

Conceptual Semantics in a Nonhuman Primate

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Some animal vocalizations have been described as *referential*, or *semantic*, because individuals respond to them as if they designate some object or event. Alternatively, subjects may simply attend to the acoustic features of calls rather than their meanings. Field playback experiments on diana monkeys (*Cercopithecus diana diana*) tested these hypotheses using the calls of leopards and eagles and the males' alarm calls to these predators. In the experiment, 2 calls were played in sequence, separated by 5 min of silence, such that they were either (a) similar in acoustic and semantic features, (b) similar in semantic features only, or (c) different in both acoustic and semantic features. Subjects readily transferred habituation across acoustic but not semantic features, suggesting that they attended to the calls' underlying meanings.

In many animal species, particular vocalizations appear to provide nearby listeners with information about some object or event—such as a predator, food, or another group—that is physically separate from the calling individual. The clearest example comes from studies of the alarm calls of vervet monkeys (*Cercopithecus aethiops*). Vervets give acoustically distinct alarm calls to leopards, eagles, and snakes (Struhsaker, 1967). When a call is played to subjects in the absence of actual predators, they respond as if they have seen the predator itself (Seyfarth, Cheney, & Marler, 1980). Similar data suggest that natural semantic communication may be widespread in the animal kingdom; for example, it may occur among rhesus macaques (*Macaca mulatta*; H. Gouzoules, S. Gouzoules, & Tomaszycki, 1998), diana monkeys (*Cercopithecus diana*; Zuberbühler, Noë, & Seyfarth, 1997), ring-tailed lemurs (*Lemur catta*; Macedonia, 1990), or domestic chickens (*Gallus domesticus*; Gyger, Marler, & Pickert, 1987). It seems that whenever a particular vocalization is produced consistently after the occurrence of

a specific event, for instance the appearance of food or a predator, that vocalization acquires strong response-evoking power and elicits the same behavior as would the corresponding event itself.

A second line of evidence for referential signaling comes from the psychological laboratory. Here, members of several species have successfully been trained to master various arbitrary signal–referent relationships assigned by their experimenters; these animals include chimpanzees (*Pan troglodytes*; Premack, 1970), bonobos (*Pan paniscus*; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rupert, 1986), bottle-nosed dolphins (*Tursiops truncatus*; Herman, Pack, & Morrel-Samuels, 1993), California sea lions (*Zalophus californianus*; Schusterman & Krieger, 1984), and African grey parrots (*Psittacus erithacus*; Pepperberg, 1990). Although these studies of captive subjects say little about the adaptive value of such communication under natural conditions, they clearly demonstrate that the necessary cognitive competence for semantic communication is present. Thus, the question no longer seems to be whether animals are able to produce and respond to semantic signals; rather, it has become one of what kinds of cognitive structures support this ability and how it has evolved.

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Perceptual or Conceptual Semanticity?

In the wild, vocalizations are considered to be semantic if the following causal relations can be shown: First, a unique environmental event (e.g., an eagle attack) causes the animal (e.g., a vervet monkey) to produce a physically unique signal (e.g., an "eagle" alarm call). Second, the signal alone is sufficient to elicit the same response as the environmental event typically does (e.g., run into cover; Macedonia & Evans, 1993).

However, by this definition one cannot distinguish in principle between, for example, the alarm call system of vervet monkeys (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 1992a, 1992b) and communication about distant food sources by honey bees (von Frisch, 1950). In both cases, a specific environmental event (a predator or a food source) elicits a signal (a specific call or dance), and this

signal alone seems to be sufficient to elicit the same behavior in nearby conspecifics as would the signal's referent. The processing of meaning by animals, in other words, could be merely perceptual (Seyfarth & Cheney, 1992a, 1992b): Recipients of a signal might simply be attending to the physical features of an alarm call or a dance motion, and it is this percept alone, rather than some intervening mental representation of the referent, that drives subsequent behavior. Alternatively, animals' processing of meaning could be of the kind that presumably underlies human language. Here, the acoustic-perceptual properties of speech sounds are only relevant insofar as they refer to associated cognitive structures (e.g., Yates & Tule, 1979). The linguistic processing of meaning by humans, therefore, seems to be conceptual.

Most research on animal semantic communication conducted so far has not specifically distinguished between perceptual and conceptual semanticity (but see Cheney & Seyfarth, 1988). Instead, ethologists have labeled instances of semantic communication as being at least functionally referential (e.g., C. S. Evans, L. Evans, & Marler, 1993; Hauser, 1996, p. 508), without distinguishing among the different mechanisms that might underlie such behavior.

Semantic Communication in the Diana Monkey (*Cercopithecus diana diana*)

The diana monkey is an arboreal guenon species that inhabits the West African rain forest belt between Gambia and Ghana (Wolfheim, 1983). Because of poaching and deforestation, populations have vanished in most areas, and the species is now highly vulnerable to extinction (Oates, 1994). Adults produce acoustically distinct alarm calls in response to both eagles and leopards, two of their main predators. There is a striking sexual dimorphism in the structure of the alarm calls of the adults (see Figure 1).

Prior research has shown that when the alarm calls of a male are played back to a group of dianas, the females respond with their own corresponding alarm calls, suggesting that the calls function as semantic signals (Zuberbühler et al., 1997). In what sense, however, do female diana monkeys understand the meaning of the male alarm calls? Do they access a stored representation of an eagle when they hear a male's eagle alarm call or are they simply and reflexively responding to the acoustic features of the calls? This study investigates whether the females' response to males' alarm calls is based on attending (a) to the calls'

