerecorded calls to mothers in standardized contexts and measuring their responsiveness to those produced by their own infant versus those produced by another familiar but unrelated infant in the group matched for age and sex. The experiment was designed to match our acoustic analyses and therefore focused on maternal recognition of single contact calls and distress screams, rather than protracted bouts of either type.

A. Methods

1. Subjects

The subjects of experimental trials were the mothers of the same infants used in acoustic analyses, thereby providing the most direct test possible of the results of our acoustic

analyses of individual differentiation in these infants' calls. Limiting the experiment to only these females, however, would have yielded a precariously small experimental sample of only eight subjects for this test. Therefore, to increase the sample of subjects, the power of our test, and the potential generality of its findings, we included as subjects additional group females with infants of similar age to those used in acoustic analyses.

2. Experimental design

The experiment was conducted as a set of matched playback trials. For each call type, a given female was the subject of two trials: one trial involving the calls of her own infant ("own" infant trials) and the other trial involving the calls of a familiar, but unrelated, age- and sex-matched infant in the group ("other" infant trials). In each trial, the subject was played two different exemplars of the same call type (either contact calls or distress screams) produced by their own or another infant separated by a 1 s interval of silence. We played a pair of calls in each trial, rather than only a single vocalization, to reduce the chance that, given the exigencies of ambient noise and activity, subjects might not hear or register a single call. In effect then, the first of the two calls in a pair primed subjects for the second call, and the short interval between calls increased the likelihood that they could be coming from the same caller.

Specific vocalizations were chosen as stimuli for use in the experiment if they were of uniformly high quality, uncontaminated by background noise or other calling. The set of playback stimuli ultimately used in experiments consisted of 19 pairs of contact calls (38 different exemplars) originally recorded from 15 different infants and 14 pairs of distress screams (28 different exemplars) originally recorded from 13 different infants.

Following the logic of many similar studies testing vocal recognition abilities, we reasoned that if mothers could recognize the calls of their own infant and discriminate them from the calls of other infants in the group, then they should respond more strongly to their own infant's calls. Because social rank (particularly matrilineal rank in Old World monkeys) is an additional important dimension of primate sociality potentially affecting animals' responses to the vocalizations of others, trials were conducted to systematically control for the influence of this factor. Thus, in other infant trials, half the subjects were played the calls of an infant whose mother ranked above them in the hierarchy, and the other half were played the calls of an infant whose mother ranked below them in the hierarchy.

3. Playback trials

Playback trials were conducted during the course of focal observations on mothers as appropriate conditions arose. Hence, the choice of subject for any given trial was determined by the ongoing regimen of behavioral sampling (see Rendall *et al.*, 2000). Trials on the same mother were separated by several days. The order of own versus other infant trials was balanced across subjects. Trials were conducted only if the mother's infant (and, in the case of other infant

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trials, the unrelated infant whose calls were to be played) was some distance away and out of sight and could reasonably be located in the direction from which calls were to be played. Because mothers and their infants were frequently separated from one another, these conditions occurred regularly. Trials were also only conducted when the mothers were either resting, self-grooming, moving slowly on their own, or foraging in place and therefore were undistracted by other group members or their activities. Calls were played through a Nagra DSM loudspeaker positioned approximately 20 m from the subject in the direction from which the infant was last seen. The same speaker amplitude settings were used for all playback trials and were established during a pretesting period to naturally simulate a caller at approximately 50 m.

4. Maternal response assays

Playback trials were videotaped for later scoring. Response assays included (1) whether or not the subject actively attended to call playback as evidenced by deliberate head or body orientation in the direction of the speaker, (2) how rapid was the orientation (latency to orient), and (3) for what period of time it lasted (duration of orientation) in the 10 s immediately following stimulus presentation. In conducting trials, care was taken to ensure that subjects were facing away from the speaker prior to stimulus presentation so that changes in orientation toward the speaker after stimulus presentation could be evaluated unambiguously. In the few cases (four trials) where subjects were oriented in the direction of the speaker for a brief portion of the 10 s interval preceding stimulus presentation, the duration of this incidental orientation toward the speaker in the preplayback period was subtracted from the duration of the subjects' orientation in response to the calls in the postplayback period to arrive at a conservative measure of the subject's response. The latency and duration of subjects' orienting responses were calculated from the onset of the first call in each playback stimulus.

