Assessment of meaning and the detection of unreliable signals by vervet monkeys

DOROTHY L. CHENEY & ROBERT M. SEYFARTH

Departments of Anthropology and Psychology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, U.S.A.

and

Institute of Primate Research, National Museums of Kenya, P.O. Box 24481, Karen, Nairobi, Kenya

Abstract. Free-ranging vervet monkeys, *Cercopithecus aethiops*, who had learned to ignore playbacks of one type of call by an unreliable signaller subsequently also ignored playback of an acoustically different call by the same individual if the calls had similar referents. Such transfer did not occur if either the identity of the signaller changed or if the two calls had different referents. After repeatedly being played an intergroup call in the absence of other groups, vervets also ignored an acoustically different intergroup call given by the same individual. The monkeys did not transfer habituation, however, if the new call was given by a different individual. In tests where the referents of two calls were different, the monkeys also failed to transfer habituation across call types. Vervet monkeys who had learned to ignore an unreliable leopard alarm call did not later ignore an eagle alarm call, even when the signaller remained the same. Results suggest that vervets, like humans, process information at a semantic, and not just an acoustic, level.

Humans make judgments about the similarity or difference between words on the basis of an abstraction, their meaning. By contrast, it is often assumed that animals respond to signals not according to some abstract feature such as meaning but according to the signals' physical features (e.g. Morton 1977). Is this dichotomy valid? One method for determining how group-living animals assess the meaning of calls is through their ability to detect anomalous or unreliable signals. For example, if signallers occasionally attempt to deceive others by using multiple signals with the same information (Andersson 1980), selection should favour the ability of recipients to compare signals on the basis of their meaning, and to transfer information about the reliability of a signaller's calls from one context to another.

We investigated whether vervet monkeys, *Cercopithecus aethiops*, were capable of transferring information gained in one context to another context by repeatedly playing recordings of either the intergroup call or the alarm call of one individual to establish that individual as an unreliable signaller. We then tested whether subjects attended to this 'unreliable' individual in other contexts by playing recordings of acoustically different calls whose referents were either similar to or different from the habituating stimulus. Sub-jects' responses to 'unreliable' individuals were compared with their responses to group members whose calls had not been played previously.

METHODS

Field Experiments

Experiments were conducted on four groups of vervet monkeys living in Amboseli National Park, Kenya, over a 9-month period. Three of the groups had been observed without interruption since 1977, and one had been observed since 1983 (Cheney et al., in press). All groups were habituated to observers on foot, and the ages and maternal kin of almost all individuals were known. We conducted four series of experiments, using as stimuli calls whose referents were known from previous observations or experiments.

In the first series of experiments, we used three different calls given by vervet monkeys to the members of other groups: a grunt, a chutter and a long call or intergroup 'wrr'. Although all three calls are acoustically different from one another, each occurs only in the presence of another group, and in playback experiments each evokes a similar response: namely, orientation towards the signaller and scanning in the direction that the signaller is

Table I. A summary of the experimental protocol used in each series of trials

| | Day 1 | Day 2 | | | |
Series	Control stimulus	Habituation stimulus	Final stimulus	Signaller	Referent
1	A's ch	A's wrr × 8	A's ch	Same	Same
2	B's ch	A's wrr × 8	B's ch	Different	Same
3	A's E (L)	A's L (E) × 8	A's E (L)	Same	Different
4	B's E (L)	A's L (E) × 8	B's E (L)	Different	Different

ch: chutter; L: leopard; E: eagle. In series 1 and 2 a chutter (or in one trial, a grunt) was played. In series 3 and 4, if an eagle alarm call was played first, then the habituation stimulus was a leopard alarm call. If a leopard alarm call was played first, the habituation stimulus was an eagle alarm call (see Tables II and III).

looking (Struhsaker 1967; Cheney & Seyfarth 1982a, b; also see below). Wrrs and grunts are usually given when a group has first been spotted; only 40% ($N=96$) of all wrrs occur in encounters that include some form of aggressive interaction. In contrast, 96% ($N=47$) of all chutters are given during aggressive fights with other groups (data are based on 113 encounters that occurred during the period when the experiments were conducted). Despite their broadly similar meaning, therefore, chutters appear to be given at higher states of arousal than wrrs.

