age by an increase in the sensitivity (supersensitivity) of dopaminergic autoreceptors. The development of such supersensitivity would make the dopaminergic neuron more vulnerable to the inhibitory effects of dendritic dopamine release (*14*). This in turn would result in increased autoregulation (that is, increased self-inhibition) of dopaminergic neuronal activity, thereby causing a decreased responsiveness to the environment and possibly depression. If our speculation is correct, the dopamine autoreceptor subsensitivity, such as we have now demonstrated with both ECS and tricyclics (*5*), might gradually reverse this supersensitivity and, in so doing, ameliorate depression. The passage of time required for the reduction of sensitivity is consistent with the delayed onset of the therapeutic influence of both ECS and tricyclic antidepressants (*15*). These data tentatively suggest, as previously proposed for TCA's (*5*), that it may not be necessary for ECS to be repeatedly administered in order for it to be therapeutically effective. Instead, a single ECS (or short-term treatment) may be sufficient to trigger autoreceptor subsensitivity, which, as it progresses, becomes functionally manifest as an antidepressant effect. Alternatively, autoreceptor sensitivity reduced by ECS may be an intermediate process providing the impetus for other neuronal changes necessary to achieve clinical efficacy. In either case, the hypothesis that repeated antidepressant treatments may not always be required warrants testing in a controlled clinical trial.

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5. We have also shown that both typical (amitriptyline and imipramine) and atypical (iprindole) antidepressants reduce the sensitivity of dopaminergic autoreceptors after both 2 and 10 days of injections (10 mg/kg, injected intraperitoneally twice a day). All drug treatments significantly attenuated the inhibition of dopaminergic neuronal activity by apomorphine (0.004 mg/kg, injected intravenously):

Treatment	Inhibition of discharge (mean % ± S.E.)	*t*	d.f.	*P*
Control	73.6 ± 7.3			
Imipramine				
2 days	34.1 ± 12.4	4.134	12	.001
10 days	13.6 ± 13.9	6.550	11	.001
Amitriptyline				
2 days	40.7 ± 26.1	2.119	10	.05
10 days	2.7 ± 17.4	8.985	9	.001
Iprindole				
10 days	15.7 ± 9.4	4.832	9	.001

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16. One of the six animals in the single ECS + 7-day delay group and three of the six in the six ECS + 2-day delay group showed an increase in spontaneous activity after the administration of a presynaptic dose of apomorphine (0.004 mg/kg, intravenously). However, the dopaminergic nature of these cells was supported by the finding that they all decreased their activity when a postsynaptic dose of apomorphine was administered (50 μg/kg, intravenously) and increased their activity in response to haloperidol (0.2 mg/kg, intravenously) [L. A. Chiodo and S. M. Antelman, *Eur. J. Pharmacol.* **66**, 255 (1980)].
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Monkey Responses to Three Different Alarm Calls: Evidence of Predator Classification and Semantic Communication

Abstract. *Vervet monkeys give different alarm calls to different predators. Recordings of the alarms played back when predators were absent caused the monkeys to run into trees for leopard alarms, look up for eagle alarms, and look down for snake alarms. Adults call primarily to leopards, martial eagles, and pythons, but infants give leopard alarms to various mammals, eagle alarms to many birds, and snake alarms to various snakelike objects. Predator classification improves with age and experience.*

A central but neglected issue in the study of animal communication is that of semantics. Have species other than man evolved the ability to make systematic use of signals to refer to objects in the external world? Captive chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) can be taught to use symbols to represent different objects without support from contextual cues (*1*), but whether nonhuman species exhibit a similar ability under natural conditions has yet to be investigated.

If an organism is to communicate semantically, using different signals to represent distinct objects in its environment, it must either employ many signals or sort objects into groups. Present indications are that repertoires of natural, meaningfully distinct signals are limited in animals. Thus any study of semantic communication under natural conditions must consider how animals "categorize" objects in the external world. The extent to which nonhuman species divide objects into groups for the apparent purpose of communicating about them is not known (*2*). We present field data on responses of free-ranging vervet monkeys (*Cercopithecus aethiops*) to playbacks of recorded predator alarm calls. Additional data illustrate how vervets classify predators and suggest how such categorization develops.

