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Language and Communication: Comparative Perspectives

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When humans use words like "apple" or "eagle," we recognize the referential relation that holds between such signs and the things for which they stand. Referential relations can, for instance, be distinguished from causal relations: The word "eagle" does not cause a particular bird to appear or result in a particular pattern of behavior. Instead, the word "stands for," or "conjures up images of," an object even when that object cannot be seen.

Representational capacity occupies a pivotal role in studies of human language, animal communication, and the mechanisms that underlie them because it concerns not only how organisms communicate but also how they classify features of their environment. Given the extensive research that has documented the ability of captive nonhuman primates to learn referential communicative signals in the laboratory (e.g., Premack, 1976), we focus in this chapter on the vocalizations used by nonhuman primates under natural conditions. We begin by asking whether monkeys, apes, or any other animals ever use sounds to denote objects and events in the world around them. If so, are their vocalizations semantic in the same sense that human words are semantic? Do animals understand the referential relation that exists between calls and the things for which they stand? Finally, we consider whether...
monkeys ever use vocalizations to influence another animal's beliefs as well as its behavior.

In this chapter we ask whether the vocalizations used by East African vervet monkeys (Cercopithecus aethiops) under natural conditions can usefully be called semantic. Data are drawn from a population of vervets that we and our colleagues studied over a 12-year period in Amboseli National Park, Kenya (Cheney & Seyfarth, 1990a). Additional data, supplementing those on vervet monkeys, come from experiments recently conducted on captive rhesus (Macaca mulatta) and Japanese macaques (M. fuscata) housed at the California Primate Research Center, University of California, Davis (Cheney & Seyfarth, 1990b).

SUBJECTS

Vervet monkeys in Amboseli National Park live in stable social groups composed of a number of adult males, adult females, and their juvenile and infant offspring. Each group occupies a territory that averages around 0.3 km² in size. Territories remain relatively stable from one year to the next and are aggressively defended against incursion by the members of other vervet groups.

As in most Old World monkey species, female vervets remain throughout their lives in the groups where they were born, maintaining close social bonds with female kin through frequent grooming, proximity, and the formation of alliances. Males, in contrast, leave their natal group at around sexual maturity and join a neighboring group, often in the company of brothers or natal group peers. Within each group, males and females can be ranked in linear dominance hierarchies that accurately predict the outcome of competitive interactions over access to food, water, and social companions. Offspring acquire dominance ranks immediately below those of their mothers, such that all members of a family share adjacent ranks (Cheney & Seyfarth, 1990a).

In the wild, group composition, patterns of dispersal, and social behavior among rhesus and Japanese macaques are similar to those among vervet monkeys (e.g., Lindburg, 1971; Sade, 1972; Kawai, 1958; reviewed in Melnick & Pearl, 1987). At the California Primate Research Center, rhesus and Japanese macaques are housed in groups that retain many of the features of each species' natural social organization. Each of the four groups used in our research (two of each species) lived in an outdoor enclosure constructed from two modified corncribs (hereafter called "arenas") connected by an intercage unit. Each group was composed of one or two sexually mature males, three to five sexually mature females, and the females' juvenile and infant offspring. In each group at least two adult females were close genetic relatives (mother and daughter or half-sisters). One rhesus group had been constituted in 1984; animals in the three other groups had lived together for at least 10 years.

SEMANTICITY IN THE WEAKEST SENSE

There are at least three senses in which an animal vocalization might be called semantic. In the weakest sense, we can describe an animal vocalization as semantic whenever different calls signal the presence of different external objects or events, and when each call elicits the same response as would its referent even when the referent itself is absent (see, for example, Hockett, 1966).

As an example, consider the alarm calls given by vervet monkeys to different sorts of predator. In East Africa, vervet monkeys give acoustically different alarm calls to at least three different predators (Struhsaker, 1967): leopards (Panthera pardus), eagles (the martial eagle, Polemaetus bellicosus and the crowned eagle, Stephanoaetus coronatus), and snakes (usually the python, Python sebae). Each alarm call type (Figure 10.1) elicits a different, apparently adaptive response from other monkeys nearby. When vervets are on the ground a leopard alarm causes them to run into trees, where they are safe from a leopard's attack. Eagle alarm calls cause them to look up in the air or run into bushes; when the monkeys are in trees, eagle alarms often cause them to run out of trees and into bushes on the ground (martial and crowned eagles can capture vervets when the monkeys are in trees). Finally, snake alarms cause the monkeys to stand on their hind legs and peer into the grass around them (Struhsaker, 1967). Subsequent experiments have shown that alarm calls alone, even in the absence of an actual predator, elicit the same responses (Seyfarth, Cheney & Marler, 1980). Thus each alarm call type accurately replaces (i.e., elicits the same response as) the object for which it stands, even when that object is not itself present.