B. Results and discussion

In total, 14 mothers were tested in paired trials involving the contact calls of their own and another infant, and 13 mothers were tested in paired trials involving distress screams. In both cases, mothers were clearly interested in the calls and motivated to respond. They showed active orientation toward the playback speaker in 20 of the 28 trials (71.4%) involving contact calls and in 16 of the 26 trials (61.5%) involving distress screams, and in almost all cases immediately upon hearing the calls (Fig. 3). The average latency to respond to contact calls was 0.79 s [±0.21 s standard error of mean (SEM)] from the onset of the first call in the stimulus pair, while the average latency to respond to distress screams was 0.76 s (±0.21 s SEM). On average, then, females started responding $\frac{1}{4}$ of a second before hearing the second of the two calls in a stimulus pair. At times, females abruptly stopped their current activity (e.g., moving, foraging in place, and self-grooming) and craned their necks, or adjusted their whole posture, to look more directly in the direction of the simulated caller. In seven of the trials involv-

ing contact calls (five involving their own infant), mothers also either got up and moved some distance toward the speaker to investigate further or climbed to an elevated position in a tree or on a stump to scan the surroundings. Such additional behaviors were not observed in response to screams.

1. Maternal responses to contact calls

In the case of contact calls, females also showed clear discrimination between calls produced by their own and other infants. Females were more likely to orient toward the speaker in trials involving their own infants' calls, 13 of 14 females orienting to own infant trials compared to only 7 of 14 orienting in other infant trials (chi-square test: $\chi_1^2 = 6.30$, $P = 0.012$). They also responded significantly faster and longer to calls produced by their own infant than to those produced by other infants (Wilcoxon matched-pairs test: response latency, $Z = 2.83$, $P < 0.01$; response duration, $Z = 2.57$, $P < 0.01$).

2. Maternal responses to distress screams

In contrast, females' responses to distress screams provided comparatively little evidence that they discriminated between calls produced by their own and other infants. 10 of 13 females responded with deliberate orientation to the playback speaker in own infant trials and 6 of 13 also oriented in other infant trials. This difference suggests a similar tendency for mothers to respond preferentially to their own infants' screams but the difference was not statistically significant (chi-square test: $\chi_1^2 = 2.60$, $P = 0.11$). Similarly, females responded marginally faster and longer, on average, in own than other infant trials (Fig. 3) but here again the differences were not statistically significant (Wilcoxon matched-pairs test: response latency, $Z = 1.16$, $P = 0.12$; response duration, $Z = 1.36$, $P = 0.09$).

3. Effects of social rank

Neither set of outcomes proved to be influenced by the social rank of other infants. For contact calls, there appeared to be some tendency for females to differentiate among other infants. Thus, females oriented in five of seven trials involving other infants whose mother ranked higher than them in the social hierarchy compared to only two of seven trials involving other infants whose mother ranked lower in the social hierarchy. However, this difference was not statistically significant (chi-square test: $\chi_1^2 = 2.57$, $P = 0.11$). Furthermore, although females' responses to all other infants were markedly slower and shorter than they were to their own infants, they responded faster and marginally longer, on average, in other infant trials that involved infants with mothers of higher as opposed to lower maternal rank (latency: higher ranking mother, mean$=3.96 \pm 1.56$ s SEM; lower ranking mother, mean$=7.28 \pm 1.76$ s SEM; duration: higher ranking mother, mean$=2.01 \pm 0.91$ s SEM; lower ranking mother, mean$=1.75 \pm 1.26$ s SEM). However, here again, the differences were not statistically significant (latency: $Z = 0.96$, $P = 0.17$; duration: $Z = 0.82$, $P = 0.21$).

