



The meaning and function of grunt variants in baboons

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Wild baboons, *Papio cynocephalus ursinus*, give tonal, harmonically rich vocalizations, termed grunts, in at least two distinct, behavioural contexts: when about to embark on a move across an open area ('move' grunts); and when approaching mothers and attempting to inspect or handle their young infants ('infant' grunts). Grunts in these two contexts elicit different responses from receivers and appear to be acoustically distinct (Owren et al. 1997, *Journal of the Acoustical Society of America*, **101**, 2951–2963). Differences in responses to grunts in the two contexts may, then, be due to acoustic differences, reflecting at least a rudimentary capacity for referential signalling. Alternatively, responses may differ simply due to differences in the contexts in which the grunts are being produced. We conducted playback experiments to test between these hypotheses. Experiments were designed to control systematically the effects of both context and acoustic features so as to evaluate the role of each in determining responses to grunts. In playback trials, subjects differentiated between putative move and infant grunts. Their responses based only on the acoustic features of grunts were functionally distinct and mirrored their behaviour to naturally occurring move and infant grunts. However, subjects' responses were in some cases also affected by the context in which grunts were presented, and by an interaction between the context and the acoustic features of the grunts. Furthermore, responses to grunts were affected by the relative rank difference between the caller and the subject. These results indicate that baboon grunts can function in rudimentary referential fashion, but that the context in which grunts are produced and the social identity of callers can also affect recipients' responses.

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Much research in animal communication is aimed at identifying the meaning and function of animal signals. Recent work in this area has been guided by two contrasting theoretical approaches, both of which assume that the meaning of signals, or the information they convey to a recipient, can be assessed by observing the recipient's response. One approach, which derives from the work of Smith (1977; see also Lancaster 1975), argues that species possess too few acoustically distinct signals and use them in too many different behavioural contexts for the array of possible meanings to derive from the structure of the signals themselves. Instead, differences in the meaning of signals (that is, in the responses they evoke) must derive from differences in the contexts in which they are produced. The signals themselves are likely to provide information only about the caller's internal state or probable future behaviour.

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In recent years this view has been challenged by a number of studies. For instance, systematic acoustic analyses of vocalizations in several primate species have revealed reliable acoustic variants in what seemed formerly to be unitary call types (e.g. Struhsaker 1967; Green 1975; Snowdon & Pola 1978; Gouzoules et al. 1984; Seyfarth & Cheney 1984; Seyfarth et al. 1994; Owren et al. 1997). Subsequent experiments have shown that such variants are, in some cases, salient to the animals (Zoloth et al. 1979; Seyfarth et al. 1980a, b; Gouzoules et al. 1984, 1986; Bauers & Snowdon 1990; Fischer et al. 1995; Fischer 1998; reviewed in Snowdon 1986; Hauser 1996), that is, they elicit consistently different responses despite variation in the contexts in which they occur. Differences in the meaning of these different calls therefore seem to depend upon subtle differences in their acoustic structure. Furthermore, studies of both birds and primates have confirmed that vocalizations like alarm calls, intergroup calls, food calls, and screams can provide information about objects or events external to the signaller, even in the absence of supporting contextual cues (e.g. Seyfarth et al. 1980a, b; Cheney & Seyfarth 1982; Gouzoules et al. 1984, 1986; Gyger et al. 1987; Macedonia

1990; Evans et al. 1993; Hauser & Marler 1993; Fischer 1998; reviewed in Macedonia & Evans 1993; Gouzoules et al. 1995; Hauser 1996).

These results suggest that at least some vocalizations function referentially in a fashion roughly analogous to the words of language, where call meaning derives primarily from acoustic properties of the signal itself and calls can function to denote objects or events external to the signaller, independently of supplemental contextual cues (Marler 1977, 1984, 1985; Seyfarth et al. 1980a, b). Of course, the conclusion that signals can denote external referents does not exclude the possibility that they also provide other types of information, for example, about the signaller's identity or emotional state (Smith 1981; Marler et al. 1992).

However, although referential signalling by nonhuman primates is now well documented in the case of discrete, conspicuous vocalizations like alarm calls and intergroup vocalizations, its existence in graded, intragroup calls is largely undocumented. This disparity may reflect a difference in meaning and function between the two sorts of calls. After all, both alarm calls and intergroup vocalizations are often given over long distances that limit or even preclude support from contextual cues, and they often occur in circumstances that require rapid, unambiguous, discrete responses. By contrast, within-group vocalizations typically occur during face-to-face interactions that are rich in contextual cues from both the environment and conspecifics, and in which the consequences for failing to respond in rapid, discrete fashion are less dire.

