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The Use of Vocal Signals in the Social Play of Barbary Macaques

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ABSTRACT. Field studies in various species of *Macaca* (Cercopithecidae) provided evidence for specific visual displays that typically accompany playful interactions. The aim of our study was to examine whether and when playing individuals would use auditory displays, i.e. vocalizations that often occur during social play as well. The study was conducted on a population of semi-free Barbary macaques (*Macaca sylvanus*) with a special focus on the composition and dynamics of playful wrestling (synonymous term: 'rough-and-tumble play'). Analyses of dyadic encounters between subadult males allowed us to distinguish five types of playful behaviours and three types of vocalizations. The latter were clearly linked to encounters where effects of visual signals were impaired, e.g. during close body contact. During wrestling, vocalizations tended to increase in the beginning of an encounter, whereas the last seconds of wrestling often showed a decline in vocalization rate. Our results allowed us to conclude that these vocalizations may supplement or in many cases even substitute interactional effects of visual signals, e.g. the 'play face.'

Key Words: *Macaca sylvanus*; Social play; Play signals; Vocalization.

INTRODUCTION

The search for criteria that allow a general definition of play has a long tradition (review in FAGEN, 1981). Although many of them are still the subject of controversial debate, a number of features have been put forward that are widely accepted as operational characteristics of playful behaviour (PELLIS & PELLIS, 1996; BEKOFF & BYERS, 1998). From a formal perspective, these characteristics include, for example, a remarkable variability and plasticity of pattern performance, a high degree of flexibility in the sequential order of motor patterns, the absence of a clear target pattern (TODT, 1997), and in the case of social play, also a frequent change of interactional roles (TODT et al., 1992).

The occurrence of particular displays in social play that are not found during other kinds of behaviour provides an additional cue: most investigators agree that such displays are genuine signals that are addressed to a playmate and serve to stimulate the start or the maintenance of playful encounters (FAGEN, 1981; BEKOFF, 1974, 1995).

In many species, playing individuals use even more than one type of play-promoting displays and may also adjust their use (BIBEN & SYMMES, 1986; ZELLER, 1986). According to FAGEN (1981), the exchange of play signals in mammals may apply to any communicative channel that is available to a given species. However, special gestures and postures such as the 'relaxed open mouth display' (VAN HOOFF, 1972), also described as the 'play-face' of non-human primates (CHEVALIER-SKOLNIKOFF, 1974) or the 'play-bow' of carnivores (e.g. BEKOFF, 1977) appear particularly widespread across mammals.

Many species, and especially non-human primates, use specific vocalizations during their social play (review in ALDIS, 1975). Moreover, these show a quite similar structure: they often consist of short sound elements that occur in distinct serial succession. In some cases, e.g. the great apes (VETTIN et al., 1999) or rhesus-monkeys (SYMONS, 1978), the rhythm of vocalizations resembles the rhythm of human laughter (PROVINE & YONG, 1991; KIPPER et al., 1999; KIPPER & TODT, 2001).

The majority of vocalizations uttered during play are characterized by a low amplitude (ALDIS, 1975). This was interpreted as an adaptation to predation pressure (GOEDEKING, 1988). However, such a trait also supports the view that the signals are primarily addressed to the respective playmate. High amplitude vocalizations have only been reported for common squirrel monkeys (*Saimiri sciureus*), where loud play-accompanying vocalizations were explained as signals that would raise the vigilance of adult group members not engaged in the playful encounter (BIBEN et al., 1989).

Perhaps as a consequence of the low amplitudes of primate play vocalizations, the number of detailed analyses of their structure and application has remained rather small. In addition, such studies have been conducted only on monkeys kept in confinement (GOEDEKING & IMMELMANN, 1986; BIBEN & SYMMES, 1986; MASATAKA & KOHDA, 1988). To elucidate this issue, we have investigated both the playful behaviour and the performance of vocalizations accompanying play in a population of Barbary macaques (*Macaca sylvanus*) living in an almost natural environment (TODT et al., 1992).

Our study was guided by a hypothesis that the performance of play-accompanying vocalizations serves a communicative function and, in particular, promotes the mutual adjustment of playful interactions. This hypothesis allowed us to derive two more specific predictions. First, the use of vocal signals should be especially expedient if there is a possibility that the visual channel might be impaired, e.g. during close body contact with rapid changes of posture. In other words, we predicted that vocalizations would be frequent during specific types of playful encounters, but rare during other types. Second, to fulfil their postulated interactional role, vocalizations should preferentially occur at a particular point during a playful encounter, instead of being equally distributed throughout the encounter.

Barbary macaques (*Macaca sylvanus*) have a number of traits that allow the proposed hypothesis to be examined: the play behaviour of this species has been extensively investigated in several studies (object play: WILL & TODT, 1997; ontogenetic and functional aspects of play: BURTON, 1972; FREYTAG-GRUNERT, 1989; use and function of the 'relaxed open mouth display': PREUSCHOFT, 1992; comparison to play of other species of the genus *Macaca*: CAINE & MITCHELL, 1979). Additionally, the vocal repertoire of Barbary macaques and their communicative abilities have been documented to the same degree as their social development and organization (e.g. ZELLER, 1986; RIECHELMANN et al., 1994; FISCHER et al., 1995; HAMMERSCHMIDT & TODT, 1995; TODT et al., 1995; HAMMERSCHMIDT & FISCHER, 1997).