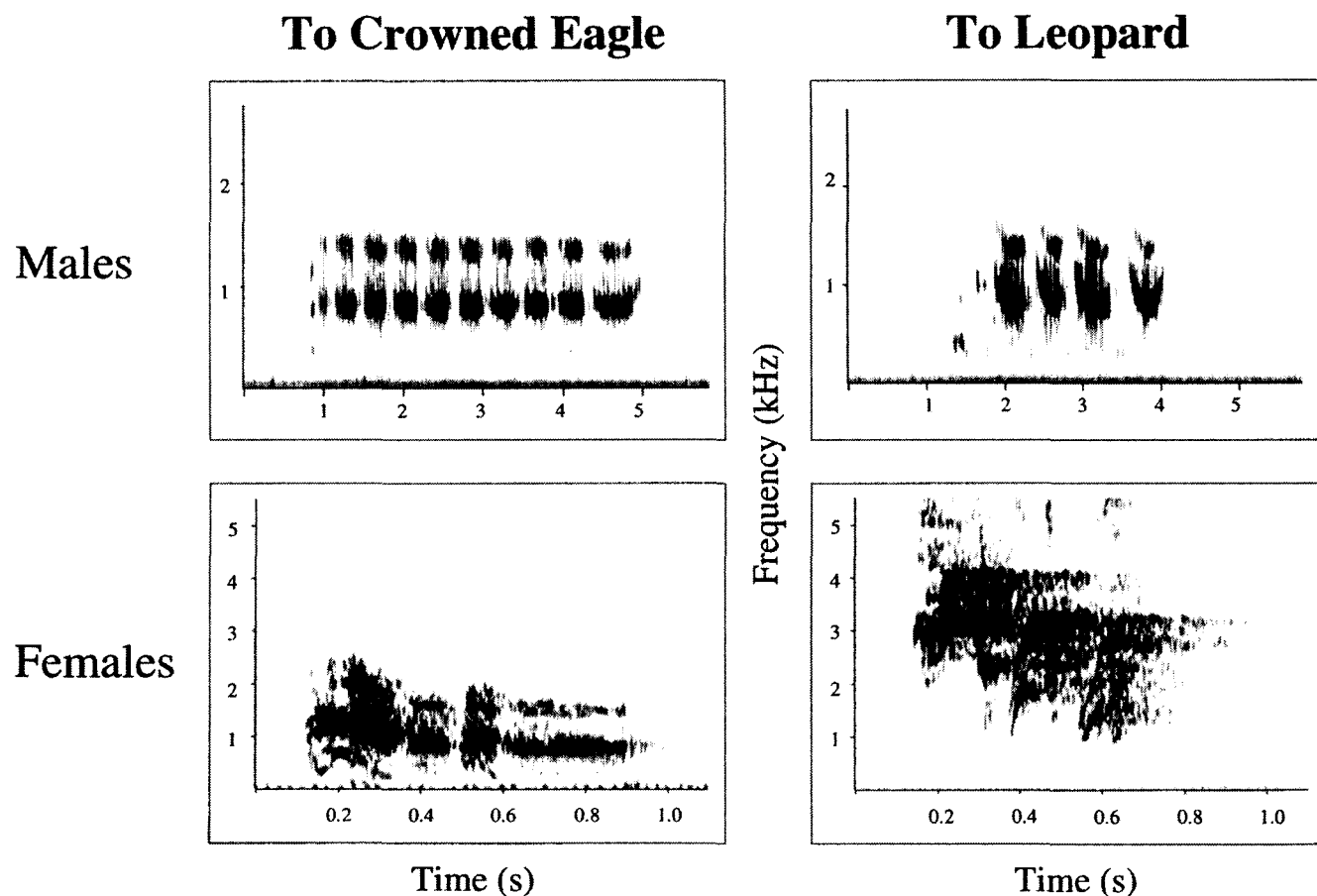


Figure 1. Alarm calls of male and female diana monkeys in response to crowned eagles and leopards.

acoustic features or (b) to a cognitive structure associated with these acoustic features, such as a mental representation or concept of the predator.

Method

Study Site and Subjects

Data were collected in the Taï National Park, Côte d'Ivoire, between July 1994 and June 1997, in an approximately 50-km² study area of primary rain forest surrounding the Institut d'Ecologie Tropicale (latitude 5° 50' north, longitude 7° 21' west). Diana monkeys (*Cercopithecus diana diana*) live in small groups of about 20 individuals with 1 fully adult male and several adult females with their offspring. None of the groups examined in this study were habituated to human observers, and most were exposed to human poaching. Because the home ranges of the groups were unknown, we could not determine exactly how many groups were tested in total. However, because the diana monkeys' home range size in the study area is approximately 0.5 km² (Höner, Leumann, & Noë, 1997) and because females are territorial (Hill, 1994), we can infer that we tested at least 30 different groups throughout the study area.

Materials

The playback stimuli were broadcast with a Sony WMD6C Professional Walkman connected to a Nagra DSM speaker-amplifier. The vocal responses of the monkeys to the playback stimuli were recorded with the Sony WMD6C or TCM5000EV recorders in combination with a Sennheiser directional microphone. Using Canary 1.2 software (Charif, Mitchell, & Clark, 1995), we digitized and displayed the monkeys' vocal responses as sonograms. Sounds were sampled at 44 kHz/16 bits and displayed using a Hanning window function (analysis resolution: 342 Hz/11.6 ms; grid resolution: 21.5 Hz/2.9 ms/75% overlap; fast Fourier transform size: 2,048 points).

Playback Stimuli

Four different vocalizations were used as playback stimuli: (a) leopard—15 s of growls of an African leopard (*Panthera pardus*), (b) eagle—15 s of shrieks of a crowned eagle (*Stephanoaetus coronatus*), (c) leopard alarms—a series of male diana monkey alarm calls given in response to a leopard, or (d) eagle alarms—a series of male diana monkey alarm calls given in response to a crowned eagle. Male alarm calls were played in a series of five calls, lasting approximately five times 2.5 s for leopard alarm calls and five times 4 s for eagle alarm calls. To control for stimulus duration, the longer lasting eagle alarm calls were played in a series of three calls in half of the cases.

Prior work on diana monkeys (Zuberbühler et al., 1997) and other monkey species in the Taï forest (Zuberbühler, Jenny, & Bshary, in press) has shown that the presentation of acoustic predator models provides a reliable way of simulating predator presence. Acoustic analyses on a smaller set of diana monkey vocalizations further indicated that the vocal response to real leopards and to playbacks of leopard growls as well as the vocal response to real crowned eagles and to playbacks of crowned eagle shrieks were identical (Zuberbühler, 1996–1997). Male diana monkeys regularly give alarm calls in long series when they detect an eagle or a leopard. The alarm calls in response to the two predators sound very similar to humans but show subtle acoustic differences in the spectral and temporal parameters (Zuberbühler et

al., 1997). Alarm calls in response to leopards also consist of fewer syllables than alarm calls in response to eagles (see Figure 1), but it is not yet clear whether the number of syllables conveys information to nearby listeners.

Recordings of leopard growls were purchased from the National Sound Archive, London. All other vocalizations were recorded in the study area. Figure 2 depicts the different predator vocalizations as sonograms.

Experimental Design

A priming technique was developed to test whether females attended to the acoustic-perceptual alone or to both the acoustic-perceptual and the semantic-conceptual features of the male alarm call. The experiment included three types of trials: a baseline, a test, and a control condition. In each trial, a diana monkey group heard two playback stimuli, a prime and a probe, separated by an interval of 5 min of silence. For example, subjects first heard male diana monkeys' leopard alarm calls; after 5 min of silence, the growls of a leopard followed. An interval of 5 min was chosen because pilot trials had shown that after this time the behavior and calling rates of nearby animals had usually returned to baseline levels. Across conditions, prime and probe stimuli varied with respect to their acoustic-perceptual and semantic-conceptual resemblance. In the baseline condition, both the acoustic and semantic features were alike (e.g., eagle shrieks were followed by the exact same eagle shrieks). In the test condition, only the semantic features were alike (e.g., males' eagle alarm calls were followed by eagle shrieks), whereas in the control condition, both the acoustic and semantic features were different (e.g., males' leopard alarm calls were followed by eagle shrieks). Figure 3 illustrates the experimental design.