Alternatively, the disparity may simply reflect a difference in research effort. Because graded, intragroup calls are often quiet, difficult to tape-record, and elicit few overt responses, they have not been subject to the sort of detailed study or playback experimentation that has characterized alarm and intergroup vocalizations. Studying the intragroup calls of vervet monkeys, *Cercopithecus aethiops* Cheney & Seyfarth (1982; Seyfarth & Cheney 1984) found that the animals used acoustically different variants of a grunt vocalization in different behavioural contexts and that playback of these different call subtypes elicited different responses. However, the different responses were subtle and could be detected only by videotaped trials in the field (see also Snowdon & Hodun 1981; Gouzoules et al. 1984; Bauers & Snowdon 1990).

We report the results of playback experiments designed to evaluate the relative roles of context and acoustic features in determining the meaning and function of baboon grunts. Baboon grunts are relatively quiet, intragroup calls used in a variety of circumstances (Cheney et al. 1995a; Silk et al. 1996; Cheney & Seyfarth 1997). The two most common and distinct contexts in which grunts occur are: (1) at the onset of a concerted move across an open area; and (2) during social approaches, especially by females to mothers with young infants. Grunts in the move context are sometimes 'answered', that is, followed quickly by grunts from others nearby. Often, individuals will also glance up in response to grunts in a move context, and look in the direction of the open terrain to be crossed. In contrast, grunts in the context of social

approach are seldom 'answered', but individuals will often look towards the caller. These observations suggest that, although grunts in these two contexts sound alike to human listeners, the baboons themselves may perceive them to be two distinct calls.

Grunts also occur in other circumstances, such as in the context of reconciliation (Cheney et al. 1995a; Silk et al. 1996). Preliminary analysis suggests that grunts given in this context are acoustically similar to those given during social approaches (R. M. Seyfarth & D. L. Cheney, unpublished data). However, grunts given during reconciliation are relatively uncommon and harder to tape-record than those given in the context of social approaches. Therefore, we focus here only on grunts given prior to group movements and during social approaches and for ease of discussion refer to these grunts as 'move' and 'infant' grunts, respectively.

To test whether move and infant grunts might in fact be different signals, Owren et al. (1997) analysed the acoustic properties of 216 grunts tape-recorded from nine adult female baboons in the study population. Baboon grunts are tonal, harmonically rich calls, with prominent vocal tract resonances (formants). Figure 1 illustrates a representative grunt of each subtype from the same individual. Owren et al. found clear differences among individuals in formant patterns. They also found evidence of a consistent difference in the spectral structure of grunts used in the two contexts. Move and infant grunts differed most consistently in the overall slope of their amplitude spectra primarily due to differences in the relative amplitudes of the first two formants (F1 and F2). In move grunts, the amplitude of the first formant (F1a) was low relative to that of the second formant (F2a), such that the amplitude difference between them (i.e. $F1a - F2a$) was small or negative (see Fig. 1). Infant grunts were characterized by a high F1 amplitude, such that $F1a - F2a$ was large and positive (Owren et al. 1997).

One hypothesis, then, argues that move and infant grunts elicit different responses because they are acoustically distinct signals that provide different sorts of information to those nearby. Alternatively, differences in response may occur simply due to differences in the contexts in which the grunts are being produced. To investigate these alternatives, we conducted a series of playback experiments designed to control systematically for the effects of both context and acoustic features. In addition, because of the pervasive effect of social status on interactions among adult female baboons (Altmann 1980), we designed trials to test the hypothesis that responses to grunts differ depending upon the rank difference between callers and recipients.

METHODS

Study Site and Subjects

Research was conducted on baboons, *Papio cynocephalus ursinus*, in the Moremi Game Reserve of northern Botswana. The reserve is situated at the southern end of the Okavango Delta, a vast wetlands created by seasonal flooding of the Okavango River. The habitat is a mixture