To test whether monkeys attend to these calls on the basis of their meaning, we designed an experiment that addressed the following question. If a monkey repeatedly hears animal A's wrr to another group when there is no other group present and hence ceases to respond to that call, will it also cease responding to A's chutter? We reasoned that, if two calls have similar meanings, and if monkeys use meaning to judge the relation between calls, habituation to one call of a given individual should produce habituation to the other. Alternatively, if monkeys use some other feature (such as acoustic similarity) to judge the relation between calls, these features, and not the calls' referents, should determine whether or not habituation is transferred.

Each experiment was conducted over a 2-day period (Table I). In series 1, on day 1, we played animal A's intergroup chutter (or, in one trial, its intergroup grunt) to a subject in order to establish the duration of that subject's response in the absence of other intergroup calls. The following day, we played animal A's wrr (long call) to the same subject eight times. Each wrr was separated by an average of 30 min. Then, approximately 30 min after presentation of the eighth wrr, we played animal A's chutter to determine whether habituation across call types had occurred.

Our second series of trials examined whether subjects would transfer information about the reliability of an intergroup call from one individual to another (Table I). Thus, on day 1 we played as a control the intergroup chutter of individual B. This was followed on day 2 by eight presentations of individual A's wrr, after which individual B's chutter was played again. All call donors were adult females (at least 4 years of age), and all females for whom we had the appropriate recordings were used as call donors.

Since vervet groups encounter each other on average once every 1·8 days, it was not always possible to conduct all eight trials in the absence of a naturally occurring intergroup call. No natural intergroup calls, however, ever occurred within 1 h of the final playback. Moreover, we made every effort to ensure that the conditions under which each subject heard intergroup calls were similar for both series 1 and 2. Thus, if an intergroup encounter occurred during the presentation of calls to a given subject in series 1, we always conducted the trials for series 2 on a day when another intergroup encounter occurred.

The third series of experiments examined whether habituation to a given individual would also occur if the signalling individual remained the same but the call's referent changed. The calls chosen as stimuli were alarm calls given to leopards

and eagles. Although both are predator alarm calls, they are acoustically distinct and evoke markedly different responses: leopard alarms evoke vigilance and running into trees, while eagle alarms cause vervet monkeys to look up or run into bushes (Struhsaker 1967; Seyfarth et al. 1980). In these experiments we first played, for example, individual A's eagle alarm call. Then on day 2 we played the same individual's leopard alarm call eight times, followed again by its eagle call. Leopard and eagle alarm calls were used alternately as habituating stimuli and test stimuli.

In the fourth series, both the referent and the signaller were changed. For example, individual B's eagle alarm call was played on day 1, followed on day 2 by eight presentations of individual A's leopard alarm, after which B's eagle call was played again. As before, all call donors were adult females and all available calls were used as stimuli.

In series 3 and 4, we were able to alternate leopard and eagle alarm calls as habituation and test stimuli. For two reasons, however, we did not alternate intergroup calls in this way, and instead always used a wrr as the habituation stimulus. First, chutters are not as loud as wrrs, and must be played back at closer range if they are to mimic reality. Since it is more difficult to conceal speakers at close range, repeated exposure to low-amplitude calls played at close range might have risked habituation to playbacks in general and potentially have jeopardized the experiments as a whole. Second, although wrrs are of longer duration than chutters (see below), chutters are more likely to be given in escalated encounters with other groups (see above). It therefore seemed likely that we would provide stronger and more conservative support for our hypothesis if we could demonstrate that subjects were able to transfer habituation from wrrs to chutters.

To control for individual differences in the strength of response, we used the same 10 animals as subjects in series 1 and 2, and the same nine animals in series 3 and 4. All trials using subjects in the same group were separated by at least 2 weeks when no other experiments occurred. For both series 1 and 2 and series 3 and 4, the order of trials was systematically varied. Thus, for example, some subjects were played series 1 before series 2, while others were played series 2 before series 1. In only four of the 38 paired trials were subjects ever played the call of a close relative (mother or maternal sibling). Every subject was at least 3 years of age,

and all vocal stimuli had been recorded within the previous 3 months. For logistical reasons (e.g. approach of Maasai and their cattle, entry of a subject into a swamp or a dense bush) the habituating stimulus was played only seven times in eight of the trials, while it was played nine times in six of the trials.

Although all individuals in each group could potentially hear the call playbacks, there was no evidence that subjects who were played calls late in the series habituated to the playback procedure in general. Subjects who were played calls towards the end of the series, 7 months after the experiments had begun, did not respond less strongly to calls than subjects who had been played calls earlier. Moreover, by varying systematically the order in which subjects heard each call type, we ensured that subjects did not habituate to one call type more than another.