In the present study, videotaped play sequences were examined in terms of behavioural categories of play. Next, the distribution and structure of vocalizations was analysed. The combination of these data allowed us to describe the occurrence of vocalizations in the course of playful encounters.

Finally, the main part of our analyses concentrated on play dyads or pairs of subadult or juvenile males. By restricting our results to dyadic encounters and to a specific age group we were able to hold back at least some of the highly variable features of social play such as differences in the performance of play that depend on the number of playmates, age, gender, or social status of playmates (e.g. HAYAKI, 1983; MENDOZA-GRANADOS & SOMMER, 1995). We were able, consequently, to improve the analytical quality of our behavioural data.

METHODS

ANIMALS AND STUDY SITE

Our subjects were Barbary macaques (*Macaca sylvanus*) living in the semi-free outdoor

enclosure 'La forêt des Singes' at Rocamadour (France). The animals fed on natural vegetation, monkey chew, apples and other fruits, and seeds and grains. The population comprised approximately 100 individually labelled animals that formed three stable social groups. The groups used to stay in different areas of the site (size: 15 ha). Data presented here were collected from one particular group with 22 adult and 9 subadult and juvenile individuals (age 1 – 5 yr). During the period of data sampling six infants were born. All members of the group were individually known to the observers.

The enclosure is a visitor park where monkeys range freely, whereas visitors are restricted to a path. Thus, animals could choose the degree of contact to humans and they are well habituated to human presence. (For details on park management and previous research projects, see: DE TURCKHEIM & MERZ, 1984; TODT et al., 1992.)

SAMPLING AND ANALYSIS OF DATA

Data were collected during a period of six weeks (May – June) in 1996. Playful encounters were videotaped with a Sony Stereo CCD-TR805E camera that was connected to a Sennheiser ME 66 microphone.

Since both the morning and the evening turned out to be core periods for playful behaviour (KIPPER, unpubl. data), most of the recordings were collected during 07:00 – 10:00 and 18:00 – 20:00. One hundred and eighty (180) hr of observation resulted in 16 hr of videotaped material of playing Barbary macaques.

We applied 'behaviour sampling' ad lib (MARTIN & BATESON, 1986). Each occurrence of social play that met the following definition was documented: an interaction between at least two individuals that was characterized by qualitative features (specific behavioural sequences, repetition, and exaggeration) that were often accompanied by specific facial and vocal signals. Behavioural data were obtained by analysing the videotaped sequences and by applying point-sampling with a period of 1 sec (MARTIN & BATESON, 1986). Categorization of behaviours and determination of hierarchy levels followed criteria suggested by TODT (1986). Using this approach, we categorized five mutually exclusive types of playful encounters, that were defined as follows:

Wrestling: Movements in close body contact, during which rump, chest, extremities, and mouth are used to gain control over the position and mobility of the playmate.

Chasing and Grabbing: One animal follows the other with or without body contact, contact occurs only over extremities, body engagement is lower than during wrestling.

Jumping: Body contact between the playmates is started or finished by a sudden jump of one or both playmates.

Resting: Playmates remain in body contact, but sit still.

Break: Playmates do not interact bodily, but stay in close proximity and engage in other behaviours. A situation was only categorized as 'Break' if it was followed by one of the other play categories within 1 min. Otherwise, the episode of play was categorized as finished.

The defined types of encounters could occur singly, but mostly an *episode of play* was composed of several successive encounters belonging to different types. An episode begins, when one of the participants directs a behaviour to its partner and ends when one or both participants

stop or change their activities. The formal application of these definitions to the videotaped sequences allowed us to determine exactly the start and end of each encounter.

Next, we quantified these types of encounters and investigated their contribution to each episode of social play, i.e. each episode of play consisted of one or more successive play encounters that belonged to one of the defined types. If one of the types occurred repeatedly during an episode of play (for example ... wrestling – chasing – wrestling ...) these encounter were analysed separately.

Owing to clear age- and sex-related differences in the playful behaviour of our subjects (KIPPER, unpubl. data; FREYTAG-GRUNERT, 1989), we only included data of six particular dyads in our further analysis. These dyads were formed by four subadult males (age: 3 and 4 yr).

Our data on vocalizations in particular were treated dyad-wise, not individually. Such treatment had two methodological advantages: first, it allowed a conservative measure because playful dyads were performed in close contact and with rapid posture changes. Additionally, vocalizations were soft and of low volume. Thus, an identification of individual contributions was difficult to achieve. Second, it seemed expedient to treat different pairs as unrelated samples (also statistically), because each episode of playful encounters was determined by a coherent complex of interactive behaviours between both playmates.