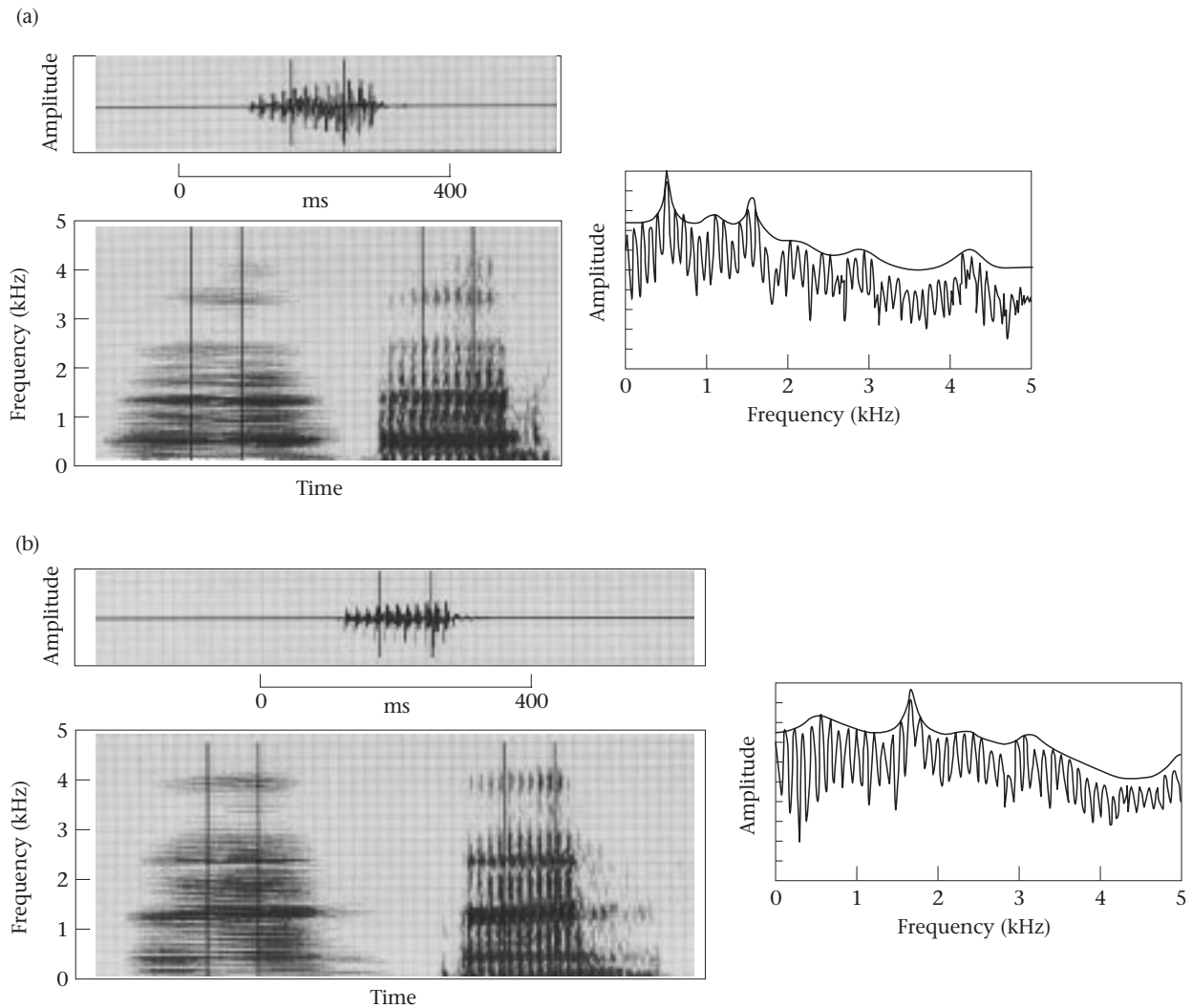


Figure 1. (a) Infant and (b) move grunts from the same adult female baboon (LX). Each grunt is represented by its waveform, a narrowband (21 Hz) and a wideband (300 Hz) spectrogram, and a spectral display comprised of a 512-point fast Fourier transform (FFT) and an overlaid, but independently derived, linear predictive coding (LPC) smoothed spectral envelope. Vertical markers in the waveform and spectrogram displays denote the segment from which FFT and LPC spectra were generated. Broad peaks in the LPC spectra indicate the location of vocal tract resonances (i.e. formants). Note that the relative amplitudes of the first two formant peaks are very different for the calls in (a) and (b). In (a), the amplitude of F1 is high relative to that of F2, while the opposite is true in (b). (See Methods and [Owren et al. 1997](#) for additional details of LPC analysis.)

of grassy floodplains, termed melapos, punctuated by numerous wooded 'islands' of varying size that rise a few metres above the melapos. In years of heavy flooding these wooded areas become islands completely surrounded by water. However, for most of this study, the area was dry and the 'islands' were therefore surrounded by open melapo.

Baboons at this site have been studied since 1977 ([Busse & Hamilton 1981](#); [Bulger & Hamilton 1988](#); [Hamilton & Bulger 1992](#); [Cheney et al. 1995a, b](#); [Silk et al. 1996](#); [Palombit et al. 1997](#)). Hence, they are fully habituated to human observers and individuals can be readily identified. The matrilineal relatedness of all natal animals is known. Subjects were the 22 adult females of a group that numbered approximately 75 individuals at the time of the study (February 1996–March 1997). Adult females

could be ranked in a stable, linear dominance hierarchy that, as in other studies of baboons, accurately predicted the direction of approach–retreat interactions.

General Experimental Design

First, during the course of behavioural observations, we recorded grunts from numerous individuals in the move and infant contexts. These recordings were then digitized and subjected to spectral analysis to select as playback stimuli calls that best exemplified the two putative grunt subtypes established previously by [Owren et al. \(1997\)](#). Finally, over the course of several months, we played back stimuli of each subtype to subjects in two distinct experimental contexts (described below). Hence, each subject heard grunts of both putative subtypes from the same

caller in each of two contexts. To investigate the potential effects of social dominance, the relative rank difference between caller and subject was controlled within, and manipulated between, subjects. Thus, individual subjects heard grunts from the same stimulus female across all four experimental conditions, with roughly half of the subjects hearing the grunts of a female that was dominant to them in the social hierarchy, and the other half hearing the grunts of a female subordinate to them.