Three groups of free-ranging vervet monkeys were studied in Amboseli National Park, Kenya, for 14 months. Groups contained a mean of 4 adult males (range 2 to 7), 7.6 adult females (range 7 to 8), 6.2 juveniles (range 1 to 11), and 6.5 infants (range 6 to 8). During 1500 hours of systematic sampling of social behavior, tape recordings were made of as many vocalizations as possible (*3*). Analysis was limited to those instances in which observers identified the vocalizer, the stimuli that occasioned vocalization, and apparent responses of nearby individuals.

Field recordings of more than 100 alarm calls supported Struhsaker's finding (*4*) that vervets in Amboseli gave acoustically different alarm calls to at least three different predators: leopards

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Table 1. Responses of monkeys to playbacks of leopard, eagle, and snake alarms. Entries indicate the number of trials in which at least one subject showed a given response for longer in the 10 seconds after playback than in the 10 seconds before. Letters indicate where there was a statistically significant difference between responses to two call types. For example, with monkeys on the ground, leopard (L) alarms caused one or more subjects to look down in 1 of 19 trials. Eagle alarms (E) caused one or more subjects to look down in 4 of 14 trials, and snake alarms (S) in 14 of 19 trials. Thus snake alarms were significantly more likely to cause animals on the ground to look down than either leopard alarms or eagle alarms. Levels of significance: letter in parentheses = .05 < *P* < .10; letter alone = .01 < *P* < .05; and starred letter = *P* < .01.

Alarm type	Responses on ground					Responses in tree				
	No. of trials	Run into tree	Run into cover	Look up	Look down	No. of trials	Run higher in tree	Run out of tree	Look up	Look down
Leopard	19	8 (E)S*	2	4	1	10	4	0	3	4
Eagle	14	2	6 LS	7 (L)S	4	17	4	5 (L)S	11 (L)	12
Snake	19	2	2	2	14 L*E*	9	2	0	5	9 L*(E)

(*Panthera pardus*), martial eagles (*Polemaetus bellicosus*), and pythons (*Python sebae*). We refer to these three calls as leopard, eagle, and snake alarms. Leopard alarms were short tonal calls, typically produced in a series on both exhalation and inhalation. Eagle alarms were low-pitched, staccato grunts, and snake alarms were high-pitched "chutters." The acoustical features of the calls were such that (i) they could be assigned unambiguously to one type, both by sound spectography in the laboratory and by ear in the field, and (ii) they were distinct from the nonalarm vocalizations that they most closely resembled. Two other vocalizations, given to baboons and to unfamiliar humans, also seemed to be discrete call types, but they were not recorded often enough for statistical comparison.

In both Struhsaker's study and our own (*5*), each alarm type was associated with a different set of responses from monkeys. The response seemed to represent adaptive strategies for coping with the hunting behavior of the predators involved. When monkeys were on the ground, leopard alarms caused them to run up into trees, where they appeared to be safest from the ambush style of attack typical of leopards. Eagle alarms caused them to look up, run into dense bush, or both, apparently to avoid an eagle's stoop. And snake alarms caused them to look down at the ground around them. Such responses suggested that each alarm call effectively represented, or signified, a different class of external danger. Alternatively, the different responses might have occurred not because of the alarm calls, but because the presumed respondents actually saw the different predators, either independently or cued by other alarmists. To test whether alarm calls alone could evoke different responses, we conducted 88 experiments in the absence of predators by playing back recorded alarms.

