

Barbary macaques categorize shrill barks into two call types

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Abstract. In response to disturbances in their surroundings, Barbary macaques, *Macaca sylvanus*, utter a distinctive call, the 'shrill bark'. Differences within this call type correlate with the stimulus eliciting the calling. I tested whether monkeys categorized calls according to the eliciting stimulus and whether their perception of calls coincided with the classification derived from the acoustic analysis. Different playback designs using the habituation–dishabituation paradigm were created in which calls exhibiting varying degrees of acoustic difference were paired. I conducted experiments in two populations of semi-free ranging Barbary macaques. The results suggest that subjects categorized calls according to the eliciting stimulus. In addition, subjects from the population in which the recordings were made were significantly better than subjects from the other population at discriminating between calls with small acoustic differences. The results suggest that call categorization is influenced by experience, mediated by individual knowledge of the caller or common call characteristics within the population.

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Many studies on non-human primate vocalizations have described factors associated with variation in call structure, for instance social context, the sender's internal state and individual characteristics in vocalizations (e.g. Green 1975; Hauser 1991; Hammerschmidt & Todt 1995). Fewer studies have asked whether the variation uncovered by such research is meaningful to the animals themselves (e.g. Seyfarth et al. 1980), and whether the acoustic categories established by human observers agree with what the animal perceives as significant units of communication (Snowdon & Pola 1978; Owren 1990). Several such studies have relied on operant conditioning under laboratory conditions (e.g. Beecher et al. 1979; May et al. 1988; Hopp et al. 1992; Brown et al. 1994). However, to identify which differences in stimuli are meaningful in the context of the natural environment, the spontaneous responses to vocalizations have to be assessed. This concept of the 'just meaningful difference' was first introduced by Nelson & Marler (1990).

In this study, I tested the perception of vocal categories in the disturbance calls of Barbary macaques, *Macaca sylvanus*. After disturbances in

their surroundings, Barbary macaques often utter series of 'shrill barks' that generally lead to increased attention in other group members (Fischer et al. 1995). Based on a visual inspection of spectrograms, these calls have been classified as a single call-type; however, a computer-based multiparametric analysis revealed significant differences correlating with the stimulus that elicited the calling (Fischer et al. 1995). My aim in the present study was to test whether the monkeys categorized these calls according to the eliciting stimulus. I first studied a population of semi-free ranging Barbary macaques living in an outdoor enclosure in Rocamadour, France. To assess the variation in perception, I then performed experiments on a second population of Barbary macaques living in an outdoor enclosure at Salem, Germany.

A further aspect of my study was to examine the correspondence between the acoustic boundary between the two categories established by the acoustic analysis and the animals' perceptual boundary. Therefore, I tested different subsets of calls which, according to the analysis, were more or less different acoustically. This approach also served as a test of the applicability of the analytical procedure used in recent studies of Barbary macaque vocalizations (Fischer et al.

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1995; Hammerschmidt & Todt 1995; Todt et al. 1995).

METHODS

Study Animals and Study Sites

The macaques' enclosures covered 15 ha (Rocamadour) and 20 ha (Salem). Both were visitor parks run by the same management where the monkeys ranged freely while visitors were restricted to a path, so the monkeys were well habituated to human observers. Each monkey was tattooed with an individual code on the inside of the thigh. Monkey chow was provided in feeder huts, and apples, grain and seeds were spread throughout the park. Visitors were allowed to feed the monkeys with popcorn provided by the park management. I conducted the experiments in Rocamadour in May, June, September and October 1994, and in March, April, June and July 1995. At that time, the population in Rocamadour consisted of approximately 100 animals, in three stable social groups. In Salem, I conducted the experiments in May 1995. The population consisted of approximately 300 monkeys in four stable social groups (one of which was housed separately). Experiments in Salem were conducted only in the main enclosure. Monkeys in both parks in part go back to a common founder population. A detailed description of the founding and management of the parks is given in de Turkheim & Merz 1984; see also Todt et al. 1992; Paul et al. 1996.