Predictions

Baseline condition. Subjects heard a predator call (the prime) followed by the same predator call (the probe). Because both the acoustic and the semantic features were repeated in the prime and probe, we expected a habituation effect. In other words, we expected subjects to respond strongly to the prime (i.e., to produce many alarm calls) but to respond weakly to the probe (i.e., to produce few alarm calls). Because both the acoustic and the semantic features had to remain constant, we always used the exact same predator vocalizations as both the prime and the probe stimuli.

Test condition. Subjects heard male diana monkey alarm calls followed by the corresponding call of the actual predator. Because only the semantic features but not the acoustic features were repeated in the prime and probe, we expected subjects to show a strong response to the prime and (a) a strong response again to the probe if they attended to the acoustic-perceptual features only or (b) a weak response to the probe if they also attended to the semantic-conceptual features.

Control condition. Subjects heard a male diana monkey alarm call followed by the call of another, noncorresponding, predator. Because both the acoustic and the semantic features were different in the prime and probe, we expected subjects to show a strong response to both the prime and the probe stimuli.

Data Collection

In conducting playback experiments, the study area was systematically searched until a group was located. When a group was located, typically by hearing their vocalizations, their geographical location was marked on a map. Unhabituated diana monkeys show

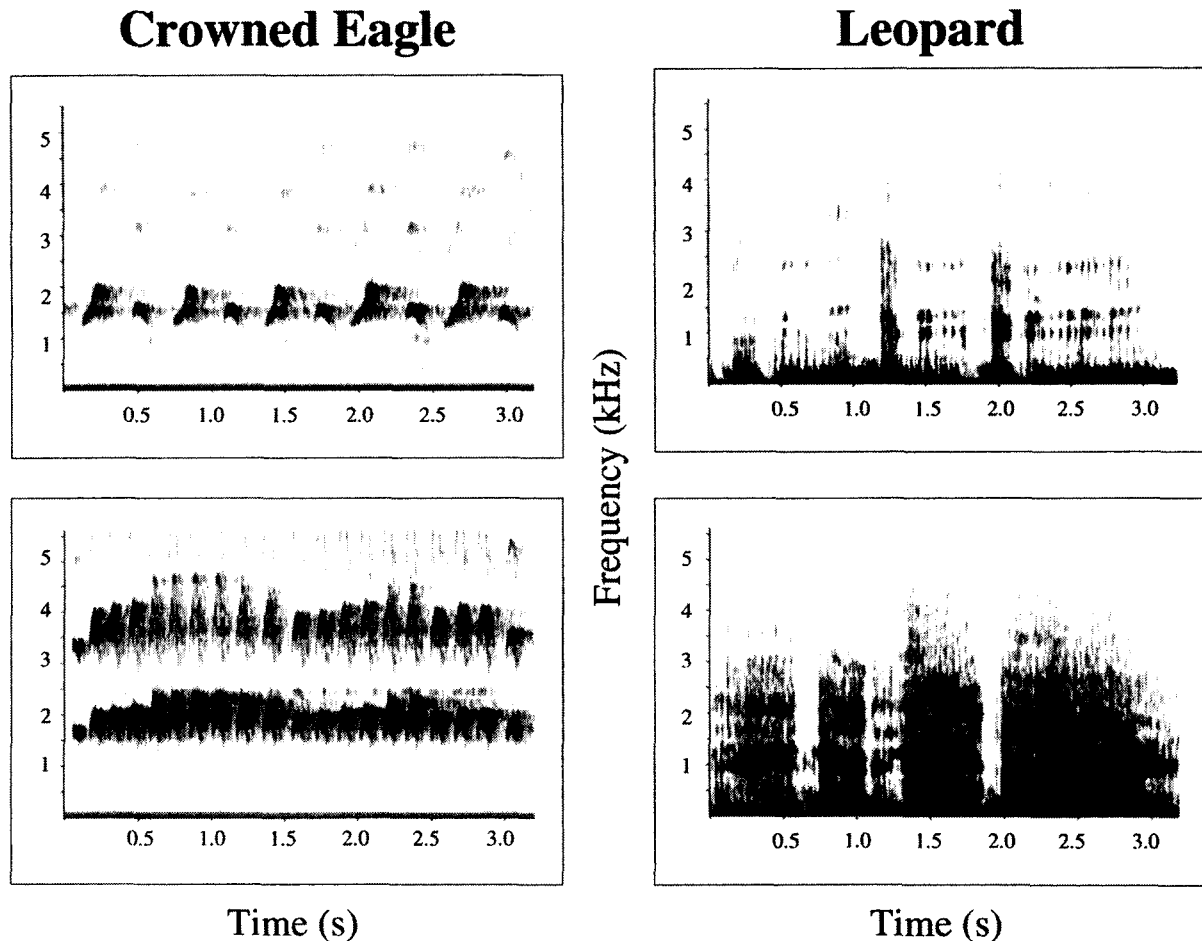


Figure 2. Representative exemplars of the predator vocalizations used as experimental playback stimuli.

a strong antipredator response when detecting humans. Typically, 1 individual gives a few alarm calls, and the group then rapidly progresses away for a few trees to hide silently in the vegetation of the upper canopy. Thus, the group's vocal behavior was monitored for at least 30 min while visual contact was avoided completely. If no predation event occurred during that time period and no monkey had detected the observer or part of the equipment, a playback trial was initiated. The speaker was positioned at an elevation of approximately 2 m from the ground and at a distance of approximately 50 m from the group (i.e., well outside of the group's visual range). Recordings of the subjects' vocal responses began 5 min before the first playback stimulus and lasted for 15 min.

To avoid unwanted dependencies in the data, we never tested a particular group more than once in each of the six experimental conditions. This procedure was ensured by testing a group only if it was located at least 1 km (i.e., two home range diameters) away from any previously conducted trial of the same series. A total of 89 playback trials was conducted. Of these trials, 31 could not be analyzed because monkeys detected the experimenter or part of the equipment ($n = 22$), a predation event occurred ($n = 5$), equipment failed ($n = 2$), or the group progressed away ($n = 2$).

Dependent Variables and Statistics

The dependent variables in all trials were the number of leopard and eagle alarm calls given by the females (see Figure 1). Because

both of these alarm calls are very loud and conspicuous stimuli that transmit over considerable distances and because groups typically forage and travel as cohesive units, we are confident that our recordings captured all the alarm calls that were actually given in response to a playback stimulus. These alarm calls are typically produced by 2 or 3 adult females in the group. Our dependent variable in all trials was therefore the number of leopard (or eagle) alarm calls jointly produced by these 2 to 3 individuals. Across trials, we calculated the median call rate and third quartile of the alarm call rates. Nonparametric statistics were used to compare the change in call rate in response to the prime and probe stimuli, to compare differences in the call rate to probes across different primes, and to investigate the relationship between the call rate in response to the prime and the probe stimuli. Nonparametric statistics and medians were used because of small sample sizes and because data were not normally distributed.