Our behavioural measurements of responses to intergroup and alarm calls were the same as those used in previous experiments (Seyfarth et al. 1980; Cheney & Seyfarth 1982a, b). Responses to intergroup calls were measured in terms of the duration that subjects looked towards the speaker. Responses to alarm calls were measured in terms of the duration that subjects looked towards the speaker and either ran towards trees (in the case of leopard alarm calls) or looked up and/or ran into bushes (in the case of eagle alarm calls).

As with previous experiments of similar design (e.g. Seyfarth et al. 1980; Cheney & Seyfarth 1982a), both the control and the final experiments in each series were filmed. Three of the 36 trials using alarm calls and one of the 40 trials using intergroup calls, however, were filmed too poorly to allow accurate analysis. In these four cases, we relied on the spoken commentary that was made during each experiment by two and usually three observers, at least one of whom did not know which individual's call was being played. In all cases, our measures were conservative with respect to the hypothesis that individuals can transfer habituation both across call types and across individuals.

Acoustic Analysis

Acoustic analysis of all calls used in the experiments was conducted in the Linguistics Laboratory at the University of Pennsylvania, using a Kay digital sonagraph and a DEC 11/23 processor with

Table II. Results of control and final trials for series 1 and 2, using intergroup calls as stimuli

Group	Subject	Signaller in habituation trials	Signaller in control and final trials	Difference between control and final trials (s)	Signaller in control and final trials	Difference between control and final trials (s)
			Series 1		Series 2	
A	TT	LS	LS	−10·0	BA	−0·4
A	GO	LS	LS	−8·5	BA	−7·2
B	TY	CC	CC*	−1·6	MA	+1·1
B	AF	MA	MA	−6·3	CC*	−0·8
B	CC	NT	NT	−0·8	AF	−1·1
C	KU	CY	CY	−3·7	AC	0·0
C	CO	AC	AC	−6·6	AO	+5·2
C	AU	AO	AO	−1·1	CY	−1·8
4	GY	AJ	AJ	−4·8	SN	−2·8
4	SY	SN	SN	−3·5	AJ	+1·6

Responses were defined as the duration that subjects looked towards the speaker in the 10 s following playback compared with the 10 s preceding playback. A negative number indicates a decrease in the duration of response from control to final trials; a positive number indicates an increase. All habituation trials used intergroup wrrs as stimuli. Control and final trials used either chutters or intergroup grunts (*).

ILS version 4·0 for waveform editing, display and analysis. Calls used as stimuli were first displayed on sonagrams, which allowed measurement of phrase length, iteration length, and the length of inter-iteration intervals, with iteration defined as any temporally continuous burst of signal energy, and phrase defined as a group of iterations separated from other similar groups by a time interval greater than that separating iterations within the phrase (Owren 1986). Examination of regular striations in calls also revealed whether voicing was present. Second, the waveform of each phrase was digitized using ILS software, and spectra of segments at the beginning and end of each phrase were obtained through Fast Fourier Transformation with a sampling rate of 20 000 Hz, a step size of 10 ms and a window size of 25·6 ms. This procedure revealed the distribution of energy at the beginning and end of each call, and allowed us to measure spectral frequency changes over time. Finally, the fundamental frequency of each call was measured using ILS command API, following a procedure described by Owren (1986). The fundamental frequency of vervet vocalizations is known to fall between 100 and 500 Hz (Seyfarth & Cheney 1984; Owren 1986). The API algorithm returns a value within this range where regular periodicity is detected, and returns negative values where the

source frequency is aperiodic. Analysis thus reveals both the value of the fundamental frequency and (through the proportion of aperiodic readings) a measure of the stability of the fundamental frequency over time.