In each field trial, an alarm call was played to monkeys (at least one adult male, two adult females, and two immature monkeys) from a speaker previously concealed. Subjects were filmed for 10 seconds preceding and 10 seconds following the playback of each call (*6*). Equal numbers of leopard, eagle, and snake alarms, recorded from known adult males, adult females, and juveniles, were used. Anticipating the possibility that call length might influence responses, we constructed long and short versions of each type of call (*7*). Calls used in some trials were broadcast at their natural amplitudes, with leopard alarms being louder than eagle alarms, which were louder than snake alarms. To control for possible effects of amplitude, we conducted a second set of trials in which the various types of calls did not differ significantly in amplitude (*8*). Fifty trials were conducted when subjects were on the ground, and 38 when they were in trees. No recordings were played twice to the same group of monkeys within 24 hours, nor was any trial run within 15 minutes of alarm-calling by nearby vervets or by the subjects' own group. Individual calls from a given monkey were used only once, except for a few cases when too few exemplars were available. The order of the various calls and the position of the speaker relative to the subjects were varied systematically.

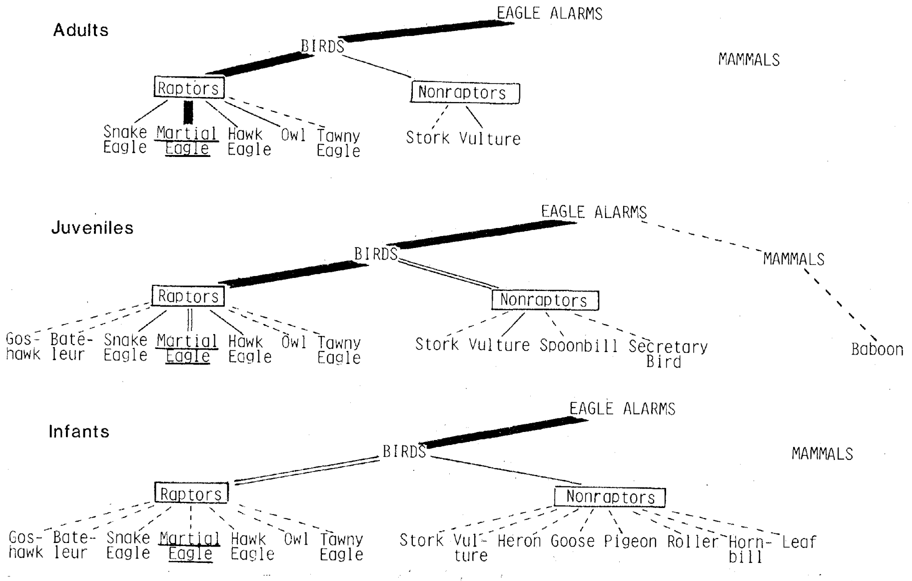

Fig. 1. Eagle alarms given by adult, juvenile, and infant monkeys to different species or objects. Broken line, 1 to 5 alarms; single line, 6 to 10 alarms; double line, 11 to 15 alarms; solid line, more than 15 alarms. Data on 149 alarms were collected over 14 months from 31 adults, 16 juveniles, and 17 infants.

Alarm-call playbacks produced two kinds of response. Subjects in all age classes and of both sexes looked toward the speaker and scanned their surroundings more in the 10 seconds after a playback than before. They behaved as if searching for additional cues, both from the source of the alarm and elsewhere. In addition, each alarm type elicited a distinct set of responses (Table 1). When subjects were on the ground, leopard alarms were more likely to cause them to run into trees. Eagle alarms made them look up and sometimes run into cover, and snake alarms caused them to look down. When subjects were in trees, eagle alarms were more likely than other alarm types to evoke looking up, running out of the tree, or both. Snake alarms were more likely to cause subjects to look down (9). The monkeys responded as though each type of alarm call designated different external objects or events.

This view of vervet alarm calls as rudimentary semantic signals contrasts with some earlier interpretations, which regard vervets' alarms, like other forms of animal communication, as manifestations of different levels of arousal that lack clearly defined external referents (10). If this were the case, responses to alarms should differ in relation to call features that mirror arousal levels, such as call length or amplitude. Our results indicated that variation in call length and equation of amplitude, as well as variation in the "arousability" of individuals as reflected by age or sex of alarmists, failed to blur distinctions among major response categories. Variation in the acoustical structure of different call types was the only feature both necessary and sufficient to explain response differences (11).