Pseudoreplication

Pseudoreplication has been recognized as a potential problem in all experimental science, including studies using playback stimuli (e.g., McGregor et al., 1992). It occurs if treatments are not repeated or if they are not statistically independent, for example, if the same subject is tested several times using the same stimulus. As described earlier, we obtained statistical independence by testing a

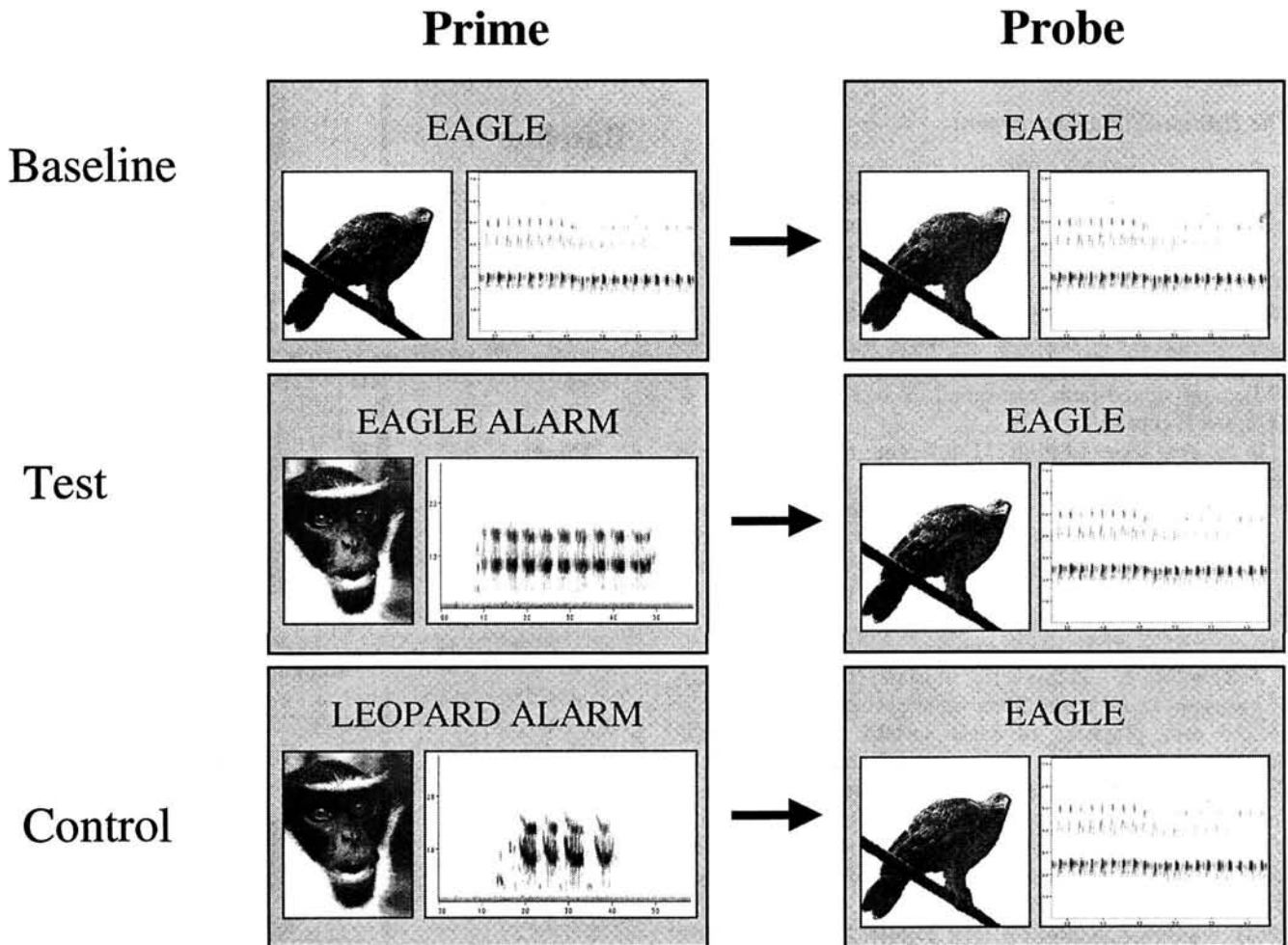


Figure 3. Example of experimental design for one set of playback experiments. Diana monkey groups were tested on two stimuli separated by 5 min of silence. Stimulus pairs differed in similarity of the acoustic and conceptual features across conditions as follows: (a) baseline condition—both the acoustic and the conceptual features remain the same; (b) test condition—the acoustic features change but the conceptual features remain the same; (c) control condition—both the acoustic and the conceptual features change.

large number of different diana monkey groups, so that each group heard a particular stimulus pair only once. To further maximize the external validity of our results, we might ideally have played different recordings of each stimulus class in every trial. The number of available master recordings (i.e., two for each predator and two for each male alarm call; see Figures 1 and 2) prevented us from doing so. The fact that real crowned eagles or leopards elicited the same vocal behavior, both quantitatively and qualitatively, as the corresponding playback stimuli made us feel confident in using a small number of high-quality recordings of these predators as representative playback stimuli.

Results

The Response-Evoking Power of the Prime Stimuli

To control for differences in stimulus duration in the male alarm calls, we used series of three or five calls as primes. This manipulation had no effect on the alarm call rate of the females: There was no significant difference in the number

of eagle alarm calls given by females in response to playback stimuli of three or five eagle alarm calls by males (Mann-Whitney U test, two-tailed: $N = 17$, $z = -0.29$, $p > .7$). It is unlikely, therefore, that differences in the stimulus duration of males' alarm calls affected the alarm call rate of females.

To control for the effects of different call types within the two predator classes, we used two different types of crowned eagle shrieks and two different types of leopard growls (see Figure 2). These acoustic differences in the vocalizations within each predator class had no effect on the alarm call rate of the females: There was no significant difference in the number of leopard alarm calls between the two leopard growls (Mann-Whitney U test, two-tailed: $N = 18$, $z = 0.35$, $p > .7$; see Figure 2), and there was no significant difference in the number of eagle alarm calls between the two eagle shrieks used as primes (Mann-Whitney U test, two-tailed: $N = 23$, $z = 0.77$, $p > .4$; see Figure 2). It is unlikely,

therefore, that acoustic differences in the vocalizations within each predator class affected the alarm call rate of females.