RESULTS

Field Experiments

In both series 1 and 2, subjects showed significant habituation following repeated exposure to wrrs. In series 1, the mean duration of response to the first wrr was 4·6 s, compared with 2·3 s to the final wrr ($r_s = -0.845$, $P < 0.01$, one-tailed). In series 2, the mean durations of response to the first and final wrrs were 4·0 and 2·5 s ($r_s = -0.809$, $P < 0.05$). When compared with control trials, all 10 subjects showed a decrease in the duration of their response to the chutter or grunt of a given individual following repeated exposure to that individual's intergroup wrr (Fig. 1 and Table II; two-tailed Wilcoxon matched-pairs test, $T = 0$, $P < 0.01$). There was no similar decrement when a different individual's grunt or chutter was played. In this case six subjects decreased their response while three increased their response (Fig. 2, Wilcoxon test, $N = 10$, 1 tie, $T = 16.5$, NS). Overall,
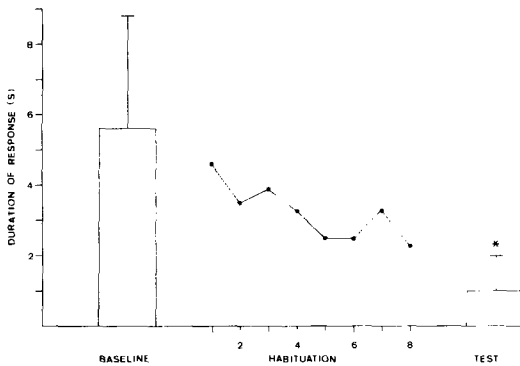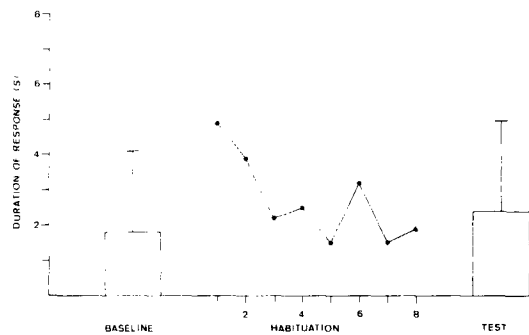
Figure 1. The duration of responses shown by 10 subjects to playback of a given individual's intergroup chutter following repeated exposure to that individual's wrr (test), compared with their responses to the same chutter in the absence of such exposure (baseline). Histograms show means and SD for all subjects. The mean duration of subjects' responses during the eight habituation trials is also shown. *$P < 0.01$ when baseline and test conditions are compared. Data are taken from Table II.
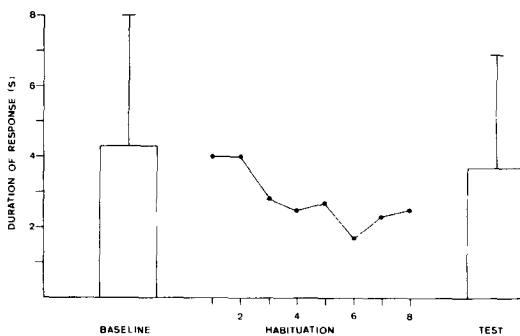
Figure 2. The duration of responses shown by 10 subjects to playback of a given individual's chutter following repeated exposure to a different individual's wrr (test), compared with their responses to the same chutter in the absence of such exposure (baseline). Legend as in Fig. 1.

subjects showed significantly greater decrement in response when played a call with a similar referent from the same individual than when played a call with a similar referent from a different individual (Wilcoxon test, $N = 10$, $T = 2$, $P < 0.01$; Table II).

In contrast to trials using intergroup calls, subjects exposed to unreliable alarm calls showed no transfer of habituation to another type of alarm call, regardless of whether the signaller was the same or different (Figs 3 and 4; Table III). This occurred even though subjects did habituate to

Figure 3. The duration of responses shown by nine subjects to playback of a given individual's leopard (or eagle) alarm call following repeated exposure to that individual's eagle (or leopard) alarm call (test), compared with their responses to the same alarm call in the absence of such exposure (baseline). Legend as in Fig. 1. Data are taken from Table III.

repeated exposure to the same alarm call. The mean durations of response to the first and final alarm calls in series 3 were 4·9 and 1·9 s ($r_s = -0.708$, $P < 0.05$). In series 4, the mean durations of response to the first and final alarm calls were 3·6 and 0·5 s ($r_s = -0.922$, $P < 0.01$). In series 3, when the caller remained the same, three of nine subjects showed a decrement in response to the final call compared with the control call. When the caller was changed, five of nine subjects showed such a decrement. Thus, subjects who had habituated to individual A's leopard alarm call after eight unreliable exposures did not subsequently ignore A's eagle alarm call.