Behavioural Observation and Vocal Recording

Typically, we located the group at 0600–0700 hours as the baboons left their sleeping trees, and we followed them for 5–7 h each day. We gathered behavioural data on the 22 adult females during 1-h focal samples (Altmann 1974), yielding a total of 734 h of data. The order in which females were sampled was randomized. Two observers collected data simultaneously, one gathering data on general activity state (e.g. feeding, foraging, moving, resting) and social behaviour, and the other making audio recordings of vocalizations, particularly grunts. Recordings were made on Sony type IV metal tapes using a Sony WM-D6C Professional Walkman cassette recorder and a Sennheiser ME 80 directional microphone with K3U power module. Because the baboons were well habituated to researchers and their equipment, recordings were readily made at close range (0.5–1.0 m).

Playback Stimulus Selection

As noted earlier, previous analysis indicated that putative move and infant grunts differed acoustically in the relative amplitudes of the first two formants (the variable F1a–F2a). To select stimuli for playback experiments, we first selected only those grunts recorded from adult females in the two unambiguous social contexts, move and infant. From this sample, we selected calls from the top and bottom 10% of the distribution of F1a–F2a values. In this way, we selected as playback stimuli putative move and infant grunts that were maximally different from one another on the F1a–F2a dimension. The F1a–F2a cut-offs for this selection were +17.8 and –6.3 dB, respectively.

The acoustic analysis used in stimulus selection was performed in the field using a Toshiba 2130 CS laptop computer and the CSRE version 4.5 software package (AVAAZ Innovations 1995). F1 and F2 amplitude differences were measured from smoothed spectral envelopes derived from autocorrelation-based linear predictive coding (LPC) as described by Owren & Bernacki (1998). LPC spectra were generated from a 512-point (46.5-ms) segment from the midpoint of each grunt using a Hanning window, 15 coefficients and no pre-emphasis (see Fig. 1 for LPC spectra of move and infant grunts). For this analysis, grunts were low-pass filtered at 4.8 kHz and sampled at 10.0 kHz.

Playback stimuli were constructed using two different grunts of the same putative subtype from the same female

separated by an interval of 860 ms of silence. This interval represented the mean intergrunt interval in our sample of two-grunt bouts of both move and infant grunts. We used a sequence of two grunts for all playback trials for two reasons. First, previous observations indicated that naturally occurring move grunts are typically given in bouts of one to four calls (mean=2.34, $N=9$ adult females), whereas infant grunts are given in longer bouts of two to eight, or more (mean=6.41; Owren et al. 1997). Thus a playback bout of two calls, while more representative of move than infant grunts, would not be unusual in either case, and allowed us to control for bout length across context and putative grunt subtype. Clearly, preserving the natural differences in bout length between move and infant grunts, and thus playing move grunts in short bouts and infant grunts in longer bouts, would have seriously biased the cues to grunt type available from bout length, and so compromised any test of the effects of differences in the acoustic structure of the two grunt subtypes. Second, by presenting two calls instead of a single vocalization, we decreased the chance that subjects might miss the stimulus, for instance due to attending to other activities, or due to ambient noise during a trial.

Our stimulus set for experiments comprised 14 pairs of matched move and infant grunts (i.e. 28 two-grunt sequences constructed from 56 different grunts) that had originally been recorded from 11 different adult females. Three females contributed two sets of matched move and infant grunts. Playback stimuli were assembled using the Canary version 1.2.1 software package (Charif et al. 1995) on a Macintosh Powerbook 520C laptop computer. Grunt stimuli were digitized with 16-bit accuracy from audiotapes by low-pass filtering at 10.0 kHz and sampling at 22.05 kHz. Stimuli were then rerecorded on Sony type IV metal tapes for use in experiments.

Experimental Contexts

We conducted playback trials in two distinct contexts, 'move' and 'rest'. We chose these two contexts for two reasons: first, to preserve the natural circumstances associated with the production of move and infant grunts, while providing clearly distinct contextual cues to grunt meaning; and second, so that the context of each trial could be clearly specified. The move context was defined as occurring whenever the group gathered at the edge of an island and paused prior to crossing an open melapo to another island. At such times, animals generally sat calmly or foraged in place, periodically looking out over the melapo while intermittently grunting. The rest context was defined as occurring whenever the group had been relatively inactive for at least 30-min in a location away from the edge of an island. Typically, this situation arose when the group converged on a shady site in the middle of an island to sleep, groom, or engage in other social activities for an extended period. During these rest periods, social approaches involving putative infant grunts occurred at high rates.