Our analyses concentrated on the sequence of vocalizations in time and also on their relationships to playful episodes and encounters. Thus, the beginning and the end of each episode or encounter as well as the beginning and the end of each vocalization were recorded. We analysed the temporal parameters of the vocalizations by visualizing them in spectrograms using Avisoft-SASLab Pro software (R. Specht, Berlin) with 16-bit resolution and a sampling rate of 16 kHz. Each sound element that was not interrupted by breaks longer than 20 msec counted as a vocalization. If a vocalization started in 1 second of an encounter and ended in the next second, it was counted within the first second. However, due to the short duration of vocalizations, such cases rarely occurred. By processing videotaped pictures and acoustic recordings in parallel, we were able to relate each vocalization to the associated play encounter as well as to examine the distribution of vocalizations throughout the course of a play episode. Results are expressed in terms of a 'vocalization rate' that was calculated by dividing the number of vocalizations (of a certain type) by the duration of an encounter.

ACOUSTIC ANALYSIS

Besides the temporal placement of vocalizations during play, we also analysed their acoustic structure. For this acoustic analysis we only used recordings with less than 3 m distance between the playing individuals and the microphone. We conducted a visual examination of the recordings using RTS 1.31 (Engineering Design, Boston), and sampled vocalizations that were not distorted by background noise. The digitized calls were transformed in their frequency-time domain with SIGNAL 2.29 (Engineering Design, Boston) (FFT 1024, sampling rate 22.5 kHz, time increment 5 msec). The resulting frequency-time spectra were analysed using LMA 6.11 computer software developed by K. HAMMERSCHMIDT. This procedure resulted in 169 acoustic parameters for each vocalization. They included frequency parameters, spectral characteristics, peak amplitude, and temporal parameters (see HAMMERSCHMIDT & TODT, 1995). A detailed description of this multi-parametric approach is given in SCHRADER and HAMMERSCHMIDT (1997).

The acoustic parameters most decisive for the categorization of the vocalization types were then used for an auditory-visual assignment of our observed vocalizations (n=4240) to one of these types. Only few of these calls (1%) could not be assigned clearly and were therefore excluded from the analysis.

Statistics

Differences in the frequency and distribution of vocalizations were tested with nonparametric statistics. All tests were two-tailed. In some tests, only five pairs were included on account of the small sample sizes for the sixth pair.

The results of the multi-parametric sound analysis were processed using multivariate statistical techniques. A discriminant analysis allowed us to compare multivariate patterns resulting from any interaction within the variables. It also provided a classification procedure that assigned each acoustic pattern to its appropriate group as revealed by visual and auditory cues, and calculated a rank order in which parameters contribute to this assignment. To examine these parameters for differences between vocalization types we used Friedman tests with average values for pairs.

RESULTS

Examination of our videotaped material revealed that all subadult individuals (six males aged 3 – 5 yr, three females aged 1 – 3 yr) of the observed social group took part in play sessions but with strong varying portions. Episodes of play were performed by two to five playmates, with dyadic episodes occurring most often (65% of all play-episodes). In total, we observed 575 episodes of play. The following analysis includes data from only six dyads (see Methods).

Playful Encounters and Temporal Placement of Vocalizations

All 118 episodes analysed and classed as social play consisted of one or more types of playful encounters. In addition, most encounters contained a significant non-vocal play marker, i.e. the 'relaxed open mouth display' (van Hooff, 1972). In line with the results of Preuschoft (1992), this facial expression could often be observed during encounters of playful 'Wrestling' and 'Chasing and Grabbing,' but less frequently during 'Jumping,' 'Resting,' or 'Break.' However, since the display was not completely absent during encounters of the latter categories, this supported our decision to accept these two play categories as relevant elements of a play episode. A summary of the frequencies and durations of the play categories is given in Table 1. Our results show that 'Wrestling' was the most frequently performed play category and also the longest lasting type of encounter. Although pairs differed slightly in the proportion of play types, for all pairs 'Wrestling' was by far the most frequently performed category. (Number of play episodes/ encounters for pairs: P1=45/204; P2=13/33; P3=18/33; P4=5/39; P5=35/73; P6=2/7.) Pairs did not show any differences in the duration of encounters of the different play types (Kruskal-Wallis H tests, n=5; 'Wrestling': χ^2=5.91; 'Chasing and Grabbing': χ^2=4.02; 'Jumping':χ^2=7.13; 'Resting': χ^2=3.70; 'Break': χ^2=2.56; all n.s.).

In most play encounters vocalizations occurred that were characterized by a low amplitude and a serial organization. However, our examination revealed that not every encounter of a play episode was accompanied by vocalizations. The proportion of 'silent' episodes was related to the play type (Table 1). During 'Wrestling,' 'Chasing and Grabbing,' and 'Jumping,' encounters without vocalization were rare (under 16%). Interestingly, subjects vocalized during all encounters of 'Resting,' but only in 42% of cases of 'Break.'

Differences among encounter types were also found with respect to the frequencies of vocalizations (Fig. 1). The greatest number was found for 'Jumping' followed by 'Wrestling' and 'Chasing and Grabbing.'

Table 1. Observed frequencies and duration of different play types and proportion of 'silent' encounters per play type.