Recordings and Acoustic Analysis

I recorded calls used for playback in Rocamadour in autumn and winter 1992, and in spring 1993. A more detailed description of the recording conditions is given in Fischer et al. (1995). At that time, the population consisted of 240 animals, divided into two stable social groups, the 'small group' (50 subjects) and the 'large group' (190 subjects), resulting from a split of the single group in 1990. Except for the vocalizations of one subject, I recorded all calls from animals in the large group. In autumn 1993, 140 animals from the large group were removed from the park.

From the recordings, I selected calls that were given in two contexts: when I approached the

monkeys on their sleeping trees after dusk; and when a dog, for instance the neighbouring shepherd's dog or the dog of one of the park staff, was in the monkeys' vicinity. I term these calls 'nocturnal disturbance calls' and 'dog calls', respectively, not implying that these calls actually denote a nocturnal disturbance or a dog, or that these calls would be given exclusively in such contexts. From the monkeys whose dog calls I recorded, only two subjects were still present in Rocamadour at the time of the study. I recorded the nocturnal disturbance calls from nine subjects and the dog calls from 16 subjects. The individual identity of the animals recorded at night could not be established. However, from the sleeping habits of different animals in the park and the age- and sex-class of the callers I concluded that I recorded nine different subjects. I estimate that two-thirds of the subjects whose calls were used in the experiments were no longer present. Thus, monkeys in Rocamadour were tested with calls from present and former members of their own population, whereas monkeys in Salem were tested with calls from an unfamiliar population.

I recorded vocalizations with a Sony WM DC6 cassette recorder and a Sennheiser directional microphone (KN3 power module and ME80 recording head with Sennheiser windscreen; frequency response 50–15 000 Hz \pm 2.5 dB re 20 μ Pa) and transferred them to a DAT tape (SONY TCD-D3) for storage. I visually inspected the recordings and sampled calls that were not disturbed by background noise (i.e. bird song, other animals calling) for analysis using RTS (Engineering Design, Boston, U.S.A.). Altogether, I sampled 537 nocturnal disturbance calls and 379 dog calls.

I digitized the calls with a sample frequency of 37.5 kHz and used the SIGNAL sound analysis system (Engineering Design, Boston) to conduct a fast Fourier transform (1024-pt FFT; time resolution: 5 ms; frequency range: 15 kHz; frequency resolution: 36.9 Hz). I used a custom software program (LMA 5.0) developed by K. Hammerschmidt (Hammerschmidt 1990) to calculate 84 parameters, characterizing the call in terms of frequency and time dynamics. I used a 3×3 sliding average filter (see Schrader & Hammerschmidt 1997) to enhance the signal to noise ratio. From the filtered frequency-time spectrum, I determined three dominant frequency bands: for each time segment I identified the

frequency ranges in which the amplitude exceeded a threshold set at the mean+SD for this time segment. Adjacent frequency bands were separated by at least three cells in which the amplitude did not exceed the threshold, that is, 110.7 Hz (for details, see [Schrader & Hammerschmidt 1997](#)). I calculated several features such as the start and end frequency, the maximum frequency, the mean and the modulation for each frequency band. From the unfiltered frequency-time spectrum, I determined the distribution of the amplitude in the frequency spectrum. From the power spectrum, I calculated the frequency range and frequency peaks. Finally, I determined temporal parameters such as the call duration and the temporal location of the maximum and the minimum amplitude ([Hammerschmidt & Todt 1995](#)). For a discussion of the multiparametric approach to animal vocalizations, see also [Schrader & Hammerschmidt \(1997\)](#).

The acoustic parameters were analysed by a discriminant function analysis which compares multivariate patterns resulting from any interaction of variables. The discriminant function analysis provides a classification procedure that assigns each call to its appropriate group (correct assignment) or to another one (incorrect assignment). To test the reliability of the discriminant function it is possible to split the data set and use half to establish a discriminant function. The remaining data can then be used separately in the assignment procedure. Similar results in the assignment procedures indicate that the sample size is appropriate. I thus tested the results of the discriminant function analysis by establishing a new discriminant function with a 50% random sample and running an additional assignment procedure with the other 50% of the data. Furthermore, the discriminant function analysis calculates the rank order in which parameters contribute to a correct assignment (identification of predictor variables). I calculated multivariate analyses using the statistical package SPSSWIN 6.1.2.