It is important to note that, although the move and rest contexts were clearly differentiated, grunts of either

putative subtype might be heard occasionally in either context. It was not unusual, for example, for one female to approach a mother with an infant and grunt to her while the group was on a move, nor was it unusual for a female to utter a move grunt when a rest period was drawing to a close but the group was still clearly resting. Thus, grunts of both putative subtypes could potentially occur in both experimental contexts, and our playback trials, therefore, did not involve anomalous call presentations.

Playback Protocol

We conducted playback trials opportunistically whenever the appropriate experimental contexts arose during the 1-h sampling sessions. Hence, the ongoing sampling regimen determined the subject being tested on any given trial. The particular calls played were, on each subject's first trial, governed by two factors. First, the animal whose calls were to be played had to be unrelated to the subject. Second, this animal also had to be out of sight of the subject and plausibly located in the area from which the calls were to be played. On all subsequent trials involving that particular subject, we used sounds from the same calling animal. Each subject heard the same set of move grunts and infant grunts in both the move and rest contexts.

In conducting trials, one observer videotaped the subject while the other prepared the playback stimulus and concealed a Nagra DSM loudspeaker in dense vegetation near the subject ($\bar{X} \pm SD$ subject–speaker distance = 15.1 ± 3.81 m). Videotaping began 1 min before stimulus presentation and continued for at least 1 min afterward. Trials were conducted only if subjects were sitting or foraging calmly with no other adult within 5 m, and were not conducted on oestrous females. Following each playback, we made a sketch of the area noting the positions of the subject, the speaker, the videocamera, various landscape features, and other animals in the vicinity. We timed stimulus presentation so as to ensure that neither the subject nor others in the vicinity had grunted in the preceding 30 s. If any of these conditions was not met, the trial was aborted before playback occurred.

Response Measures and Predictions

Response scores were of two types. First, because our observations suggested that baboons sometimes 'answer' move grunts but not infant grunts, we noted whether or not subjects produced a grunt of their own within 10 s of stimulus presentation. Second, given the observed differences in orienting responses to naturally occurring grunts in the two contexts (see Introduction), we also included three orienting response measures. These were the direction of the subject's orienting response, defined as a change in the subject's orientation within 10 s of stimulus presentation to either the speaker or the melapo, as well as the latency and duration of such movements. Because subjects could conceivably orient in the direction of both the melapo and the speaker (in either order) in

the 10-s interval following stimulus presentation, we scored only the direction of their first orienting response. We predicted that the subjects that interpreted grunts as pertaining to a group move (whether due to context or acoustics) were likely to grunt, look to the melapo (i.e. the direction of a move), or both. In contrast, subjects that interpreted grunts as pertaining to a social approach were unlikely to grunt but would orient to the speaker (i.e. the direction of the 'caller').

To facilitate evaluation of orienting responses, in each playback trial we placed the speaker in a direction that was, relative to the subject, away from the melapo (and thus the direction of a potential move), and waited until the subject was looking at neither speaker nor melapo before presenting the playback stimulus. In this way, we could unambiguously assign changes in the subjects resulting gaze direction as being either towards the melapo, towards the speaker, or neither. In most cases, the direction of the melapo was simply the direction of the nearest melapo/island edge border. In a few trials that were conducted on larger islands, the direction of the melapo was the direction in which the group habitually moved when leaving the area en route to a more distant melapo/island edge border. We scored responses using a frame-by-frame analysis of the videotape records at 30 frames/s (Panasonic AF-DS540 Hi-Fi VCR, Panasonic AG-A350P editing controller, and Sony KV-20S30 video monitor). We scored trials without information about the grunt subtype presented or the identity of the animal whose calls were played. All response measures were made starting from the onset of the first grunt in the two-grunt stimulus sequence. Because the two grunts in each experimental stimulus were separated by an interval of 860 ms, subjects effectively had 9 s to respond after hearing the second call. Statistical analyses were conducted using SYSTAT, version 5.0 (Wilkinson 1992) and the Number Cruncher Statistical System, version 5.01 (Hintze 1987).

RESULTS

In total, 122 trials were conducted on the 22 adult female subjects. The resulting data set included 19 cases in which all four experimental conditions were filled for a given subject, yielding a total of 76 trials. These complete series involved 17 different female subjects. Two females experienced two complete series each, in both cases hearing the grunts of a different female in the two sets of trials. The balance of trials ($N=46$) consisted of a variable number of the four experimental conditions completed on the remaining females. Trials were split roughly evenly by grunt subtype (move: $N=59$; infant: $N=63$), context (move: $N=67$; rest: $N=55$), and dominance status of the stimulus animal relative to that of the subject (dominant: $N=69$; subordinate: $N=53$). An analysis of the effects of seven potentially confounding variables on the various measures of response yielded no significant results (Table 1). Furthermore, there was no indication that our use of a bout of two grunts in these experiments predisposed subjects to interpret calls as pertaining to a group move