	Frequency		Duration(s)	
	Observed encounters	Encounter without vocalizations (number/%)	Total	Median (first/third quartile) for play types
Wrestling	144	6/4.2	1330	8 (4.25/11)
Chasing and Grabbing	79	12/15.2	380	4 (2/6)
Jumping	39	3/7.7	53	1 (1/2)
Resting	36	0/0.0	346	7 (3.25/11.75)
Break	91	58/63.7	646	3 (1/9)
Sum	389	79	2755	

With this as a reference, we analysed the temporal distribution of play vocalizations throughout the course of a play encounter. As 'Wrestling' was the most frequently performed and longest lasting play type, we concentrated on this category in subsequent analyses. Here, we tested for a possible correlation between the duration of 'Wrestling' encounters and the number of vocalizations. First, we found that very short 'Wrestling' encounters (duration 1 – 3 sec) were often characterized by a large number of vocalizations. In the case of longer encounters, a significance test revealed that the duration of 'Wrestling' and the frequencies of vocalizations were significantly different from a non-correlation (Spearman rank correlation, n=144, p<0.01); the correlation coefficient was only −0.21. In other words: there was a slight tendency for the production of vocalizations to decrease if the duration of 'Wrestling' encounters increased.

Next, we analysed the temporal distribution of play vocalizations throughout the course of 'Wrestling' encounters. Here, we compared the number of vocalizations in the first and last 3

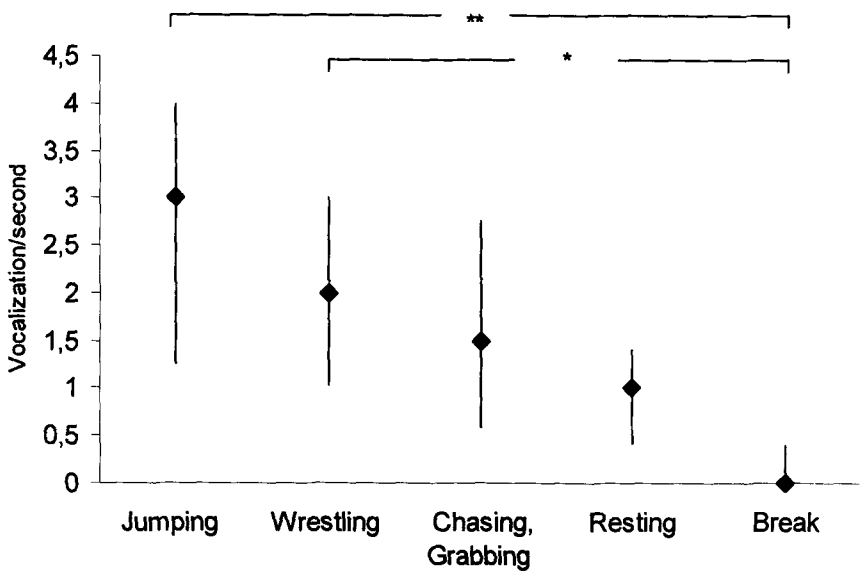

Fig. 1. Rate of vocalizations: Median, first/third quartile for the play types are shown. Data of all pairs are only pooled for illustration. Differences between the play types in the relative number of vocalizations are significant (Test: Friedman for pairs, k=5, n=5, χ^2=17.24, p<0.01). *Significant differences between play categories that were revealed by *post-hoc* multiple comparison tests (k=5, n=5, see SIEGEL & CASTELLAN, 1988).