Although we have no direct empirical evidence that vervet monkeys are able to distinguish between the alarm calls of different individuals, for several reasons it seems unlikely that the monkeys' failure to habituate to alarm calls occurred simply because the calls were not individually identifiable. Alarm calls do show considerable individual acoustical variation, and individual recognition has been demonstrated in all other calls that have been tested thus far (e.g. screams, grunts, wrrs, chutters, pant threats: Cheney & Seyfarth 1980, 1982a, b; Seyfarth & Cheney 1984; Owren 1986). Moreover, it is far easier for the human observer to learn to recognize different individuals' alarm calls than their grunts or screams.

Acoustic Analysis

To determine whether the responses of vervet

Table III. Results of control and final trials for series 3 and 4, using alarm calls as stimuli

		Series 1			Series 2	
		Signaller in habituation trials	Signaller in control and final trials	Difference between control and final trials (s)	Signaller in control and final trials	Difference between control and final trials (s)
Group	Subject					
A	GO	BA (E)	BA (L)	+0·5	LS (L)	+0·7
A	ES	BA (E)	BA (L)	+3·0	LS (L)	−0·3
B	WM	AM (L)	AM (E)	−3·2	AF (E)	−3·7
B	CC	NT (L)	NT (E)	+4·8	MA (E)	0·0
B	NU	NT (L)	NT (E)	+2·3	AF (E)	+0·4
C	AC	LO (E)	LO (L)	+0·5	CY (L)	+1·4
C	CZ	LO (L)	LO (E)	0·0	AC (E)	−2·3
C	AO	LO (L)	LO (E)	−2·0	CY (E)	−0·5
4	HH	AJ (E)	AJ (L)	−1·2	SN (L)	−2·5

Responses were defined as the duration that subjects either looked towards the speaker or ran into trees (in the case of leopard alarms) or looked up or ran into bushes (in the case of eagle alarms) in the 10 s following playback compared with the 10 s preceding playback. A negative number indicates a decrease in the duration of response from control to final trials; a positive number indicates an increase. E: eagle alarm calls; L: leopard alarm calls.

Table IV. Results of an analysis of the acoustic features of alarm calls to leopards, alarm calls to eagles, intergroup wrrs, and intergroup chutters and grunts*

	Vocalization			
	Alarm calls to		Intergroup calls	
Acoustic feature	Leopard	Eagle	Wrrs	Chutters/Grunts
Call length (ms)	128·9 (47·3)	141·3 (50·0)	6128·0 (1758·5)	302·7 (210·0)
No. of iterations per phrase	1·22 (0·44)	3·0 (1·5)	6·4 (2·5)	4·9 (2·7)
Iteration length (ms)	103·9 (35·9)	37·7 (21·4)	511·6 (336·6)	46·8 (67·8)
Inter-iteration length (ms)	55·0 (35·4)	23·2 (6·8)	460·4 (197·4)	35·1 (23·1)
Percentage of signal energy†	93·0% (14·0)	70·1% (10·3)	47·5% (18·2)	54·7% (19·1)
Voiced/Unvoiced	Voiced	Unclear	Voiced	Unclear
Strongest frequency at beginning (Hz)	3417 (841)	1289 (729)	1190 (299)	2190 (1253)
Strongest frequency at end (Hz)	3211 (1069)	2000 (1655)	1270 (695)	1959 (1353)
Frequency change‡	8/9 f	6/9 s	6/10 s	10/11 s
No. of calls with secondary peaks	5/9	7/9	8/10	10/11
Fundamental frequency (Hz)	667 (276)	371 (274)	294 (231)	191 (69)
Stability of fundamental frequency§	39·0%	32·6%	19·8%	16·7%

* Values shown represent means, with standard deviations in parentheses, for nine leopard alarms, nine eagle alarms, 10 intergroup wrrs and 11 intergroup chutters or grunts. Phrase, iteration, and inter-iteration interval are defined in the text.
† The proportion of a signal that contains acoustic energy as opposed to intervals of silence.
‡ Change in peak frequency over the duration of the call (s: stable; f: falling).
§ The proportion of frames in which the ILS command API returned a valid value for the fundamental frequency; this provides an indirect measure of the stability of fundamental frequency over time (see Methods).
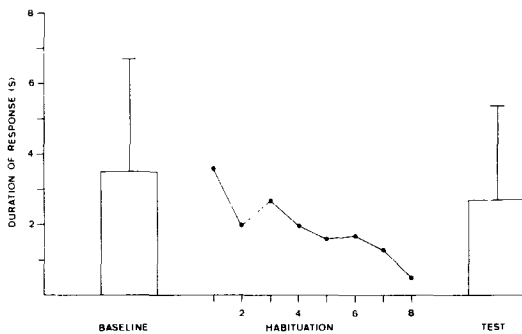
Figure 4. The duration of responses shown by nine subjects to playback of a given individual's leopard (or eagle) alarm call following repeated exposure to a different individual's eagle (or leopard) alarm call (test), compared with their responses to the same alarm call in the absence of such exposure. Legend as in Fig. 1. Data are taken from Table III.