Experimental Design

To test whether monkeys categorized calls of one context as 'same' and discriminated between calls given in the two contexts, I used the habituation-dishabituation paradigm ([Eimas et al. 1971](#); [Cheney & Seyfarth 1988](#); [Nelson &](#)

[Marler 1989](#); [Seyfarth & Cheney 1990](#); [Rendall et al. 1996](#)). With this technique, stimuli of one category are repeatedly presented until the subject habituates, that is, until the response strength of the subject declines below a predetermined level. Then, a stimulus from a putative different category is presented. A revival of response, that is, a dishabituation, suggests that the test stimulus is perceived as different from the ones used for habituation. The working hypothesis was that subjects would discriminate between calls given in the two eliciting contexts; in other words, they were expected to dishabituate after presentation of a test stimulus different in context from the habituating stimuli. This habituation-dishabituation paradigm has been successfully applied under laboratory conditions ([Eimas et al. 1971](#)) and in the field ([Cheney & Seyfarth 1988](#)).

I selected the calls for playback according to the results of the discriminant function analysis. I created different pairings in which the calls used for habituation and the calls used as test stimuli had large, medium or small acoustic differences. In addition, I conducted experiments in which I tested calls from the category boundary. These were originally given in the two contexts, but were indiscriminable by the discriminant function analysis, that is, they received the same discriminant coefficient, and were assigned to the same context (incorrect assignment). As a control, I conducted sessions during which the test trial stimulus was a novel call from the same category as the habituating stimuli (see [Fig. 1](#)). Subjects from which the recordings were made were equally distributed in the different assignment categories (Haldane-Dawson test of contingency according to [Bortz et al. \(1990\)](#) for dog calls: $\chi^2_{39} = 18.84$, NS; for nocturnal disturbance calls: $\chi^2_{27} = 7.01$, NS).

In the test trials, I always used calls from different individuals to control for any effects of individuality. For each playback tape, I randomly chose five calls from five animals. Four of these calls were used to create a sequence in which the order of calls varied and each call was separated by at least two other calls. A sequence consisted of 30 calls, but the number of calls actually played back depended on the subject's behaviour (see below). The fifth call served as the test stimulus. Calls were separated by 20 ± 2 s of silence. I created four tapes in this way for each design (i.e. large, small, etc.), except for the medium

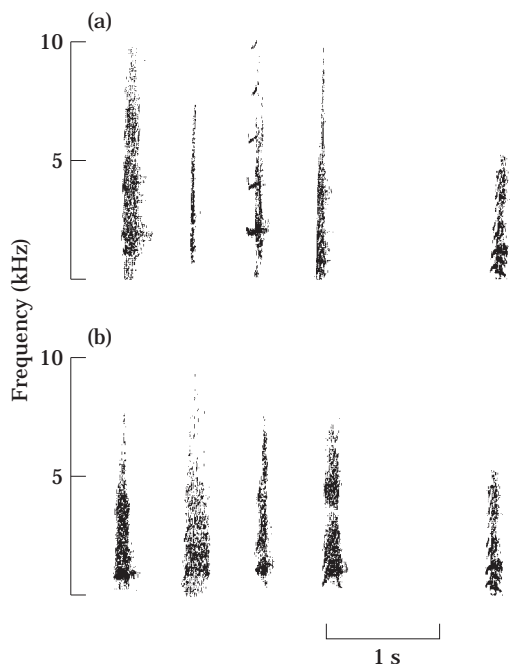


Figure 1. Examples of calls used for habituation and as test stimuli. (a) Large differences design: four nocturnal disturbance calls that were used for habituation and a call given in response to a dog that was the test stimulus. (b) Control: four calls given in response to a dog that were used for habituation and a novel call given in response to a dog that was the test stimulus. Note that the same call exemplar was used as the test stimulus in both designs. (a) and (b) both show spectrograms of the calls of one playback tape.

differences design in which I used three tapes for habituation. Thus I also used four test exemplars for each design (three for the medium differences design). In Salem, I used two additional test exemplars in the large and in the small differences design. I prepared the playback tapes and edited the signals using the ESPS/waves+ program (Entropic Research Laboratory). The amplitude of the habituation calls and the test calls was carefully controlled: sound pressure level (SPL) measurements in the laboratory yielded a mean \pm SD maximum amplitude of 74 ± 1 dB SPL (re $20 \mu\text{Pa}$; flat) of both the habituation and the test calls (precision sound pressure level meter CEL-314, Lucas-CEL Instruments, Hertfordshire, U.K.; amplitude range: $20\text{--}140$ dB ± 0.5 dB; frequency range $15\text{--}16\,000$ Hz). The sound level meter was calibrated prior to measurements with a reference value of 94 dB at 1 kHz.