For distress screams, there were no similar hints of discrimination among other infants according to maternal social rank. Females oriented in an equal number of the trials involving other infants of either higher or lower maternal rank (three of seven trials in each case; chi-square test: $\chi_1^2 = 0.07$, $P = 0.80$). And their response latencies and durations to these two classes of other infant were nearly equal (latency: higher ranking mother, mean $= 5.34 \pm 2.09$ s SEM; lower ranking mother, mean $= 6.06 \pm 1.86$ s SEM; duration: higher ranking mother, mean $= 1.58 \pm 0.97$ s SEM; lower ranking mother, mean $= 0.93 \pm 0.48$ s SEM) and not significantly different (latency: $Z = -0.39$, $P = 0.35$; duration: $Z = 0.23$, $P = 0.41$).

4. Recognition asymmetries

Taken together, these results suggest that females can readily discriminate the contact calls of their own infant from those of other infants in the group, but that they cannot do so as clearly when it comes to distress screams. This perceptual outcome for contact calls corroborates the results of our acoustic analysis which indicated significant individual differentiation in the structure of these calls and good practical success in classifying calls to the correct infant. The perceptual outcome for distress screams is more difficult to reconcile. Acoustic analysis of these calls showed substantially lower levels of individual differentiation and successful classification than were observed for contact calls; however, statistically significant individual differentiation and moderate degrees of successful call classification were nevertheless observed for screams as well.

It is, of course, possible that females in our experiment were able to discriminate screams just as well as they did the contact calls but simply chose not to do so. It is, after all, notoriously difficult to definitively establish the lack of some kind of discriminative ability based on overt behavioral responses alone. At the same time, if females could discriminate both call types equally well, why would they have chosen to do so in trials involving contact calls but chosen not to do so in trials involving screams? This kind of motivational asymmetry is equally difficult to reconcile. Both call types mediate situations of some urgency to infants. Indeed, if anything, screams mediate contexts with more immediate dire consequences for infants (e.g., injury and infanticide). Furthermore, females' behavioral responses in experimental trials demonstrated a clear interest in both call types. They responded equally often in trials involving screams and their response latencies to screams were as fast, or faster, than they were to contact calls. Hence, the lack of clear discrimination of screams compared to contact calls is not easily explained by an asymmetry in their motivation to respond to the two call types.

Nor can it easily be accounted for by some kind of response (or motivational) ceiling in our playback trials that precluded detection of mothers' actual discrimination of the calls. Although females probably could not have responded much faster in scream trials, the 10 s postplayback analysis period certainly provided ample opportunity for them to respond for longer than they did. Indeed, in contact call trials, females responded for longer, on average, than they did in scream trials and, in the course of these more protracted responses to contact calls, showed their discrimination of calls produced by their own and other infants. The same opportunity was available for showing their ability to discriminate screams.

Ultimately, it seems that despite mediating contexts of similar need for infants and despite acoustic results indicating some individual differentiation in both call types, contact calls and distress screams differ in their effective discriminability.

IV. GENERAL DISCUSSION

A. Reconciling the recognition asymmetry

The apparent maternal asymmetry for recognizing infant contact calls and distress screams contradicts our initial predictions based on the proposed functions of these calls. At the same time, the asymmetry is not without precedent. The same asymmetry was found in analogous research on closely related rhesus monkeys (Rendall *et al.*, 1996, 1998). Like baboons, rhesus also produce harmonically rich contact calls, called "coos," during group progressions through dense vegetation where visibility is limited and also when individuals ultimately become physically separated from the group (Hauser, 1991; Rendall *et al.*, 1998). These calls, like the contact calls of baboons, are proposed to function in maintaining contact among group members and facilitating reunion of separated individuals. Rhesus monkeys also produce loud broad-band scream vocalizations when physically attacked (Rowell and Hinde, 1962; Gouzoules *et al.*, 1984). These calls are structurally similar to the noisy screams produced by baboons and are proposed to function similarly in recruiting support from kin and other social allies. Previous analyses by Rendall *et al.* (1998) showed that the contact calls (coos) and distress screams produced by adult female rhesus showed some degree of acoustic differentiation between individuals, but much greater individual distinctiveness in contact calls than screams. And, in playback experiments analogous to those conducted here with baboons, adult female rhesus readily differentiated contact calls produced by close female kin from those produced by familiar but unrelated adult females in the group, but they did not make the same distinction for those females' scream vocalizations (Rendall *et al.*, 1996, 1998; see Fig. 4).