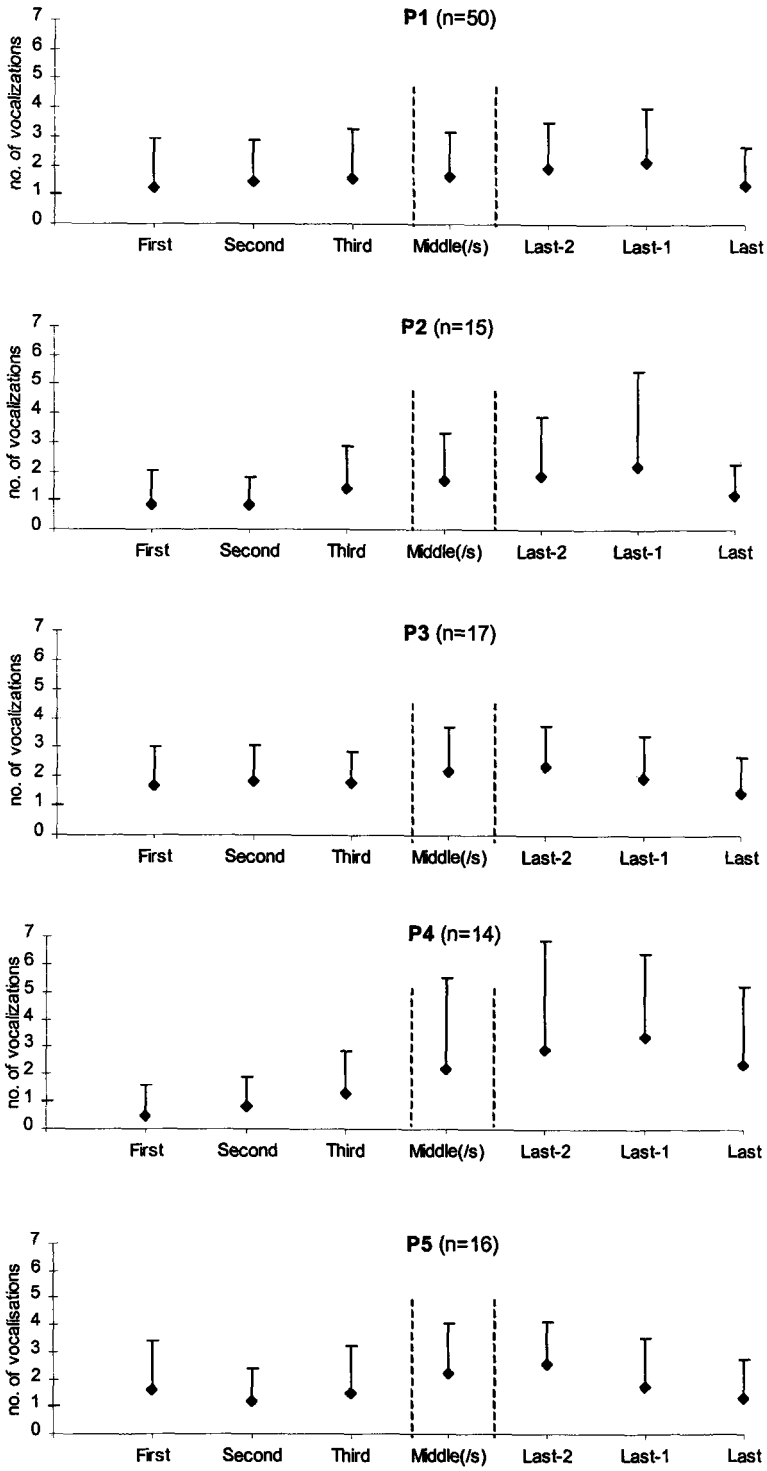

Fig. 2. Number of vocalizations recorded from five different pairs during encounters of playful 'Wrestling' (mean and standard deviation). The middle part of each figure shows the rates of vocalizations for the middle part of each 'Wrestling' (see text for further explanation).

sec of each instance of 'Wrestling' and calculated one value (vocalizations per second) for the middle part (Fig. 2). To apply this approach, we only included 'Wrestling' encounters with durations over 6 sec, thus the middle part could vary in length (range 1 – 36 sec). Vocalizations per second differed significantly between the initial, middle, and terminal part of 'Wrestling' (Friedman test, n=5, k=3, χ^2=7.6, p<0.05). The distribution of vocalizations in the first and last 3 sec was analysed in more detail. Vocalizations either started at a specific level at the beginning of 'Wrestling' and remained on that level (P1, P3, and P5), or they started at a comparatively low level and increased during the beginning (P2 and P4). The following trend emerged in all pairs for the terminal part of 'Wrestling' encounters: the number of vocalizations decreased and fewer vocalizations occurred in the last second of a 'Wrestling' encounter than in each of the two preceding seconds. These differences were statistically significant (Friedman test, n=5, k=3, χ^2=7.6, p<0.05).

ACOUSTIC FEATURES OF VOCALIZATIONS

A visual and auditory examination of recordings revealed that vocalizations produced during episodes of social play could be classified into three different types (see Fig. 3 for examples). In order to investigate the differences in the acoustic parameters of these types in more detail, we used a multi-parametric approach. A large number of acoustic parameters (169) were calculated for 289 suitable vocalizations (121 Type A; 136 Type B; 32 Type C).

There was a very good match between the assignment produced by the classification of the discriminant analysis and our classification by visual and auditory inspection of vocalizations (average correct assignment 85.5% compared with 33.3% by random assignment, χ^2=241.88, df=2, p<0.001). The discriminant analysis also provided information on which variables con-

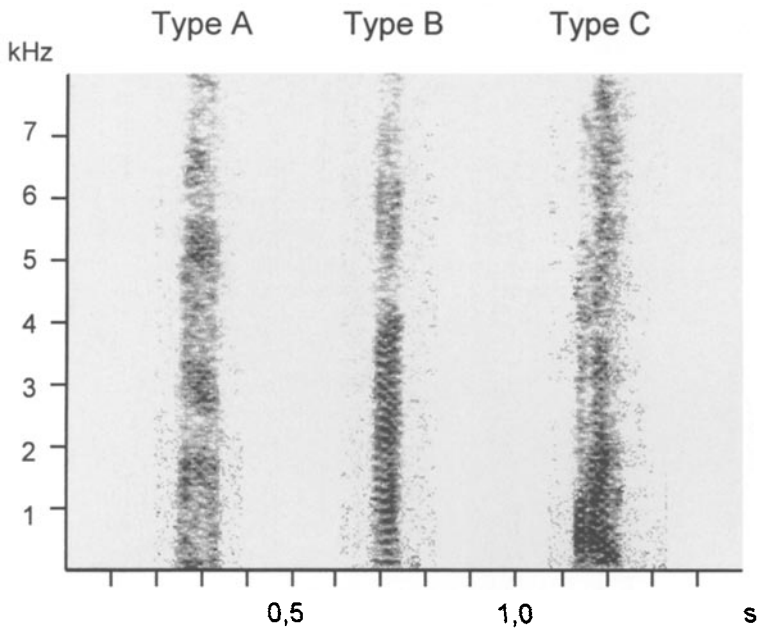

Fig. 3. Spectrograms of play signals vocalized by juvenile Barbary macaques. Identification of pattern types (A, B, and C) was confirmed by a multi-parametric measurement of 289 suitable vocalizations from 6 individuals. The most decisive parameters for discrimination between types were those describing the duration and spectral distribution of energy of vocalizations.