By giving alarm calls to some species but not to others, and by giving acoustically distinct alarms to different predators, vervet monkeys effectively categorized other species. More than 100 species of mammals, birds, and reptiles were seen regularly by the monkeys without eliciting alarm calls. When giving alarms, adults were most selective. Adults gave leopard alarms primarily to leopards, eagle alarms primarily to martial eagles, snake alarms to pythons, and baboon alarms to baboons. Sixty-four percent of all well-documented adult alarm calls ($N = 122$) were given to these four species. In contrast with adults, infants gave alarms to a much wider variety of species (two-tailed Mann-Whitney U tests, $P < .05$), and were more likely than adults to give alarms to things that posed no danger to them such as warthogs, pigeons, and falling leaves (12). Even for infants, however, the relation between type of alarm call and the stimulus that elicited it was not arbitrary. Infants gave leopard alarms primarily to terrestrial mammals, eagle alarms to birds, and snake alarms to snakes or long thin objects. Age-related differences in alarm-calling behavior (Fig. 1) indicate that while infants distinguished between relatively general predator classes (for example, between a terrestrial mammal and a flying bird), adults distinguished between particular predator species within such classes (for example, between leopards and other terrestrial mammals and between martial eagles and other birds). Evidently as infants grow older they sharpen the association between predator species and the type of alarm call. They behave as though their ability to classify other organisms improves with age and experience. The precise nature of the process of perceptual categorization that is implied and the possible roles of individual experience and adult tutelage in this development remain to be determined.

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7. Long alarms contained a mean of five acoustic units, with a mean duration of 3.7 seconds (standard deviation = 2.5). Short alarms contained a single unit, with a mean duration of 0.3 second (S.D. = 0.2).
8. Sound intensities were measured on a General Radio sound level meter, model 1933, A weighting.
9. In only one trial did a monkey respond to a playback by giving an alarm.
10. See, for example, J. C. Marshall, in *New Horizons in Linguistics*, J. Lyons, Ed. (Penguin, Harmondsworth, England, 1970), p. 234; W. J. Smith, *The Behavior of Communicating* (Harvard Univ. Press, Cambridge, Mass., 1977), p. 181.
11. It has also been argued [for example, by Smith (10), pp. 181 and 270] that animal signals encode a limited number of generalized messages, such as attack, escape, or frustration, with the specificity of responses being highly context-dependent. In our experiments, however, context was not a systematic determinant of responses. Different alarms evoked different responses in the same context, and responses to some alarms remained constant despite contextual variation. The most parsimonious interpretation is that each alarm represented a certain class of danger and that monkeys responded according to their vulnerability to that danger at the time.
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Endogenous Potentials Generated in the Human Hippocampal Formation and Amygdala by Infrequent Events

Abstract. *Infrequent, attended, auditory and visual stimuli evoke large potentials in the human limbic system in tasks that usually evoke endogenous potentials at the scalp. The limbic potentials reverse polarity over small distances and correlate with unit discharges recorded by the same electrodes, indicating that they are locally generated.*

Long-latency potentials that are dependent on the cognitive context in which a stimulus occurs, but are independent of the sensory characteristics of the stimulus and overt motor response required by the task, can be recorded from the human scalp. These potentials (N2, P3, and slow wave) are thus termed endogenous (1). Typically, they occur when the subject is actively attending to the stimuli, and the evoking event is infrequent (2, 3). Reliable changes in endogenous potentials occur in relation to cognitive variables (4) and neurological status, for example, in dementia and retardation (5). The functional interpretation of these changes has been limited because the location and nature of neural activity within the human brain during endogenous potentials is unknown (6). Here we report that large field-potential and unit responses are evoked in the human hippocampal formation and amygdala by infrequent, attended events.

Recordings were obtained from six adults of normal intelligence and personality with bilateral electrodes implanted in the hippocampus ($N = 20$), hippocampal gyrus ($N = 13$), and amygdala ($N = 8$) to locate epileptic foci for possible surgical removal (7). A simple method used to evoke endogenous scalp potentials is to present tone bursts of two different fixed pitches at random intervals. The subject's task is to count silently the number of "rare" tones (20 percent of the total presented) randomly interspersed among the "frequent" tones (3). We found that during this task,