Once again, the recognition asymmetry could not be attributed either to a motivational asymmetry or to some kind of response ceiling that might have precluded detection of the animals' discrimination of screams. Furthermore, follow-up perceptual experiments were conducted to test how well human listeners could discriminate identity in these two types of rhesus monkey calls (Owren and Rendall, 2003). Like the monkeys themselves, human listeners readily discriminated between callers' contact calls but fared much worse when the discrimination involved their screams. Similar results have been reported recently by Fugate *et al.* (2008) based on short bouts of screams.

Taken together, this corpus of work involving two closely related primate species is consistent in showing some greater capacity for discriminating individual identity from

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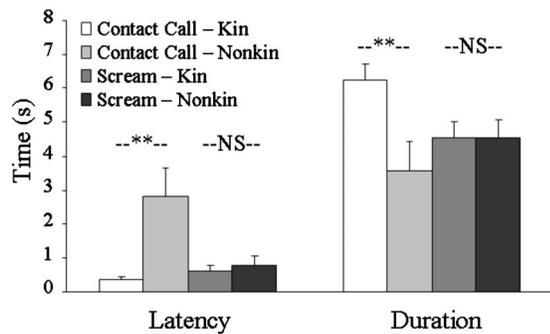Rendall *et al.*: Vocal cues to identity in baboons   1801

FIG. 4. Results of playback trials conducted previously on rhesus monkeys testing the ability of adult females to discriminate between the contact calls and distress screams of an adult female relative and a familiar but unrelated adult female in the group. The data plotted represent the mean (+SEM) latency and duration of orienting responses by adult females in the different experimental conditions. Females responded significantly faster and longer to the calls of their adult female relatives than they did to the calls of unrelated group females in the case of contact calls (**$P<0.01$) but not screams (NS, $P>0.05$). See Rendall *et al.* (1998) for details of test statistics. Figure redrawn from Rendall *et al.* (1998).

species' contact calls compared to distress screams. It is important to emphasize that this conclusion does not necessarily mean that scream vocalizations are not individually distinctive, or recognizable, at any level, and hence that they cannot serve to recruit support as originally proposed. Our acoustic analyses and playback experiments, for both baboons and rhesus monkeys, focused on single vocalizations, and, in many situations, contact calls and distress screams are produced in more protracted bouts. It is, therefore, possible that some additional cues to identity might be carried in the organization of these more protracted bouts of calling (see Cheney and Seyfarth, 1980, 1999; Seyfarth and Cheney, 1984; Gouzoules *et al.*, 1986; Fugate *et al.*, 2008).

Therefore, an important caveat on the recognition asymmetry reported here, and in previous work on rhesus monkeys, is that it might apply only to single vocalizations of each type. However, that point is potentially also extremely informative. The fact that single screams are not so readily identifiable whereas single contact calls are (as are single calls of other types in these same species; Cheney and Seyfarth, 1997; Owren *et al.*, 1997; Rendall *et al.*, 1999; Fischer *et al.*, 2002) strongly suggests that some other factor might be influencing the design of screams in ways that limit or constrain salient individual differentiation at this level.