In half of the sessions in the large differences design and in the control trials, subjects were habituated with nocturnal disturbance calls, while in the other half they were habituated with dog calls. In the other experimental designs, I habituated the subjects with nocturnal disturbance calls and tested them with dog calls since the number of overall sessions possible was constrained by the number of subjects available in Rocamadour, and by time in Salem. Table I provides an overview of the test designs and the number of sessions conducted in Rocamadour and Salem. I performed tests opportunistically when the test subject was in

Table I. Experimental design and number of test sessions conducted in Rocamadour and Salem

| Design | Δ^* | Call category | | Rocamadour <i>N</i> | Salem <i>N</i> |
|-------------------|------------|---------------|------|------------------------|-------------------|
| | | Habituation | Test | | |
| Large difference | 6.15 | Ndc† | Dog | 8 | 11 |
| | | Dog | Ndc | 8 | |
| Medium difference | 3.45 | Ndc | Dog | | 10 |
| Small difference | 0.85 | Ndc | Dog | 8 | 10 |
| | | Dog | Ndc | | |
| Incorrect | 0.12 | Ndc | Dog‡ | 8 | |
| Control | 0.11 | Ndc | Ndc | 8 | |
| | | Dog | Dog | 8 | |

*Difference between the median discriminant coefficients between call pairings. The maximum difference in the entire data set was 10.

†Ndc: nocturnal disturbance call.

‡Calls were originally given in response to a dog but assigned to the category nocturnal disturbance call by the discriminant function analysis.

a quiet situation, for example during foraging or resting. For the playback experiments, I used a SONY DAT TCD-D7 and a BOSE Roommate II battery-powered loudspeaker (frequency response 40–16 000 Hz \pm 2 dB). Once a suitable subject was identified, I hid the loudspeaker behind a bush or in tall grass. The volume was set at 62–66 dB SPL (flat) maximum amplitude measured at a distance of 1 m. At the subject's distance from the speaker, this was below ambient noise SPL (averaging 60 dB SPL (flat)).

I started the playback session when the test subject had been looking away from the loudspeaker for 20 s prior to the playback of the first stimulus, so that no baseline looking time had to be taken into account. The minimum number of turns towards the loudspeaker in response to the habituation calls for a session to be classified as valid was three to ensure that the animals were sufficiently motivated to respond at all. The time interval between consecutive trials was 20 s. The test stimulus was played back not after a fixed number of habituation trials (Cheney & Seyfarth 1988), but instead after the subject failed to respond on a given number of consecutive trials (Rendall et al. 1996). After three consecutive trials in which the monkey showed no response, the test stimulus was broadcast. Thus, the minimum number of habituation trials was six. I aborted sessions during which other animals approached the subject to a distance of less than 3 m. A second observer videotaped the sessions using a Panasonic NV-M7 EG or a SONY CCD-TR 750. Videotapes were later used to measure the duration of responses and to check the animal's reaction after playback of the test stimulus. Two observers naive to the hypothesis tested were asked to assess the animal's response on a yes/no basis. All three observers agreed in all the cases. To measure looking time, I analysed the tapes on a frame-by-frame basis using a Panasonic Video-Cassette Recorder NV-FS 88 HQ (25 frames/s). In nine sessions in Rocamadour, I failed to videotape all the subjects' responses, and discarded these sessions from analyses regarding response duration and response frequency. To test whether subjects' responses in the test trial differed significantly from their response in the last trial of the habituation series, I used a Wilcoxon signed-ranks test, corrected for 'zero differences' in the two conditions according to Bortz et al. (1990), assigning a positive sign to half of the zero differences,

and a negative sign to the other half. When the number of zero differences was unequal, I omitted one of the zero cases from the analysis and reduced N to $N-1$ (N).