Table 2. The most decisive acoustic parameters for the discrimination between vocalization types A, B, and C.

Parameter	Median (first/third quartile) Type A	Type B	Type C	χ^2/significant
Duration (msec)	90 (75/110)	50 (40/65)	130 (110/170)	8.4*
Median second quartile (Hz)	4270 (3771/4623)	4884 (4526/5109)	4228 (3808/4477)	7.6*
Median third dfb (Hz)	2798 (2214/4234)	3090 (2409/3835)	2372 (1873/3427)	8.4*
Minimum numbers of dfb	4 (2/5)	8 (6/10)	4 (3/4)	8.3*
Frequency of peak amplitude at end (Hz)	3771 (1825/5912)	4453 (3090/6472)	5961 (3808/7062)	5.2 n.s.

dfb: Dominant frequency band, frequencies with an amplitude exceeding a statistical threshold in a consecutive number of cells.

tribute most to the discrimination of groups. The five most decisive parameters are listed in Table 2. To test for differences between the three vocalization types, we applied Friedman tests for the averages per pair and type (n=5, k=3, results in Table 2). In this fashion, we found that the differences in the parameters were not only due to differences between pairs. Parameters most clearly distinguishing between the groups were those characterizing the duration and the spectral distribution of energy.

As three different types of vocalizations occurred during the playful encounters, we examined whether there were differences in the serial distribution of these types. Our analysis uncovered the following relationships: Type A was the most frequent vocal pattern and was found during all types of encounters (Fig. 4). Type B occurred mainly during encounters of 'Wrestling' and 'Jumping' and less often during other encounters. Type C, finally, was rather rare, but nevertheless occurred in all play categories.

In order to analyse the use of the three vocal types during the course of playful 'Wrestling' in

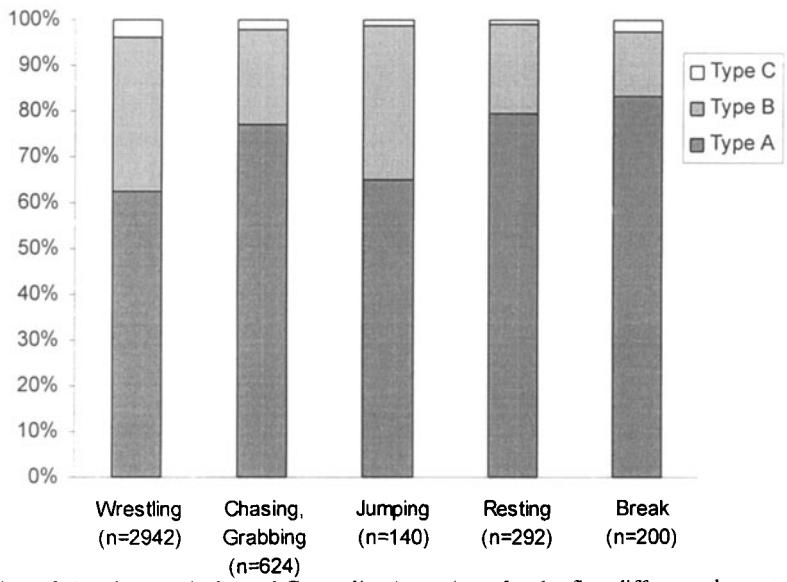

Fig. 4. Proportion of signal types A, B, and C vocalizations given for the five different play categories.