Table 1. Analysis of the effects of seven potentially confounding variables on two dichotomous and two continuous measures of subject response in playback experiments

Variable	Grunt response (yes/no)*		Orient response (speaker/melapo)*		Latency to orient (s)†		Duration of orient (s)†	
	χ^2	<i>P</i>	χ^2	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Subject's activity before playback trial (feed, move, rest, groom)	0.12	0.726	1.72	0.190	-1.15	0.253	-1.31	0.196
Source amplitude of playback stimulus (root mean square amplitude)	2.30	0.130	1.17	0.279	-1.25	0.215	-1.90	0.063
Habitat type for playback trial (four categories of habitat visibility)	0.86	0.354	0.32	0.574	-0.55	0.584	-1.05	0.300
Subject-speaker distance (metres)	0.36	0.550	0.17	0.678	1.29	0.201	0.85	0.401
Speaker position relative to subject (left, right, in front, behind)	0.08	0.771	0.35	0.555	-0.29	0.771	1.13	0.262
Day during study (1-379)	0.00	0.987	0.05	0.819	1.30	0.200	-0.33	0.746
Time of day (0600-1800 hours)	0.05	0.823	0.15	0.700	-0.69	0.492	0.89	0.376

*Dichotomous response variables analysed using logistic regression.

†Continuous response variables analysed using multiple regression.

and thus to orient preferentially in the direction of the melapo (see below).

Grunt Responses

Grunt responses were not evenly distributed among the four experimental conditions (Table 2; multiway frequency analysis for overall effect: $G^2=97.60$, $N=121$ trials, $P<0.001$), a result attributable to the effect of both grunt subtype and context. Grunt responses occurred more frequently than expected when the playback stimulus was a move grunt than when it was an infant grunt (chi-square test: $\chi^2_1=4.62$, $P<0.05$), and were more likely in the move than in the rest context ($\chi^2_1=11.74$, $P<0.001$). There was also an interaction between grunt subtype and context, with the majority of 'answering' grunts occurring in response to move grunts when presented in a move context (Table 2). However, the sample of grunt responses was too small to permit statistical evaluation of this interaction. There was no effect of social dominance (i.e. the relative rank difference between stimulus and

subject animals) on the probability of responding with a grunt (chi-square test: $\chi^2_1=1.28$, NS).

Orienting Responses

Of the 122 trials, 70 elicited an orienting response. The probability of showing any orienting response, whether to the speaker or to the melapo, was unaffected by either grunt subtype (chi-square test: $\chi^2_1=0.62$, $N=122$ trials, NS) or context ($\chi^2_1=2.81$, NS), but was influenced by the relative dominance ranks of caller and subject ($\chi^2_1=8.64$, $P<0.01$). Subordinate subjects hearing the grunts of a dominant were more likely to respond with some orienting response, while dominant subjects hearing the grunts of a subordinate female were more likely to show no response. Within rank classes, the probability of orienting was unaffected by the absolute rank difference between subject and caller (Mann-Whitney *U* test: caller dominant to subject: $U=444$, $N=69$ trials, NS; caller subordinate to subject: $U=371.5$, $N=53$ trials, NS).

Orienting responses to the speaker and melapo were not evenly distributed among the four experimental conditions (Fig. 2; multiway frequency analysis for overall effect: $G^2_{11}=25.80$, $N=122$ trials, $P<0.01$). Differences in orienting responses were influenced by all three factors: grunt subtype, context and social dominance. Across dominant and subordinate subjects, females were more likely to look to the melapo in response to move grunts and to look to the speaker in response to infant grunts (chi-square test: $\chi^2_1=5.93$, $N=122$, $P<0.05$), and more likely to look to the melapo in a move context and to look to the speaker in a rest context ($\chi^2_1=8.67$, $P<0.01$). Multiway frequency analysis (Tabachnick & Fidell 1989) revealed an interaction between grunt subtype and context (SYSTAT log-linear model: $\chi^2_1=20.12$, $P<0.01$). In other words, subjects were most likely to look towards the melapo when move grunts were presented in a move

Table 2. Grunt responses (yes/no) as a function of the grunt subtype played (move grunts/infant grunts) and the playback context (move/rest)

Context	Grunt responses to			
	Move grunts		Infant grunts	
	Yes	No	Yes	No
Move	10	23	3	31
Rest	0	26	0	28

During one trial, the subject grunted to a young infant that approached her shortly after the playback stimulus was presented. This trial was excluded from analyses of grunt responses leaving the sample of 121 trials presented in this table.