RESULTS

Acoustic Analysis

The discriminant analysis revealed two call categories that exhibited a transition (Fig. 2). The classification procedure yielded an average correct assignment of 95.85% to the two contexts. A test with a 50% random sample confirmed the discriminant function: the average correct assignment was 95.2% for the base data set and 96.3% for the validation set. The most decisive parameters for discrimination between groups were 'mean first dominant frequency band' and 'call duration' (Fig. 3).

Playback Experiments

In both populations, a considerable number of trials had to be aborted because subjects responded fewer than three times. This apparently became more likely with an increasing number of experimental sessions. I tested this effect with the trial number as the dependent variable for the 1994 experiments in Rocamadour and it proved to be significant (Mann-Whitney U -test: $U=218$, completed trials $N_1=22$, insufficient responses $N_2=39$, $P<0.01$). The median duration of the first response was significantly lower in sessions that had to be aborted owing to insufficient responses than in sessions that could be completed, both in Rocamadour and in Salem (Table II).

I completed 48 trials in Rocamadour on 45 adult subjects. Three subjects were tested twice in 2 consecutive years in different experimental designs. The median number of habituation trials per session was 7, ranging from 6 to 20. Figure 4a shows the median looking time to the test stimulus. In the large differences design, subjects showed a significant dishabituation to the test stimulus (Wilcoxon signed-ranks: last trial versus test trial, $T_+=133$, $N=16$, $P<0.001$). The same was true in the small differences design ($T_+=34.5$, $N=8$, $P<0.01$). After presentation of a novel call from the same category, in contrast, only two subjects showed a revival of response ($T_+=25.5$,

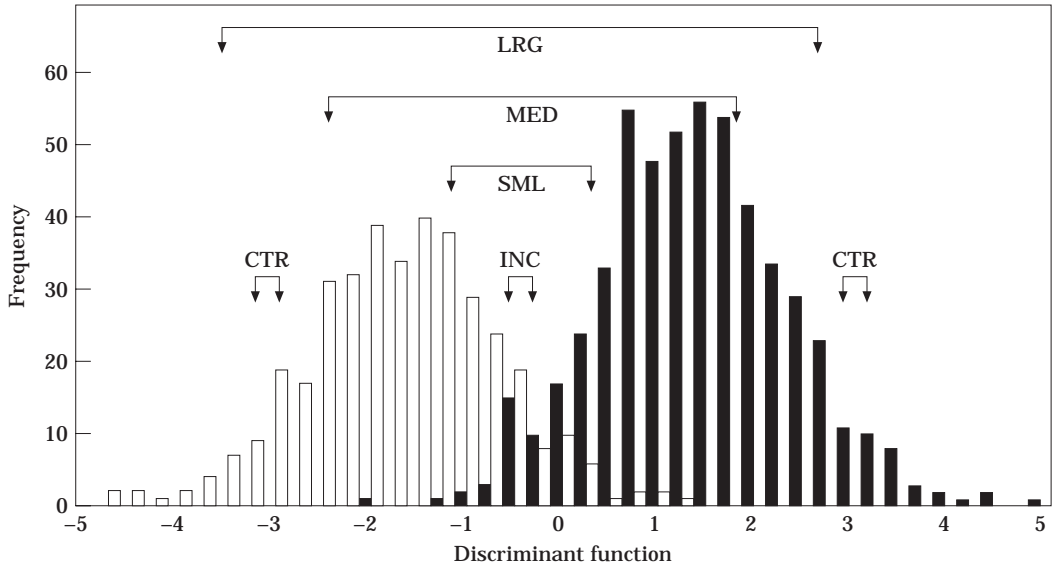


Figure 2. Frequency distribution of discriminant coefficients and selection of calls for playback. Arrows indicate the midpoint of the subset of calls from which different exemplars were drawn at random. Connected arrows denote corresponding test pairs. Calls exhibited large (LRG), medium (MED) or small (SML) acoustic differences. CTR indicates control trials in which subjects were tested with a call from the same category. INC: the test call was originally given in the other context than the calls used for habituation, but was incorrectly assigned by the discriminant function analysis to this latter category.

$N=8$, NS). In the incorrect assignment design, however, half of the subjects showed a revival of response ($T_+=31$, $N=8$, $P<0.05$), indicating that the subjects discriminated calls indiscriminable to the acoustic analysis.