monkeys were influenced more by the calls' physical properties than by their meanings, we conducted an acoustic analysis of all vocalizations used during the experiments (Table IV). Since it is not known precisely what acoustic features are most salient to the monkeys, a number of measurements were taken of the overall physical properties of each call, characteristics of the underlying waveform, and characteristics of the call's spectrum.

Alarm calls given to leopards were voiced, with peak frequencies higher than most other vocalizations, around 3400 Hz (Fig. 5). They consisted of a single, or at most two, iterations, with a rapidly falling frequency over the duration of the call. By contrast, while most eagle alarms showed evidence of voicing this was not always apparent (see also Owren 1986). The peak frequency for eagle alarms was around 1290 Hz. They contained an average of three iterations, and exhibited a stable peak frequency over the duration of the call. Among intergroup vocalizations, wrrs were clearly voiced, while chutters and grunts varied. Wrrs had a mean peak frequency of 1190 Hz, chutters and grunts a mean peak frequency of 2190 Hz. Both calls had stable frequency peaks over the duration of the call, wrrs contained on average six iterations while chutters and grunts contained four. Eagle alarm calls were of longer duration than leopard alarm calls, while wrrs were longer than chutters.

To summarize, there was no evidence that intergroup calls were consistently more similar or different from each other than were alarm calls. It

therefore seems unlikely that any differences in subjects' responses across trials could be explained by the acoustic structure of the call types used.

DISCUSSION

It is important to emphasize that the calls used in these experiments were acoustically different from one another. Thus when subjects ignored an individual's intergroup chutter following repeated exposure to that individual's intergroup wrr, they had habituated not to a particular acoustic signal but to a particular referent. Such habituation suggests the ability to classify physically dissimilar stimuli into abstract categories based on their meaning. Vervet monkeys, like humans (e.g. Yates & Tuhl 1979), appear to process information at a semantic level, and not just according to acoustic similarity. The fact that subjects showed less transfer of habituation when played the call of another animal suggests that vervet monkeys attended to both the identity of the signaller and the call's meaning.

Subjects showed no transfer of habituation when they were played different alarm calls, even when they came from the same individual. This may have occurred because vervet monkeys simply could not afford to ignore a new call by a previously unreliable individual in a potentially dangerous context, although subjects did habituate to repeated exposure of the same alarm call. It also suggests that subjects may have perceived unreliable signallers as 'mistaken' rather than as generally deceitful. This is perhaps not surprising, since the experiments were conducted on group-living animals who interacted regularly with each other, and whose relationships were comprised of both cooperative and competitive interactions.