The Prime-Probe Experiment

Baseline condition. In the first series of trials, 11 different groups of diana monkeys were played eagle shrieks; after 5 min, playback of the same eagle shrieks followed. Because both the acoustic and semantic features remained the same, the probe stimulus was expected to cause only a weak response. Indeed, females produced significantly fewer eagle alarm calls in response to the second playback of eagle shrieks in comparison with the first (Wilcoxon signed-rank, one-tailed: $N = 11$, $z = 2.94$, $p < .002$; see Figure 4).

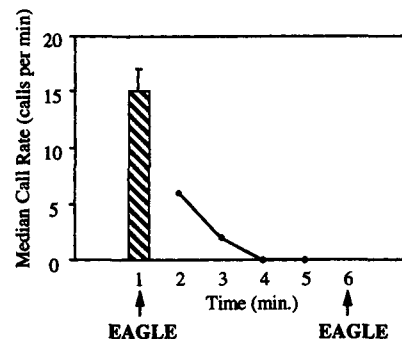
In the next series of trials, 11 different groups of monkeys were played leopard growls; after 5 min, playback of the same growls followed. Again, because both the acoustic and semantic features remained the same, only a weak response was expected to the probe stimulus. Females did give significantly fewer leopard alarm calls to the probe than to the prime stimulus (Wilcoxon signed-rank, one-tailed: $N = 11$, $z = 2.52$, $p < .01$; see Figure 5).

Test condition. In this series of trials, 10 different groups of monkeys heard male diana monkeys' eagle alarm calls; after 5 min, playback of eagle shrieks followed. If the monkeys only attended to the acoustic features of these two different calls, we expected a strong response to both stimuli. However, if they also attended to the semantic features, we expected a weak response to the probe stimulus. In fact, monkeys did respond weakly to playbacks of eagle shrieks, even though this stimulus was highly effective under unprimed conditions (see Figure 5). Females produced significantly fewer eagle alarm calls to the probe than to the prime (Wilcoxon signed-rank, one-tailed: $N = 10$, $z = 2.66$, $p < .004$; see Figure 4).

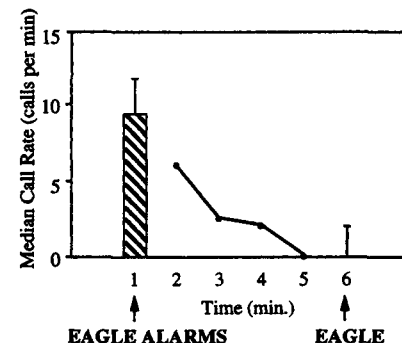
When we compared the females' response to the probe (i.e., eagle shrieks) between the baseline and test conditions, we found no statistical difference. There was no difference in the number of eagle alarm calls females gave in response to eagle shrieks after they had already been primed with eagle shrieks or after they had been primed with males' eagle alarm calls (Mann-Whitney U test, two-tailed: $N = 21$, $z = 1.75$, $p > .08$; see Figure 4). Also, the number of eagle alarm calls by males used as a prime had no apparent effect. There was no significant difference in the number of eagle alarm calls by females in cases when three or five eagle alarm calls by males were used as a prime (Mann-Whitney U test, two-tailed: $N = 10$, $z = 0.46$, $p > .6$).

In another series, nine different groups heard males' leopard alarm calls; after 5 min, leopard growls followed. If the monkeys only attended to the calls' acoustic features, they should have responded strongly to the probe stimulus, whereas if they also attended to the semantic features, they should have responded weakly. Monkeys responded weakly to playbacks of leopard growls even though this stimulus is normally highly effective. Females gave significantly fewer leopard alarm calls to the probe than to the prime (Wilcoxon signed-rank, one-tailed: $N = 9$, $z = 2.67$, $p < .004$; see

Baseline $N = 11$



Test $N = 10$



Control $N = 9$

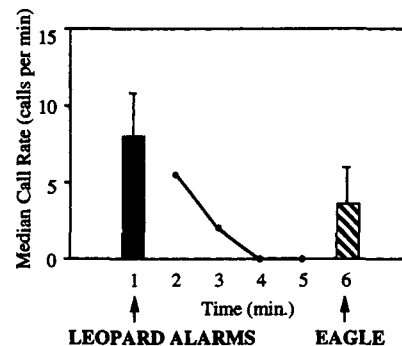


Figure 4. Females' responses to eagle call probes as a function of priming history. In the baseline condition, females are primed with eagle shrieks; in the test condition, females are primed with male monkeys' eagle alarm calls; and in the control condition, females are primed with male monkeys' leopard alarm calls. The x axis represents the length of time after starting the first playback stimulus. The y axis represents the median number of calls per minute. Error bars indicate the third quartile. Female monkeys' leopard alarm calls are represented by solid bars; female monkeys' eagle alarm calls are represented by hatched bars. N = number of groups.

Figure 4). As predicted, there was again no statistical difference in the number of leopard alarm calls by females between baseline and test condition. In other words, females responded equally weakly regardless of whether they were primed with leopard growls or with males' leopard alarm calls (Mann-Whitney U test: $N = 20$, $z = 1.14$, $p > .2$; see Figure 5).

Control condition. In this series, nine different groups heard males' leopard calls; after 5 min, eagle shrieks followed. Because the two stimuli differed both in acoustic

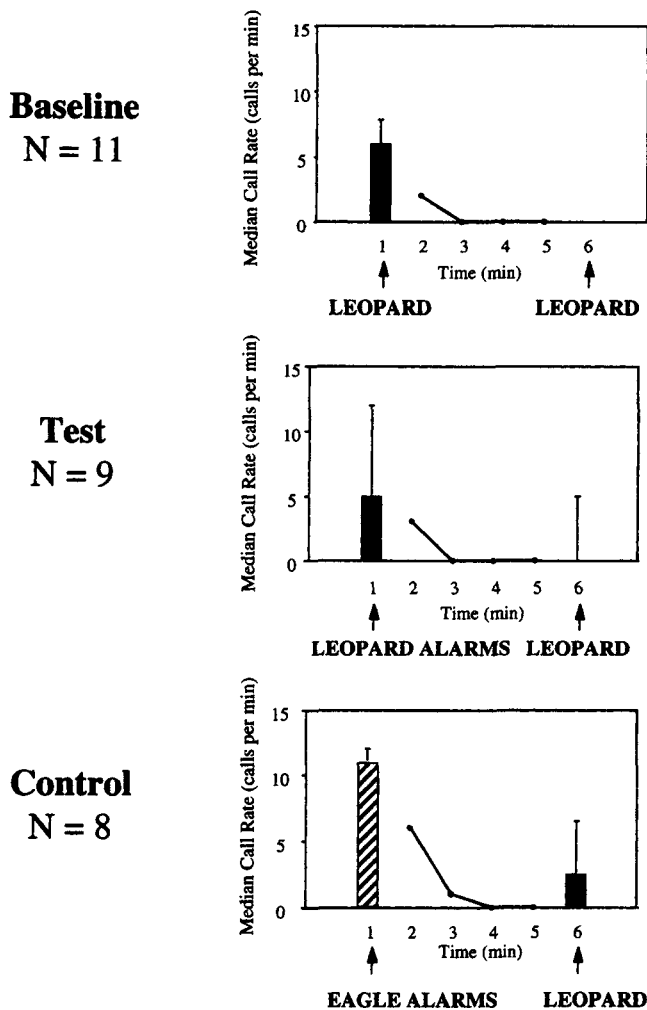


Figure 5. Females' responses to leopard call probes as a function of priming history. In the baseline condition, females are primed with leopard growls; in the test condition, females are primed with male monkeys' leopard alarm calls; and in the control condition, females are primed with male monkeys' eagle alarm calls. The x axis represents length of time after starting the first playback stimulus. The y axis represents the median number of calls per minute. Error bars indicate the third quartile. Female monkeys' leopard alarm calls are represented by solid bars; female monkeys' eagle alarm calls are represented by hatched bars. *N* = number of groups.