In Salem, I completed 31 experiments involving 31 subjects. The median number of trials was 13, ranging from 6 to 32. This was significantly more than in Rocamadour (Mann-Whitney U -test: $U=237.5$, $N_1=31$, $N_2=39$, $P<0.001$). Figure 4b shows the median looking time after presentation of the test stimulus in Salem. Both in the large differences design (Wilcoxon signed-ranks: last trial versus test trial, $T_+=64.5$, $N=11$, $P<0.01$) and in the medium differences design ($T_+=40$, $N=9$, $P<0.05$) I observed a significant rate of dishabituation. In the small differences design, in contrast, only two out of 10 subjects showed a dishabituation ($T_+=37$, $N=10$, NS).

Responses in the two populations did not differ significantly in the large differences design (Mann-Whitney U -test: $U=40$, $N_1=8$, $N_2=11$, NS; Rocamadour data in the large differences design are confined to those in which monkeys were habituated with nocturnal disturbance calls). In

the small differences design, in contrast, monkeys in Rocamadour showed significantly more dishabituations than monkeys in Salem (Mann-Whitney U -test: $U=16$, $N_1=8$, $N_2=10$, $P<0.05$).

DISCUSSION

The discriminant function analysis of Barbary macaque calls given in response to a dog versus a nocturnal disturbance revealed significant differences in call structure that correlated with the stimulus eliciting the calling. The discriminant function analysis identified two acoustic categories connected by a series of intermediate calls. The experiments in Rocamadour showed that these monkeys categorized the calls according to the eliciting stimulus, regardless of whether the calls exhibited large or small acoustic differences. Accordingly, the subjects seemed to perceive a boundary in the transition between the two categories. This conclusion is supported by the control trials in which the monkeys failed to dishabituate to calls given in the same context. Although it remains undecided whether subjects

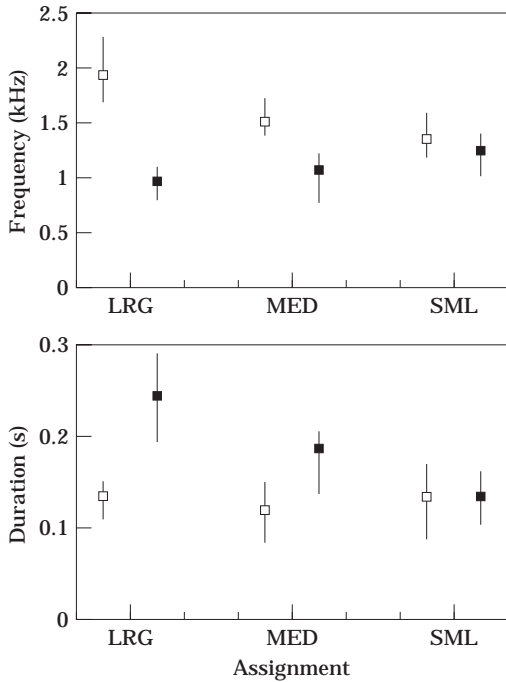


Figure 3. Distribution of the two acoustic parameters (mean first dominant frequency band and call duration) that were most decisive in discriminating between calls given in the two contexts (median \pm first and third quartile), for calls that were assigned to the large (LRG), medium (MED) and small (SML) differences categories. □: Nocturnal disturbance calls; ■: dog calls.

Table II. Median looking time (s) during the first response in trials with three or more or fewer than three responses, for subjects in Rocamadour and Salem

| | ≥ 3 | <i>N</i> | < 3 | <i>N</i> | <i>U</i> * | <i>P</i> |
|------------|----------|----------|-------|----------|------------|----------|
| Rocamadour | 2.44 | 39 | 1.36 | 22 | 293 | <0.05 |
| Salem | 5.0 | 31 | 1.74 | 12 | 113 | <0.05 |

*Mann-Whitney *U*-test.

failed to dishabituate because they could not perceive a difference between the calls or because the perceived difference did not warrant a renewed response, the latter seems more likely. Rendall et al. (1996), for instance, using the habituation-dishabituation paradigm, found evidence for discrimination between both kin and non-kin and between individuals by voice in rhesus macaques, *Macaca mulatta*. Thus, it seems more likely that the monkeys would be able to discriminate