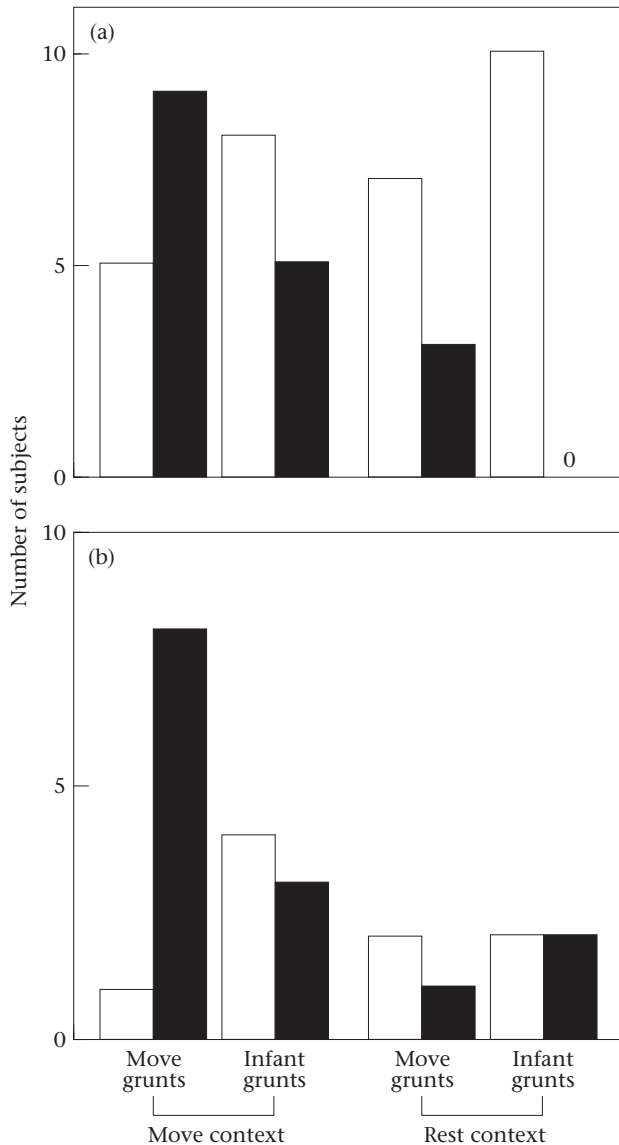


Figure 2. The number of subjects orienting towards either the speaker (□: the simulated caller) or the melapo (■: the direction of a move) in response to move grunts or infant grunts presented in a move or rest context. Trials in which subjects did not orient to either the speaker or the melapo have been excluded. The data have been partitioned for purposes of presentation according to the relative rank difference between the caller and the subject. (a) Caller dominant to subject; (b) caller subordinate to subject.

context, and similarly to look towards the speaker when infant grunts were presented in a rest context. Thus, orienting responses were most distinct when the grunt subtype and the context were consonant. In addition, subjects' orienting responses were affected by the relative rank difference between themselves and the simulated caller. Across contexts and grunt subtypes, subjects were more likely to look to the speaker when the grunts of individuals dominant to themselves were played (chi-square test: $\chi^2_1=3.82$, $P=0.0507$). This tendency was not affected by the absolute rank difference between subject

and caller (Mann-Whitney U test: caller dominant to subject: $U=225$; $N=47$ trials, NS).

Latency and Duration of Orienting Responses

Neither the latency nor the duration of orienting responses varied as a function of any of the three main factors. However, orienting latencies and durations did vary as a function of whether the subject oriented to the speaker or to the melapo. The mean \pm SE latency of orientation to the speaker was 1.93 ± 0.40 s, while that to the melapo was 3.50 ± 0.48 s (Mann-Whitney U test: $U=850$, $N=70$ trials, $P<0.01$). The mean \pm SE duration of orientation to the speaker was 1.63 ± 0.17 s, while that to the melapo was 2.68 ± 0.38 s ($U=780$, $P<0.05$). Thus, animals oriented faster to the speaker but looked for a shorter time, whereas they oriented more slowly to the melapo but looked for a longer time.

DISCUSSION

Results from playback experiments indicated that the two grunt subtypes given by baboons elicited functionally distinct responses from listeners that were appropriate to the referent of each call. Subjects were more likely to grunt and look towards the melapo (i.e. the direction of a move) when played move grunts and more likely to remain silent and look towards the speaker (i.e. the direction of the caller) when played infant grunts. Moreover, orienting responses towards the melapo were slower and more protracted than were those towards the speaker. The responses elicited by playback experiments mirrored those given in response to naturally occurring grunts and support the hypothesis that the different grunts convey different sorts of information to those nearby. Because this information can concern events that are external to the signaller (e.g. the onset of group movement), we suggest that baboon grunts have a rudimentary referential function.

This hypothesis is, however, subject to several important caveats. Although baboons discriminated between grunts with different acoustic features, their responses were also affected by context. While listeners responded differently to move and infant grunts when they were presented in a move context, they did not do so when the grunts were presented in a rest context. Irrespective of the grunt subtype played, subjects in this context typically showed no response at all or simply oriented towards the speaker; they never responded with 'answering' grunts. Similarly, when played infant grunts in the move context, several subjects oriented towards the melapo rather than the speaker. Finally, although move grunts, but seldom infant grunts, elicited grunts from listeners, they did so only in the move context.