It is also possible that transfer of habituation did not occur whenever listeners judged the meanings of two calls to be different. Thus, given evidence that one individual was unreliable when signalling about leopards, subjects did not assume that the same individual would be unreliable when signalling about eagles. The monkeys appeared to judge leopard alarms and eagle alarms as different from one another, even when they seem (from our perspective) to be of the same general referential class. Thus, in contrast to language-trained chimpanzees, *Pan troglodytes* (e.g. Premack 1976; Savage-Rumbaugh et al. 1980), vervet monkeys
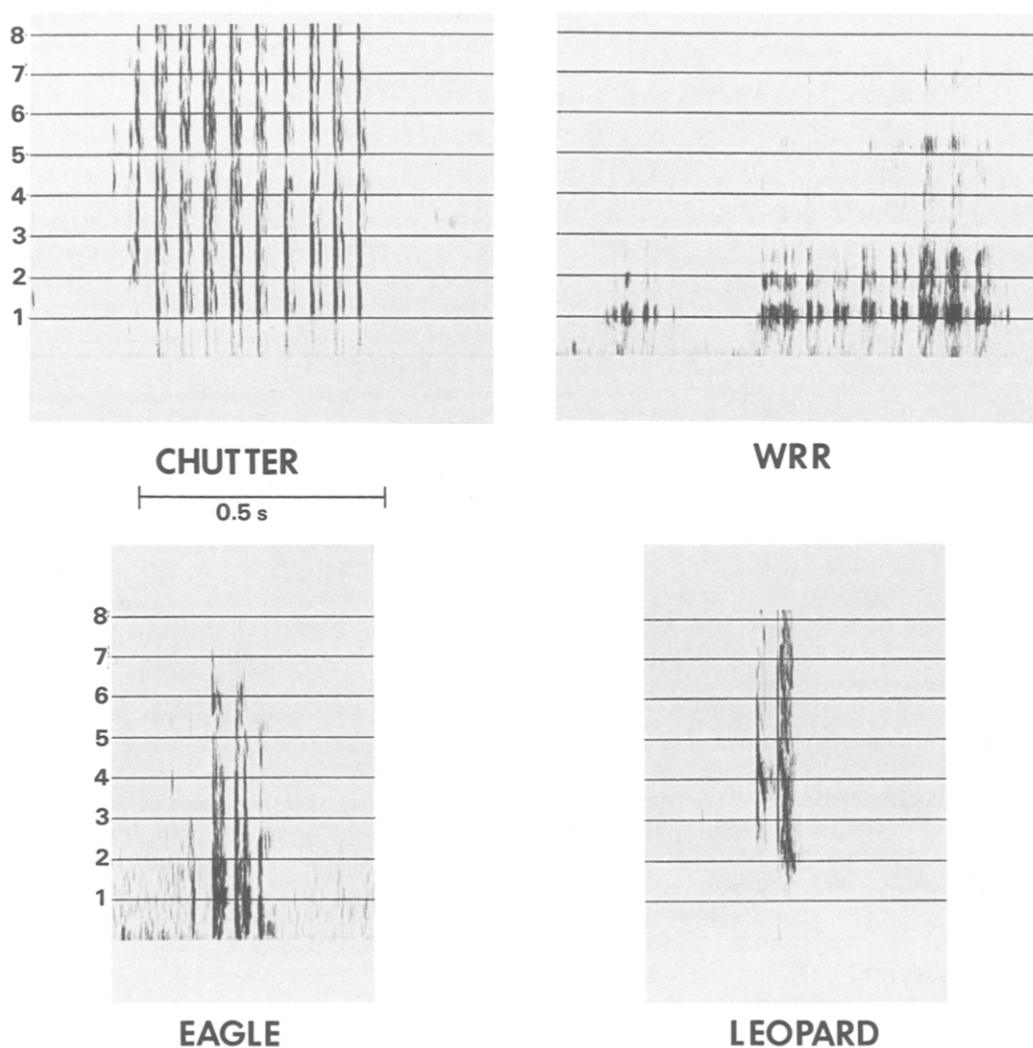
Figure 5. Chutter and wrr vocalizations given by adult female SN, and alarm calls to eagles and leopards given by adult female AM. Horizontal lines show frequency in units of 1 kHz.

gave no indication that different alarm calls were grouped into a higher order unit; for example, a general 'warning' or 'predator' category. Instead, such classification appeared to be restricted to calls whose referents were more similar.

The habituation/dishabituation procedure described in this paper is widely used in psychological tests of pre-verbal infants (e.g. Eimas et al. 1971). The test determines whether subjects can perceive a particular distinction, and it assumes that subjects make use of any distinctions that they can perceive. There is some evidence, however, that chimpanzee infants who can perceive relational distinction when tested using the habituation procedure may nevertheless be unable to make use of the same distinction in a match-to-sample test (Oden et al., in press). This suggests that habituation data alone cannot be used to argue that vervet monkeys are aware of their ability to make abstract judgements when assessing a call's meaning. The habituation

data suggest that they have the requisite skills, but we still cannot say definitively that they regularly make use of such skills.

It could be argued that the results described here resemble a form of 'sensory preconditioning', in which two stimuli are treated as similar because of their prior temporal association (e.g. Brogden 1939; Jacobson & Premack 1970). Thus, for example, intergroup wrrs and chutters may have been judged as similar not because they have similar referents but because they are temporally associated, whereas alarm calls to leopards and eagles were judged as different because they rarely occur in close temporal association. Moreover, if individuals often give different intergroup calls in rapid sequence, subjects might have been particularly likely to habituate to trials involving the same signaller.