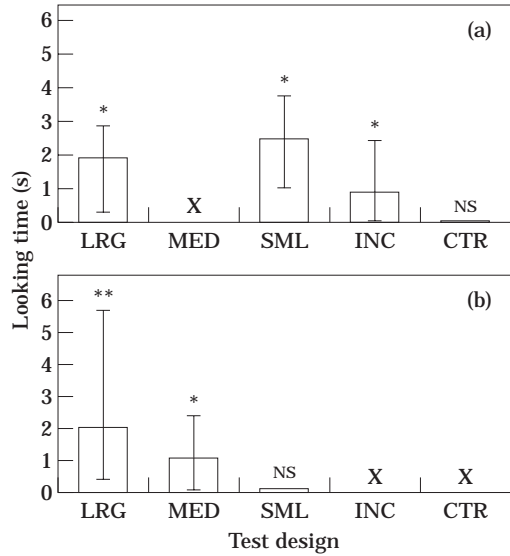


Figure 4. Looking time after presentation of the test stimulus (median \pm first and third quartile) for the different test designs (see legend to Fig. 2). (a) Rocamadour; (b) Salem. 'X' indicates that no tests were conducted in this design. **P* < 0.05; ***P* < 0.01.

between calls within a category when tested using a different criterion.

Half of my subjects discriminated between calls that were indiscriminable by the analysis. Thus, monkeys were able to extract meaningful information in addition to that measured in the acoustic analysis, suggesting that their perceptual space differs in some ways from the linear model established by the discriminant function analysis. Nevertheless, the monkeys' assessment of the call categories coincided in general with the outcome of the discriminant function analysis. Therefore, the results support the use of this multiparametric analysis of primate vocalizations (Fischer et al. 1995; Hammerschmidt & Todt 1995; Todt et al. 1995).

The combination of call analysis and perceptual experiments is essential to identify meaningful units of communication. Whereas my results indicate that meaningful variation may occur within a group of calls that represent the same general call type ('shrill bark'), a study by Cheney & Seyfarth (1988) on vervet monkey, *Cercopithecus aethiops*, calls suggested that different call types ('chutter' and 'wrrr') effectively convey the same meaning (see also Macedonia & Evans 1993). Thus,

perceptual experiments are crucial for establishing a functional vocal repertoire of a given species. These results highlight the importance of combining analyses of call features with those of their perception (e.g. Owren 1990; Fitch & Hauser 1995) to gain a full understanding of a species' communication system. Further research will be needed to evaluate the features eliciting particular call types and the selective advantage of the formation of different calls.

Differences between Populations

In Salem, I tested subjects with calls recorded in Rocamadour, from unfamiliar callers. Whereas the Salem subjects were able to discriminate calls with large acoustic differences, they discriminated poorly between calls with medium acoustic differences, and failed to discriminate calls with only small acoustic differences. One explanation for the differences in the discrimination of call categories between subjects in Rocamadour and Salem may be that Salem subjects were not able to identify the individual calling. Cheney & Seyfarth (1988) suggested that knowledge of caller identity, and in particular a specific individual's call variability, is essential to assign a call to its correct category. However, in Rocamadour the population had been split into two stable social groups, and the majority of subjects whose calls were used as stimuli had been removed several months before the first suite of experiments. It seems unlikely that all the subjects in Rocamadour were equally familiar with the call characteristics of subjects that were no longer present. Therefore, detailed knowledge of the individual caller does not seem likely in Rocamadour either. Clearly, further studies are needed to address the issue of familiarity with the caller on the classification of calls.

A second plausible hypothesis for the observed difference between populations is that callers in Rocamadour exhibited common call characteristics that differed from those in Salem. An acoustic analysis of the dog calls from both Rocamadour and Salem indicated that subjects revealed slight but significant differences in their acoustic characteristics (Fischer 1996), presumably resulting in slightly different call categories. The differences in subjects' responses in Rocamadour and Salem suggest that, while broad categories may be universal to the species, the specific location of

acoustic boundaries may be established by experience. Alternatively, subjects of the two populations may attend to different cues to discriminate between categories. Work by Seyfarth & Cheney (1986) and Hauser (1988) suggests that auditory experience is important for the subsequent assignment of meaning and the appropriate behavioural response. In summary, the perceptual system seems to be fine-tuned by experience to differences in call production.

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