There are several possible explanations for these patterns. For example, contextual cues may have served to 'prime' listeners' expectations and response tendencies. In this case, subjects in the rest context may have oriented preferentially to the speaker irrespective of the grunt subtype played because, given the low probability

of a move, they expected whatever grunts they heard to pertain to a social approach. However, it is also possible that the subjects discriminated between move and infant grunts in the rest context, just as they did in the move context, but that when the probability of a move was low they looked to the caller for additional information. Our data simply do not allow us to distinguish between these alternatives.

Furthermore, while our results suggest a role for context in influencing listeners' responses to grunt subtypes, they do not allow us to specify the precise nature of the contextual cues involved. In our experiments, we attempted to control for contextual cues associated both with local environmental conditions and with the general activity of conspecifics. As a result, the relative roles of environmental and social conditions in contributing to observed contextual effects remain to be determined.

Most conservatively, then, we conclude that context and the acoustic features of grunts can both affect subjects' responses. Because the acoustic features alone permitted accurate inferences about external events at least in the move context, grunts can be considered functionally referential according to current formulations (e.g. Macedonia & Evans 1993).

However, this conclusion applies only to the meaning of grunts from the listener's perspective. Our experiments reveal nothing about the meaning of grunts to signallers. Although grunts may have functioned to allow listeners to infer information about external events, there is no evidence that signallers actively intended to convey such information. To date, there is little evidence for intentional signalling in nonhuman primates (reviewed in Cheney & Seyfarth 1996). Even in the case of vervet monkey alarm calls, which clearly function referentially, there is little evidence that vervets call with the intent of informing others (Cheney & Seyfarth 1990). In the case of baboon grunts, it is entirely possible that the acoustic differences between move and infant grunts do not denote different semantic labels but instead reflect differences in signallers' affective states in these two contexts. If so, the calls could still provide listeners with information about external events, and thus function referentially, so long as there was some consistent matching of arousal or motivation between signallers and listeners in the two contexts (Premack 1972; see also Evans et al. 1993; Macedonia & Evans 1993).

The possibility that baboon grunts might, despite index signaller affect, function referentially, may seem especially likely given that our experiments used grunts that represented the extremes of what appears to be an acoustically graded continuum. As a result, the extent to which move and infant grunts represent truly distinct call types with specific external referents remains unclear. Of course, an acoustic continuum may be perceived categorically (reviewed in Harnad 1987). Barbary macaques, *Macaca sylvanus*, for example, respond differently to alarm calls given in response to humans as opposed to dogs, even though these alarm calls are acoustically graded (Fischer 1998). Similarly, many of the phonetic contrasts of speech grade continuously but are perceived discretely (reviewed in Borden et al. 1994). In a similar

fashion, move and infant grunts may be perceptually discrete to baboons despite continuous variation between the calls. Furthermore, an acoustically graded continuum need not simply reflect a continuum in underlying arousal or motivation, as the example of speech makes clear. Many speech signals have high semantic (i.e. referential) content and are produced completely independently of speaker affective state but nevertheless grade continuously. The resolution of these issues in baboons will require systematic perceptual testing.

In addition to grunt subtype and context, the relative ranks of signallers also influenced listeners' responses to playbacks. Across grunt subtypes and contexts, subjects oriented towards the speaker upon hearing the grunts of females dominant to themselves, but showed no response to the grunts of more subordinate females. These response differences were not due to acoustic differences in grunts that signalled anything about rank directly because the same calls were used in trials both 'up' and 'down' the dominance hierarchy (i.e. the same female's grunt appeared as a 'subordinate's' grunt in some experiments and as a 'dominant's' grunt in others, depending upon the subject to which the call was being played). Instead, subjects appeared to be able to identify the individual whose grunt they heard and rank her according to whether she was dominant or subordinate to themselves. These results support previous observational, experimental and acoustical research indicating that cues to individual identity are a significant and perceptible feature of baboon grunts that complement and enrich other information provided by these calls (Cheney et al. 1995a, b; Silk et al. 1996; Cheney & Seyfarth 1997; Owren et al. 1997). They also contribute to a growing body of evidence that many nonhuman primate calls are individually distinctive (reviewed in Snowdon 1986; Hauser 1996; Rendall et al. 1996, 1998).

In summary, the playback experiments described here indicate that baboons' responses to grunts are affected by the acoustic structure of call variants, the context of call production, and the individual identity and rank of callers. The fact that different grunt variants elicit functionally distinct responses from listeners in at least some contexts suggests that baboon grunts can function referentially. At the same time, contextual cues also play a role in determining listener's behaviour, although the precise nature of the cues involved remains unclear. Finally, baboons are also sensitive to the identity and rank of calling animals, particularly in the case of subordinate individuals responding to the calls of dominants.

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