and semantic properties, we predicted a strong response to both prime and probe. Indeed, in this series, monkeys responded strongly to the eagle shrieks even though they had just responded strongly to males' leopard alarm calls 5 min earlier. There was a significant difference in the number of eagle alarm calls given by females in response to the probe stimulus between the baseline and the control conditions (Mann-Whitney *U* test, two-tailed: $N = 20$, $z = 3.63$, $p < .001$; see Figure 4).

In the final series, eight different groups heard males' eagle alarm calls followed by leopard growls. Again, we predicted a strong response to both prime and probe.

Monkeys responded strongly to leopard growls, even though they had just responded strongly to males' eagle alarm calls 5 min earlier. There was a statistical difference in the number of leopard alarm calls females gave in response to the probe stimulus in the baseline and the control conditions (Mann-Whitney *U* test: $N = 19$, $z = 2.94$, $p < .004$; see Figure 5).

Alternative Hypotheses

Data show that diana monkeys exhibit consistent variation in response strength to normally powerful stimuli as a function of priming history. Although both the acoustic and the semantic properties of the calls varied between the prime and the probe stimuli, only variation in the semantic properties explained the females' vocal response pattern in response to the probe stimuli.

However, one alternative explanation is that the monkeys failed to respond to the probe stimulus in the test condition not because the two playback stimuli had similar referents but because subjects had recently given that vocal response. If this were true, there should have been a quantitative relationship between call rate to the prime stimulus and call rate to the probe stimulus. Specifically, the more calls subjects gave in response to the prime, the fewer calls of the same type they should have given in response to the probe. Conversely, a weak response to the prime should have resulted in a relatively strong response to the probe. Data do not support this hypothesis. There was no significant relationship between the number of eagle alarm calls females gave in response to the prime and probe (Spearman rank: $N = 21$, $r_s = -.324$, $p > .14$). Contrary to prediction, there was also a significant positive relationship between the number of leopard alarm calls females gave in response to the prime and probe (Spearman rank: $N = 20$, $r_s = .678$, $p < .004$).

Another alternative explanation is that monkeys failed to respond to the probe stimulus in the baseline and the test condition not because prime and probe stimuli had similar referents but because females had habituated to the alarm calls of their own resident males' responses to the playback stimuli. Data do not support this hypothesis either. Although males almost always gave alarm calls in response to the prime stimuli, they only responded to approximately one third of all probe stimuli when the semantic features remained the same. Thus, the females' failure to respond to the probe stimuli could not have been the result of a simple habituation to the males' alarm calls because most males did not call in response to the probe. Moreover, there was no statistical difference in the number of eagle alarm calls the females produced in response to the eagle probes between trials in which the resident male did and trials in which he did not respond with his own eagle alarm calls (Mann-Whitney *U* test, two-tailed: $N = 21$, $z = -0.311$, $p > .7$). In an analogous manner, there was no statistical difference in the number of leopard alarm calls produced by females in response to leopard probes between trials in which the resident male did and trials in which he did not respond with his own leopard alarm calls (Mann-Whitney *U* test, two-tailed: $N = 20$, $z = -1.18$, $p > .2$), indicating that females did not simply habituate to the acoustic features of the

males' alarm calls but that they attended to the meaning associated with a playback stimulus.

Discussion

Female diana monkeys respond to male alarm calls by giving their own acoustically distinct alarm calls (Zuberbühler et al., 1997). These vocal responses are highly selective, in the sense that playbacks of both eagle shrieks and male diana monkeys' eagle alarm calls elicit one type of alarm call from females, the females' eagle alarm call, whereas playbacks of leopards growls and males' leopard alarm calls elicit an acoustically different type of call, the females' leopard alarm call (see Figures 1, 4, and 5).

The semantic content of prime stimuli, but not their acoustic features, explained the response pattern of females to the probe stimuli. This fact was demonstrated when both eagle shrieks and leopard growls, two very powerful stimuli, lost their effectiveness in eliciting alarm calls when subjects were primed with the corresponding male alarm calls (see Figures 4 and 5). Apparently, subjects took the male calls as evidence for the presence of the predator and were therefore not surprised to hear the vocalizations of the real predator following the alarm calls.

Presumably, refraining from giving alarm calls is adaptive in these cases because the benefits of alarm calling (i.e., the warning of conspecifics; Maynard-Smith, 1965) or the signaling of detection to the predator (Zuberbühler et al., in press, 1997) cannot be increased. The costs of giving an alarm call, however, may steadily increase with each additional call. Indeed, two other predators, chimpanzees and humans, are known to hunt monkeys using auditory cues (C. Boesch & H. Boesch, 1989; Martin, 1991).

This fact may also explain the comparably weaker response to the probe stimuli in the control conditions. As is apparent in Figures 4 and 5, groups produced fewer eagle or leopard alarm calls when hearing eagle or leopard vocalizations as probe stimuli compared with when they heard them as prime stimuli. The production of conspicuous vocalizations over long periods of time is likely to be costly because it attracts other predators. We had the strong impression that in the aftermath of any kind of predation event, both natural or experimentally induced, groups tended to fall into cryptic behavior for the next hour or so, such that any stimulus presented during this period failed to elicit strong vocal responses. The generally high predation pressure on monkeys caused by four different predators in the Tai forest might have favored this behavioral adaptation. Given this general behavioral pattern, it is important to note that in the control conditions subjects nevertheless produced a substantial number of alarm calls to predators although at a somewhat lower rate (see Figures 4 and 5).

If diana monkeys attend to the referential properties of their alarm calls, as these data suggest, then the following variations in the experimental design should yield analogous results. First, priming with female instead of male alarm calls should have similar decremental effects on vocal response to a probe predator vocalization. Unfortunately, however, this experiment proved difficult to conduct. Diana

monkeys, like many other primate species, live in female-bonded groups (Wrangham, 1980), and adult males often live solitarily or associate with monkey groups of another species. Hence, although playback of the alarm calls of an unfamiliar male at 50 m from the group simulates a natural event, playback of unfamiliar female calls would be entirely anomalous.