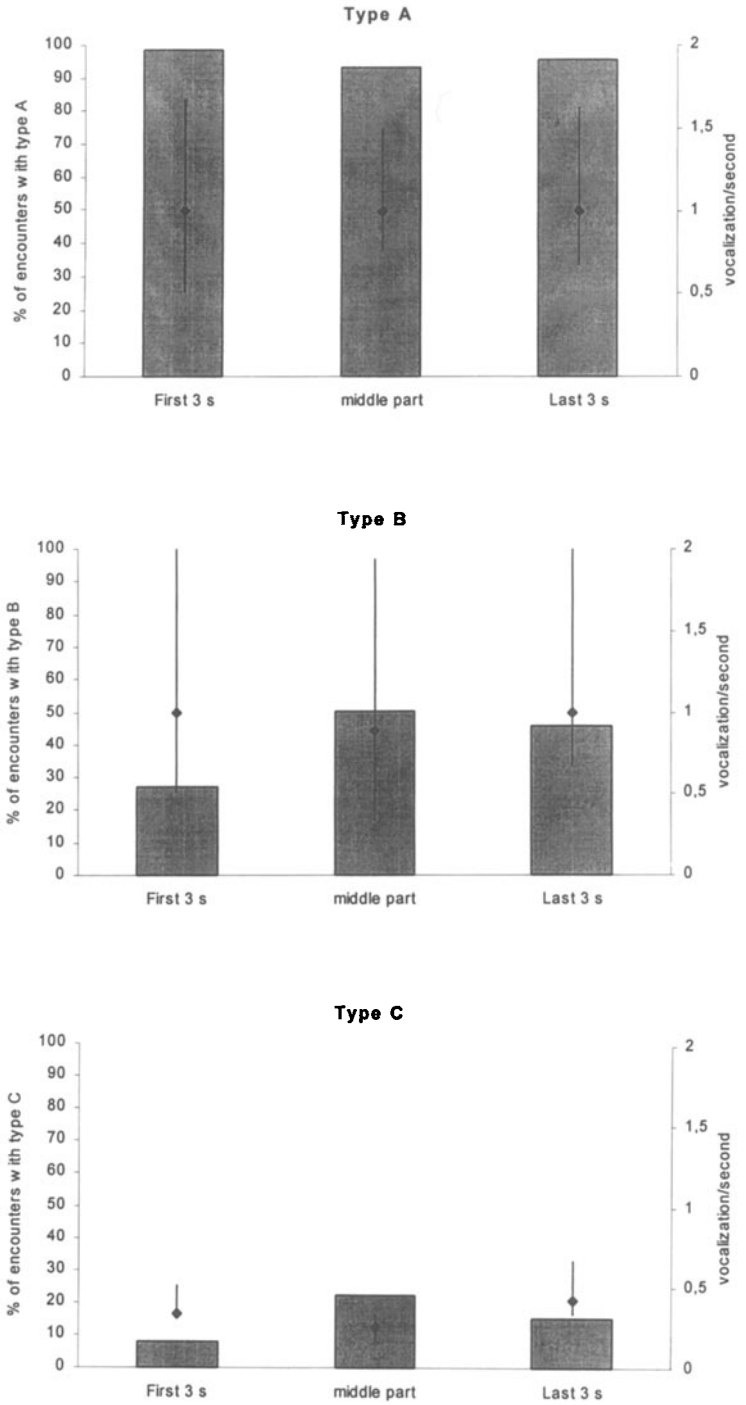

Fig. 5. Percentage of 'Wrestling' episodes with vocalizations (columns) and frequency of vocalizations per second (dots, median, and first/third quartile; episodes without any occurrence of the vocalization type were not included).

more detail, the percentage of wrestling episodes with the vocalization types were determined. Additionally, for those parts, in which the respective type was performed, we compared vocalizations in the first and last 3 sec of these 'Wrestling' encounters with the vocalizations per second in the middle part (with varying length, Fig. 5).

We found that vocalizations of Type A occurred in almost any part of each 'Wrestling' at a rate of approximately 1 per second, but with high variances (see Fig. 5, top). A different distribution was obtained for Type B. Here, vocalizations occurred only in less than 30% of starting phases and in about 50% of the middle and end phases of 'Wrestling.' However, when subjects vocalized Type B, the rate was approximately as high as that one of Type A, i.e. 1/sec (Fig. 5, middle). As referred to above, vocalizations of Type C were the least frequent ones. Also, they were produced at a considerably lower rate than the other types (around 0.3/sec) in all phases of 'Wrestling' (Fig. 5, bottom).

Finally, we examined which types were uttered as the *first* of all vocalizations during the 'Wrestling' encounters (total: 138, because 'Wrestling' encounters without any vocalization were excluded): Type A was the first vocalization in 88% of the cases, Type B in 12% of the cases. In contrast, none of the encounters were initiated by a Type C vocalization.

DISCUSSION

Our study showed that the social play of juvenile Barbary macaques is often accompanied by soft, low-volume vocalizations, which are especially frequent during bodily interactions such as wrestling, or during sudden movements such as jumping. These results confirmed the predictions derived from our hypothesis that vocal play signals may supplement and in many cases may even substitute interactional effects of visual signals, e.g. of the so-called 'play face.' A multi-parametric analysis of acoustic features validated the discrimination of three types of vocal patterns. Analyses of relationships between these signals and non-vocal interactions revealed a specific distribution of the vocalizations identified throughout a sequence of different types of playful interactions or throughout the course of a given playful encounter, respectively. During 'Wrestling,' vocalizations occurred with lower rates in the initial part and with a tendency to increase towards the terminal part, but with a decrease in the last seconds. Again, these findings are in line with our hypothesis. At the beginning of 'Wrestling,' play partners often sit face-to-face, but this is soon replaced by rapid posture-changes typical of wrestling (FREYTAG-GRUNTER, 1989). We shall discuss the implications of our findings in more detail below, and begin with some general aspects.

Social play is widespread among many taxa of mammals and is here particularly frequent in infants and juveniles (FAGEN, 1993; BEKOFF & ALLEN, 1998; PEREIRA & PREISSER, 1998). Therefore, most experts agree that playful interactions substantially contribute to the development of social competence (CHALMERS, 1980; TODT, 1986; BIBEN, 1998; BYERS, 1998), and different accounts have been proposed to explain this achievement (POIRIER & SMITH, 1974; TODT, 1997). Other investigators have also examined the communicative role of play. A major part of their research has been into the biological significance of play-accompanying signals. The mutual adjustment of playful activities is addressed for example.