B. Alternative functions of distress screams

Previously, Owren and Rendall (1997, 2001) and Rendall and Owren (2002) suggested that victims of attack might attempt to deter aggression directly by themselves in addition to indirectly by recruiting aid from allies. They argued that, on strictly functional grounds, it would certainly be more expeditious if victims could end attacks promptly themselves rather than having to wait for help from others to arrive. By definition, though, victims' capacity to resist or repel their opponents physically might be relatively limited, which is, after all, why they are the victims rather than the aggressors to begin with. Nevertheless, they might not be entirely impotent if they can make themselves unappealing
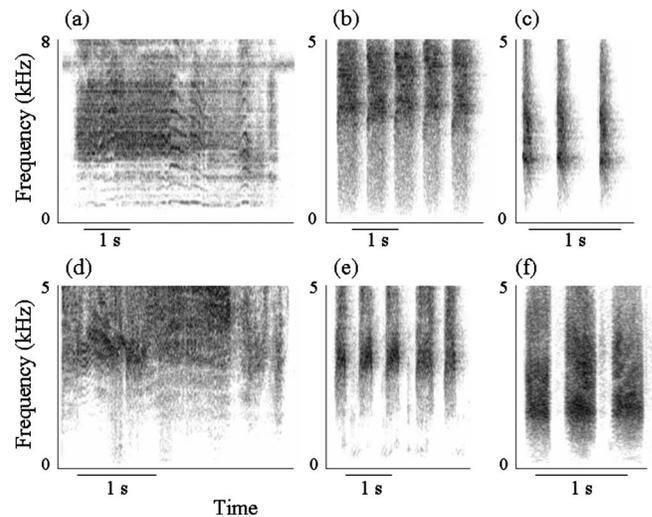

FIG. 5. Cross-species comparison of distress screams produced singly or in shout bouts of concatenated calls. Note the shared features of abrupt call onset and an extremely broad-band noisy spectral structure. The different species and contexts of call production are (a) a frog confronted by a predator, (b) a rabbit siezed by the mouth and then encircled by a constrictor snake, (c) a least weasel captured in the hand by the author (DR), and (d)–(f) infant baboons aggressively attacked by peers or adults.

targets of continued attack. Owren and Rendall (1997, 2001) thus proposed that the loud noisy screams produced by victims of attack might be designed in part to inhibit or attenuate aggression through the calls' aversive effects on opponents.

This kind of repellent function for scream-type vocalizations has seldom been explicitly considered for primates. However, it is an acknowledged function for vocal signals in a variety of nonprimate taxa. For example, various frogs, birds, and mammals are known to produce loud distress calls when captured by a predator. These calls are variously labeled "fear," "distress," "desperation," or "death" screams and they are thought to function as a last-ditch attempt to startle or repel the predator sufficiently that it hesitates for an instant, or releases its grip marginally, or even accidentally drops its victim, allowing some opportunity for escape (Driver and Humphries, 1969; Kruuk, 1972; Schaller, 1972; Conover and Perito, 1981; Gochfeld, 1981; Conover, 1994; Wise *et al.*, 1999). Although their detailed form can vary, they are commonly described as "sudden," "powerful," "high-intensity," and "piercing" calls (see Fig. 5 for several examples).

Owren and Rendall (1997, 2001) noted that primates' distress screams share these qualities as similarly powerful high-intensity signals (often the loudest calls in the vocal repertoire) with sudden (i.e., abrupt) call onsets and often chaotic (noisy) spectral structures, which give them a jarring, plosive, and grating quality commensurate with a similar kind of repellent function. In fact, comparative research indicates that these characteristics of screams are among those that best induce the acoustic startle reflex when experienced at close range (Davis, 1984; Eaton, 1984). This reflex has been demonstrated in a wide range of animal taxa (including monkeys and apes) and is thought to occur in every hearing species. It includes a cascade of behavioral and physiological

changes in listeners that involve the immediate cessation of ongoing activity and abrupt shifts in attention toward, and in movement away from, the stimulus; a host of reflexive autonomic changes, including heart rate and blood pressure changes, increased muscle tonus and stimulation of brainstem circuits that control overall brain activity and glucose metabolism (Davis, 1984; Eaton, 1984). Together, these changes represent a broad systemic reaction readying the listener for a "fight-or-flight" response. Inducing such effects, or anything even approximating them, could be quite aversive or repellent to listeners and thus highly functional to signalers in deterring aggression.

Even if primate distress screams have not been selected specifically to induce the startle reflex *per se*, the reflex confirms the degree to which signals can contact and influence listener nervous systems and automatic response processes at foundational levels, thereby potentially returning a degree of freedom to signalers in aggressive contexts where they might otherwise be relatively impotent.