Although different intergroup calls might almost by definition be expected to occur in closer temporal association than alarm calls to different predators, it should be emphasized that wrrs and chutters occurred contiguously in only 27% of all intergroup encounters ($N = 113$). Usually, wrrs and chutters were given by different individuals; these calls were given by only one individual in only 3% of all encounters. Thus, although the two calls appeared to have closely related referents, they did not necessarily occur in close temporal association.

A major issue in animal communication concerns whether vocalizations should reliably signal information and how unreliable signals might be detected (e.g. Andersson 1980; Caryl 1982; Krebs & Dawkins 1984; Cheney & Seyfarth 1985). The results presented here suggest that the detection of unreliable signals is influenced by the ways in which animals assess and compare signals based upon their meaning. Deception will be constrained if recipients can recognize a false relation between a call and its apparent referent, and it will be further constrained if recipients can transfer information about the reliability of a signaller's calls from one context to another. In the case of vervet monkeys, and perhaps other primates as well, selection may have favoured the ability to recognize 'spheres' of meaning and the transfer of information gained in one sphere to other, related ones. Individuals who have come to recognize that one type of call by a given signaller is unreliable appear to transfer their scepticism to other calls of broadly similar meaning, but not to calls whose referents are different. Thus deception, if it occurs, is less likely to be detected when contexts are changed between successive deceptive acts than when contexts remain the same.

ACKNOWLEDGMENTS

REFERENCES

Andersson, M. 1980. Why are there so many threat displays? *J. theor. Biol.*, **86**, 773–781.

Brogden, W. J. 1939. Sensory pre-conditioning. *J. exp. Psychol.*, **25**, 323–332.

Caryl, P. G. 1982. Telling the truth about intentions. *J. theor. Biol.*, **97**, 679–689.

Cheney, D. L. & Seyfarth, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. *Anim. Behav.*, **28**, 362–367.

Cheney, D. L. & Seyfarth, R. M. 1982a. How vervet monkeys perceive their grunts: field playback experiments. *Anim. Behav.*, **30**, 739–751.

Cheney, D. L. & Seyfarth, R. M. 1982b. Recognition of individuals within and between free-ranging groups of vervet monkeys. *Am. Zool.*, **22**, 519–529.

Cheney, D. L. & Seyfarth, R. M. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour*, **94**, 150–166.

Cheney, D. L., Seyfarth, R. M., Andelman, S. J. & Lee, P. C. In press. Reproductive success in vervet monkeys. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock). Chicago: University of Chicago Press.

Eimas, P. D., Siqueland, P., Jusczyk, P. & Vigorito, J. 1971. Speech perception in human infants. *Science, N. Y.*, **171**, 303–306.

Jacobson, E. & Premack, D. 1970. Choice and habituation as measures of response similarity. *J. exp. Psychol.*, **85**, 30–35.

Krebs, J. R. & Dawkins, R. 1984. Animal signals: mindreading and manipulation. In: *Behavioral Ecology. An Evolutionary Approach*, 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Sunderland, Massachusetts: Sinauer.

Morton, E. S. 1977. On the occurrence and significance of motivation–structural rules in some bird and mammal sounds. *Am. Nat.*, **111**, 855–869.

Animal Behaviour, 36, 2

Oden, D., Thompson, R. K. R. & Premack, O. In press. Spontaneous transfer of matching by infant chimpanzees. *J. exp. Psychol.: Anim. Behav. Proc.*

Owren, M. J. 1986. The acoustic features of alarm calls in vervet monkeys (*Cercopithecus aethiops*): perspectives on primate vocal behavior and the evolution of human speech. Ph.D. thesis, Indiana University, Bloomington.

Premack, D. 1976. *Intelligence in Apes and Man*. Hillsdale, New Jersey: Lawrence Erlbaum.

Savage-Rumbaugh, E. S., Rumbaugh, D. M., Smith, S. T. & Lawson, J. 1980. Reference: the linguistic essential. *Science, N.Y.*, **210**, 922–925.

Seyfarth, R. M. & Cheney, D. L. 1984. Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature, Lond.*, **308**, 541–543.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim. Behav.*, **28**, 1070–1094.

Struhsaker, T. T. 1967. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: *Social Communication Among Primates* (Ed. by S. A. Altmann), pp. 281–324. Chicago: University of Chicago Press.

Yates, J. & Tuhl, N. 1979. Perceiving surprising words in an unattended auditory channel. *Q. J. exp. Psychol.*, **31**, 281–286.