In another variation of the experiment described here, the presentation order of the stimuli in the test and the control condition were reversed, so that monkeys were primed with a predator's vocalization and then heard the corresponding or noncorresponding male alarm call. Although results of this experiment were analogous to the ones in this study (Zuberbühler, 1996–1997), no strong conclusions could be drawn because predator vocalizations elicited alarm calls not only from females but also from the resident male. Hence, if females failed to respond to the playback of male alarm calls in the probe, one could not determine whether this was due to prior habituation to the acoustic features of resident males' own alarm calls or to the referential similarity between the prime and the probe stimulus (McGraw, personal communication).

Conceptual Semantics?

The design of this study may be viewed as a case of noncontingent stimulus presentation (Rescorla & Holland, 1976). Subjects experience an event (S_1) at a given time (t_1) and are assessed on the effect of this experience at a later time (t_2), and the critical observation is the response-evoking power of a probe stimulus (S_2) at t_2 . Several types of experiences at t_1 are known to have an attenuating effect on the response to S_2 at t_2 , including the number of stimuli and the spacing between them, the presentation of a novel stimulus before assessing S_2 , the time interval between S_1 and S_2 , an increasing intensity of S_1 toward S_2 , a higher constant intensity of S_1 relative to S_2 , and the similarity of S_1 relative to S_2 (Rescorla & Holland, 1976). Only the last experience appeared to matter in this study. Note, however, that S_1 (the male alarm call) and S_2 (the corresponding predator vocalization) did not resemble each other physically. The monkeys, therefore, had to attend to a common associate of both the conspecific alarm call and the predator vocalization. This common associate allowed functional equivalence of two highly different acoustic stimuli.

At this point, one might want to argue that the critical mediator is not the predator category, but the fact that the two predators appear in the air or on the ground. However, this rule does not hold for rain forests, where monkeys may encounter leopards in the upper forest canopy (i.e., higher than they are themselves), and crowned eagles are also encountered on the ground (e.g., Bshary & Noë, 1998). Moreover, results of another experiment on wild diana monkeys showed that males do not label the relative threat posed by a predator, such as its relative distance or vertical position in the canopy, but instead reliably label the predator's biological category regardless of its distance or vertical position (Zuberbühler, 1998).

In light of these results, what can one conclude about the content and structure of these underlying common associates that

governed the alarm call behavior of the monkeys? Using mentalistic terminology, do these monkeys possess higher level mental representations of the two predator types as appears to be the case for humans? Are these mental representations also concepts of the kinds that underlie words in a natural language?

The notion of animal concepts remains controversial (e.g., Cheney & Seyfarth, 1998). Difficulties have arisen in part because many theories of concept formation have been developed to explain the structure and content of linguistic concepts in humans (e.g., Armstrong, L. Gleitman, & H. Gleitman, 1983). Moreover, human concepts and natural language are so closely tied together that some have questioned whether the former should even be given independent psychological status (Chater & Heyes, 1994). Others are convinced that concepts are empirically accessible with nonlinguistic methodology (e.g., Herrnstein, 1991). Pigeons, for instance, can learn to discriminate exemplars of trees from non-trees (Herrnstein, Loveland, & Cable, 1976), and long-tailed macaques can distinguish mother-offspring dyads from other types of social bonds (Dasser, 1988), to mention just two of many examples.

Nevertheless, it remains possible that the assumption that the subjects' behavior was based on a preexisting or learned concept may be unnecessary and that more parsimonious explanations describe the data sufficiently. One, the "stimulus generalization" account, argues that subjects neither possess nor form concepts but learn to identify exemplars by attending to one or a few physical dimensions. This heuristic could be sufficient to score above chance in some discrimination tasks (e.g., D'Amato & Van Sant, 1988). In this study, the stimulus generalization explanation cannot account for the monkeys' response because physically dissimilar stimuli, such as leopard growls and male monkeys' leopard alarm calls, caused similar behavior in response to the probe, whereas physically similar stimuli, such as male monkeys' leopard and eagle alarm calls, caused diverging behavior in response to the probe.

Another explanation, the "secondary stimulus generalization" account (e.g., Hull, 1943, p. 191; Thompson, 1995), also questions the presence of mental concepts in animals. According to this account, animals classify stimuli together if they are associated with the same response; in other words, the only means subjects have to categorize the environment is to attend to their own behavior as opposed to the stimulus properties. Unfortunately, animal learning studies have so far failed to determine whether animals learn the stimulus or the response properties when forming associations (e.g., Rescorla, 1980). More recently, some experiments have suggested that during discrimination tasks, pigeons use a heuristic based on stimulus-response associations to classify stimuli (Wasserman, DeVolder, & Coppage, 1992). However, in this study the pigeons' overall classification performance was comparably poor, suggesting that attending to one's own behavior is not a key mechanism for classifying stimuli. In our study, we found no relationship in the number of female monkeys' eagle alarm calls given to prime and probe stimuli and a significant positive correlation between the number of female monkeys' leopard alarm calls given to prime and probe stimuli, suggesting that the females'

refraining from giving alarm calls to the probe stimuli in the baseline and test condition (see Figures 4 and 5) was not a consequence of the subjects' attending to their own behavior.

Similarly, females did not simply habituate to the acoustic features of the alarm calls of their resident males. Although resident males regularly produced alarm calls to the prime stimuli, thus adding another possible source for acoustic habituation to the playback stimuli, they mostly remained quiet to the probe stimuli if the semantic properties of the stimuli remained the same.

Clearly, these arguments are based on post hoc inspection of the data, and more experiments are needed to scrutinize the notion of conceptual semanticity as a governing principle of the behavior of these animals. One experimental paradigm well suited for accessing conceptual knowledge in nonlinguistic organisms, the match-to-sample technique (e.g., Premack & Dasser, 1991), is unfortunately impractical for field experiments with wild animals. Instead, variations of the habituation-dishabituation procedure (Eimas, Siqueland, Jusczyk, & Vigorito, 1971) have successfully been applied in the field (e.g., Cheney & Seyfarth, 1988; Fischer, 1998) although their inferential power is somewhat less strong. The prime-probe technique used in this study is such a variant, although with one important difference. Subjects were not habituated to a battery of repeated stimuli but were simply exposed to one brief stimulation containing specific conceptual-semantic information (the presence of a predator class). The same basic technique has been recommended by others as a tool to assess mental states in nonhuman organisms (Allen & Bekoff, 1997, p. 57). In our experiments, we gave subjects knowledge about a highly relevant environmental event and then asked whether they took this knowledge into account when faced with the same or novel conceptual information. Results showed that they did—the monkeys actively produced vocalizations to match the conceptual information when it was novel and refrained from responding when the information was repeated.