Indeed, functional effects like these might not be uncommon as demonstrated by the widespread pattern of loud crying and screaming by young infants of many species, including humans and many nonhuman primates, when denied nursing access or other physical comforts or when otherwise subdued or frustrated in their goals (e.g., Grimm, 1967; Ostwald, 1972; Lester and Boukydis, 1985; Todt, 1988; Owren *et al.*, 1992; Hammerschmidt *et al.*, 1994; Appleby *et al.*, 1999; Patel and Owren, 2007). In these situations, young individuals who are otherwise impotent to exert their will on others resort to loud vocal protests. The acoustic structures of these protests are quite consistent across taxa and involve rapidly varying combinations of loud noisy screams and piercing high-frequency tonal cries, with dramatic amplitude and frequency modulations (Owren and Rendall, 2001; Owings and Zeifman, 2004). Everyday experience and systematic perceptual studies on humans confirm that such screaming is extremely grating and aversive to listeners and very effective in catalyzing responses from them (Zeskind and Lester, 1978; Lester and Boukydis, 1985; Bradley and Lang, 2000; Owings and Zeifman 2004; Patel and Owren, 2007).

There are few perceptual tests on nonhuman primates that directly test how aversive such scream-type vocalizations might be to them. Nevertheless, the broad structural similarity of scream-type vocalizations between humans and nonhuman primates and the fundamental similarity in the auditory systems and hearing abilities of the two groups (Hienz and Brady, 1988; Sommers *et al.*, 1992; Fichtel *et al.*, 2001; Fitch and Fritz, 2006; reviewed in Ghazanfar, 2002; Heffner, 2004) together suggest that scream-type calls could be as aversive to nonhuman primates as they are to human listeners.

This proposed additional repellent function of screams thus has considerable intuitive appeal and is consistent with a variety of comparative acoustic and perceptual research. It also helps to make sense of the otherwise puzzling fact that similarly structured scream-type vocalizations occur during aggressive conflicts in a wide range of other primate and nonprimate species whose social behavior seldom involves recruiting agonistic aid from others (Owings and Morton, 1998). In fact, such screams are produced in aggressive conflicts that occur in otherwise solitary species where there is not even the potential for recruiting such support (e.g., *primates*: Aye-aye, Stanger and Macedonia, 1994; *orangutan*, Marler and Tenaza, 1977; *rodents*: Haney and Miczek, 1993; *shrews*: Andrew, 1963). Hence, inhibiting attackers might well represent the original ancestral function of screams that has been elaborated subsequently to include recruiting agonistic support in social species where that potential exists.

The additional repellent function of screams compared to contact calls might also help to account for the observed recognition asymmetry in the two call types if the design requirements associated with one function for screams influence or constrain the design requirements of the other. Such signal-design tradeoffs in the face of competing signal functions are certainly well known from other species and from multiple signaling modalities, particularly in contexts where the signals involved can have multiple potential audiences (e.g., Cade, 1975; Tuttle and Ryan, 1981; Endler, 1988). In the case of distress screams then, it is possible that the noisy spectral structure of these calls makes them functionally aversive to opponents close at hand specifically because of their unpatterned quality, and this in turn precludes, by definition, any consistent patterning associated with carrying reliable identity cues to distant recruits. This possibility remains speculative, but it is an important signal-design issue to resolve. If there is not some additional function like this at work for screams, and vocalizing when attacked is therefore only an attempt to recruit support from distant others by conveying to them clear cues to caller identity, then why, in fact, do infants (and adults) actually scream in these circumstances? Why do they not instead produce other calls which are demonstrably more individually distinctive and recognized by others? For example, contact calls.

Ultimately, then, we tentatively suggest that individual contact calls and distress screams differ in their effective discriminability because they vary in the range of functions they have been selectively designed for. Agonistic screams may serve a repellent function in addition to a recruitment function, and the balance of these functional requirements appears to emphasize aversiveness at the level of individual scream calls and identity cueing potentially in features that emerge from the organization of more protracted sequences of calling. Contact calls appear not to be similarly constrained; hence, their structure is comparatively freed to promote individual differentiation and recognition of single vocalizations.

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