To date, it is generally accepted that any engagement in social play requires a number of behavioural adjustments between mates. Such adjustments can refer to basic procedural matters and serve for example to initiate, maintain, or terminate an interaction or to affect the intensity of play (FAGEN, 1981; BEKOFF, 1974, 1995; TODT, 1997). Other adjustments seem to concern more complex matters and serve for example to regulate socially significant variables. These

may include changes between play categories (MENDOZA-GRANADOS & SOMMER, 1995), or changes of play quality depending on age, gender, and social status of playmates (HAYAKI, 1983; IMAKAWA, 1990), and especially prevent playful interactions to escalate into serious fighting (SYMONS, 1978; SMITH, 1982). There is a consensus that these different tasks are mediated by communication and thus require a differentiated signal system that, at the same time, also reliably announces the playful character of a given approach or encounter (SYMONS, 1978). Although detailed knowledge about both the composition of such a signal system and the rules of its specific application remained fragmentary, there are findings that merit some consideration. Since they are related to the results of our study, we will briefly discuss them in terms of formal, interactional, and evolutionary aspects.

From a formal perspective, signals can be subdivided into two classes: one class encompasses 'enduring displays' such as lasting postures or reiterated motor patterns that accompany a given behaviour rather coherently, and the other class comprises signals such as a specific movement or a vocalization that occurrs more sporadically (TODT & KIPPER, in press). During social play, displays of either class have been found, but the latter ones have received more attention and are given, for example, by the 'play-bow' of carnivores (e.g. BEKOFF, 1977), the 'play-face' of non-human primates (VAN HOOFF, 1972; CHEVALIER-SKOLNIKOFF, 1974; PREUSCHOFT, 1992), or the vocalizations uttered during play (GOEDEKING & IMMELMANN, 1986; BIBEN & SYMMES, 1986; MASATAKA & KOHDA, 1988; TODT et al., 1992). Now, our study provides initial evidence that juvenile Barbary macaques have access to a repertoire of alternative vocalizations and that they make specific use of these signals.

From an interactional perspective, signals are distinguished in terms of how they affect a given addressee (for play signals, e.g. PELLIS & PELLIS, 1996). As long as direct evidence for such effects is lacking, one can use indirect information to approach this issue. Such information can be gained, for example, from the typical characteristics of many playful encounters which obviously impair the visual signal channel. In other words, individuals playfully wrestling or performing a sudden jump can mutually perceive the facial expression or some other visual display of their respective mates. With this as a reference, we postulated that the use of non-visual signals should decrease in such cases. Our analyses uncovered a strong connection between vocalizations and behaviours with close body contact or sudden movements such as jumping. Therefore, we conclude that the use of vocal signals might be a strategy that substitutes the effect of visual displays. Our conclusion is supported by similar substitutions that have been mainly reported for cases of long-distance communication (TODT & NAGUIB, 2000). In addition, we have to consider that besides auditory signals tactile signals could also play a role here.

From an evolutionary perspective, signals are distinguished in terms of their adaptive value. In the study of social play, this aspect has been discussed, for example, with reference to the crucial message 'this is play' or 'what follows is play' (SYMONS, 1978; FAGEN, 1981; BEKOFF, 1974, 1995). There is a consensus that this message can be encoded by different signal patterns, which allow an individual to choose a signal channel that fits best in a given situation. On the other hand, the number of distinct signal types is often related to the range of problems that an animal attempts to solve by communication. It is thus remarkable that the subadult Barbary macaques in the present study were found to apply three different types of vocalizations. Although, as with most other play signals, it is not yet clear which specific message each vocal pattern encodes, this finding may at least indicate that there are advantages in developing and using more than one type of vocalization. In addition, it points to two further aspects. One of them concerns the plasticity of the primate voice, which is obviously well suited to generating a variety of signal patterns (TODT et al., 1988, 1995; HAMMERSCHMIDT & FISCHER, 1997). The

other is a methodological one. As methods of sound analyses are more advanced than conventional procedures used for the analyses of non-vocal displays, we cannot tell whether the identification of three types of play calls on the one hand and only one type of 'play face' (PREUSCHOFT, 1992) on the other has biological grounds or is a result of methodological differences.

Finally, we should like to address a problem that seems to be a characteristic feature of playful behaviours and concerned some variations in the use of signals in our study. Basically two aspects account here. First, the vocalizations described in this paper focussed on specific types of encounters, but could occur during other encounters as well. Second, during some of the playful encounters subjects remained completely silent, and such encounters did obviously not differ from normal, i.e. non-silent encounters. At present we are inclined to explain both cases as an expression of the widespread biological variability that is typical for the behaviour of playmates. However, a further factor should not be left out of consideration here, i.e. the domain of tactile interaction. This signal channel seems to be crucial in social play, but has hitherto hardly been treated in studies of social play. As close body contact such as that during playful wrestling comprises a major proportion of social play, we have to decide how to address and measure the interactional role of tactile signals as well.

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