We conclude that, when hearing natural stimuli, monkeys do not rely only on the acoustic features of these stimuli alone to govern their behavior but instead access a common associate, possibly a mental representation, of the predator category. Perhaps these mental representations are not unlike those linked to the human linguistic concepts of *leopard* and *eagle*.

References

- Allen, C., & Bekoff, M. (1997). *Species of mind: The philosophy and biology of cognitive ethology*. Cambridge, MA: MIT Press.
- Armstrong, S. L., Gleitman, L., & Gleitman, H. (1983). What some concepts might not be. *Cognition*, 13, 263–308.
- Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, 78, 547–573.
- Bshary, R., & Noë, R. (1998). Anti-predator behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioural Ecology and Sociobiology*, 41, 321–333.
- Charif, R. A., Mitchell, S., & Clark, C. W. (1995). *Canary 1.2 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- Chater, N., & Heyes, C. (1994). Animal concepts: Content and discontent. *Mind & Language*, 9, 209–246.

- Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, 36, 477–486.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: Chicago University Press.
- Cheney, D. L., & Seyfarth, R. M. (1998). Why animals don't have language. In G. B. Petersen (Ed.), *The Tanner lectures on human values* (Vol. 19, pp. 173–210). Salt Lake City: University of Utah Press.
- D'Amato, M. R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, 14, 43–55.
- Dasser, V. (1988). A social concept in Java monkeys. *Animal Behaviour*, 36, 225–230.
- Eimas, P. D., Siqueland, P., Jusczyk, P., & Vigorito, J. (1971, January 22). Speech perception in infants. *Science*, 171, 303–306.
- Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: Functional reference in an avian vocal system. *Animal Behaviour*, 46, 23–38.
- Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, 55, 799–807.
- Gouzoules, H., Gouzoules, S., & Tomaszycki, M. (1998). Agonistic screams and the classification of dominance relationships: Are monkeys fuzzy logicians? *Animal Behaviour*, 55, 51–60.
- Gyger, M., Marler, P., & Pickert, R. (1987). Semantics of an avian alarm call system: The male domestic fowl, *G. domesticus*. *Behaviour*, 102, 15–40.
- Hauser, M. D. (1996). *The evolution of communication*. Cambridge, MA: MIT Press.
- Herman, L. M., Pack, A. A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. L. Roitblat, L. M. Herman, & P. E. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 403–442). Hillsdale, NJ: Erlbaum.
- Herrnstein, R. J. (1991). Levels of categorization. In G. M. Edelman, W. E. Gall, & W. M. Cowan (Eds.), *Signal and sense* (pp. 385–413). Somerset, NJ: Wiley-Liss.
- Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 285–302.
- Hill, C. M. (1994). The role of female diana monkeys, *Cercopithecus diana*, in territorial defence. *Animal Behaviour*, 47, 425–431.
- Höner, O. P., Leumann, L., & Noë, R. (1997). Dyadic associations of red colobus and diana monkey groups in the Tai National Park, Ivory Coast. *Primates*, 38, 281–291.
- Hull, C. L. (1943). *The principles of behavior: An introduction to behavior theory*. New York: Appleton-Century-Crofts.
- Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology*, 86, 177–190.
- Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, 93, 177–197.
- Martin, C. (1991). *The rainforests of West Africa: Ecology, threats, conservation*. Basel, Switzerland: Birkhäuser.
- Maynard-Smith, J. (1965). The evolution of alarm calls. *American Naturalist*, 99, 59–63.
- McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, B. J., Fusani, L., Gerhardt, H. C., Gilbert, F., Horn, A. G., Klump, G. M., Kroodsma, D. E., Lambrechts, M. M., McComb, K. E., Nelson, D. A., Pepperberg, I. M., Ratcliffe, L., Searcy, W. A., & Weary, D. M. (1992). Design of playback experiments: The Thornbridge Hall NATO ARW consensus. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 1–9). New York: Plenum.
- Oates, J. F. (1994). Africa's primates in 1992: Conservation issues and options. *American Journal of Primatology*, 34, 61–71.
- Pepperberg, I. M. (1990). Cognition in an African grey parrot (*Psittacus erithacus*): Further evidence for comprehension of categories and labels. *Journal of Comparative Psychology*, 104, 41–52.
- Premack, D. (1970). A functional analysis of language. *Journal of the Experimental Analysis of Behavior*, 14, 107–125.
- Premack, D., & Dasser, V. (1991). Perceptual origins and conceptual evidence for theory of mind in apes and children. In A. Whiten (Ed.), *Natural theories of mind* (pp. 253–266). Oxford, England: Blackwell.
- Rescorla, R. A. (1980). *Pavlovian second-order conditioning*. Hillsdale, NJ: Erlbaum.
- Rescorla, R. A., & Holland, P. C. (1976). Some behavioral approaches to the study of learning. In E. Bennett & M. R. Rosenzweig (Eds.), *Neural mechanisms of learning and memory* (pp. 165–192). Cambridge, MA: MIT Press.
- Savage-Rumbaugh, S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rupert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General*, 115, 211–235.
- Schusterman, R. J., & Krieger, K. (1984). California sea lions are capable of semantic comprehension. *Psychological Record*, 34, 3–23.
- Seyfarth, R. M., & Cheney, D. L. (1992a, January 4). Inside the mind of a monkey. *New Scientist*, 133, 25–29.
- Seyfarth, R. M., & Cheney, D. L. (1992b, December). Meaning and mind in monkeys. *Scientific American*, 267, 122–128.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980, November 26). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, 210, 801–803.
- Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In S. A. Altmann (Ed.), *Social communication among primates*. Chicago: University of Chicago Press.
- Thompson, R. K. R. (1995). Natural and relational concepts in animals. In H. L. Roitblat & J.-A. Meyer (Eds.), *Comparative approaches to cognitive science. Complex adaptive systems* (pp. 175–224). Cambridge, MA: MIT Press.
- von Frisch, K. (1950). *Bees: Their vision, chemical senses, and language*. Ithaca, NY: Cornell University Press.
- Wasserman, E. A., DeVolder, C. L., & Coppage, D. J. (1992). Non-similarity-based conceptualization by pigeons via secondary or mediated generalization. *Psychological Science*, 3, 374–379.
- Wolfheim, J. H. (1983). *Primates of the world*. Seattle: University of Washington Press.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262–299.
- Yates, J., & Tule, N. (1979). Perceiving surprising words in an unattended auditory channel. *Quarterly Journal of Experimental Psychology*, 31, 281–286.
- Zuberbühler, K. (1996–1997). [Diana monkey vocalizations]. Unpublished raw data.
- Zuberbühler, K. (1998). *Referential labeling in wild diana monkeys*. Manuscript submitted for publication.
- Zuberbühler, K., Jenny, D., & Bshary, R. (in press). The predator deterrence function of primate alarm calls. *Ethology*.
- Zuberbühler, K., Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour*, 53, 589–604.

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