The behavior of young vervets provides further evidence that monkeys may be using alarm calls to denote particular predators. When an infant vervet first begins giving alarm calls, he gives alarms to many species, small hawks or pigeons, for example, that do not prey on monkeys and pose no danger to him. Such "mistakes" by infants, however, are not entirely random. Infants give leopard alarms only to terrestrial mammals, eagle alarms only to birds, and snake alarms only to long, snake-like objects (Figure 10.2). As they grow older, infants and juveniles increasingly restrict their leopard, eagle, and snake alarm
Figure 10.1. Spectrograms of alarm calls given by adult male and female vervet monkeys to leopards, martial eagles, and pythons. In each spectrogram, X-axis indicates time, Y-axis indicates frequency in units of 1 kHz. From *How monkeys see the world: Inside the mind of another species* by D. L. Cheney & R. Seyfarth, 1990, Chicago: University of Chicago Press. Reprinted by permission.

The behavior of infant vervets recalls similar behavior by human infants, who for a brief period during development may overgeneralize the meaning of a word, saying "dadoo" to refer to any male person or "ball" when pointing to any round object (e.g., de Villiers & de Villiers, 1978). And, just as the human child's behavior helps us understand what she has in mind and shows that meaning is not always the same for children and adults, the infant vervet's behavior suggests that the monkeys have some particular class of objects in mind when they use their different alarm calls.

Figure 10.2. The stimuli that elicited eagle alarm calls from vervet monkeys of different ages. Data were collected over two 9-month periods in 1983 and 1985-1986. Infants are animals less than one year old; juveniles are 1-4 years old; and adults are over 4; N = number of alarm calls from animals in each age class. Broken lines indicate < 5 alarms, single lines 6-10 alarms, double lines 11-15 alarms, and thick solid lines > 15 alarms. From "Vocal development in vervet monkeys" by R. M. Seyfarth & D. L. Cheney, 1986, *Animal Behavior*, 34, 1640-1658. Copyright, 1986, Animal Behavior Society. Reprinted by permission.
Seyfarth and Cheney

There are at least two alternatives to this "semantic" interpretation of vervet monkey alarm calls. The first (e.g., Marshall, 1970) argues that each call type does not denote a different predator but instead reflects different levels of fear and excitement. In our experiments, however, variation in the length and amplitude of alarm calls, assumed to mimic variation in the caller's emotional state, had little apparent effect on the responses each call elicited from other monkeys (Seyfarth, Cheney, & Marler, 1980).

A second alternative hypothesis (e.g., Smith, 1977, 1981) suggests that different alarm calls do not denote different predators but instead signal what the caller is likely to do next. Of course, given the close link between predator type, alarm call type, and the most appropriate escape response, there will inevitably be a predictable relationship between a specific call and the signaler's subsequent behavior. In itself, however, this does not rule out the possibility that vocalizations also serve a referential function. Recall, for example, that vervet eagle alarm calls can elicit a number of different responses. Animals on the ground may look up or run into a bush, while animals in a tree may run down from the tree; in either circumstance a listener can also do nothing. Moreover, vervets in a tree may run down from a tree even when the caller himself is on the ground and is responding by looking up. In this case, the most parsimonious explanation would seem to be that calls denote a type or class of danger rather than the caller's behavior, and that an individual's particular circumstances strongly influence the exact nature of its response (Seyfarth & Cheney, 1990).

Given these results, we have called the alarm calls of vervet monkeys semantic signals in order to emphasize that, contrary to earlier interpretations, vervet alarms do not simply reflect different levels of excitement or provide information solely about what the caller will do next. Instead, they function to denote objects in the environment in a manner that is at least to some degree independent of the caller's behavior. Of course, this is not to say that information about external referents is the only information conveyed by the vervets' vocalizations. Features such as alarm call amplitude, length, rate of delivery, and the number of individuals calling almost certainly provide listeners with information about how close a predator is and whether it poses immediate danger (e.g., Owings & Hennessy, 1984). Moreover, our understanding of a call's meaning will almost certainly be enriched as we learn more about the acoustic features correlated with a caller's level of motivation or arousal (e.g., Marler, Evans, & Hauser, in press). We emphasize the importance of external referents, in other words, not to minimize the role of emotion or the caller's subsequent behavior as determinants of call meaning, but instead to suggest that

the communication of monkeys, long known to be highly expressive, can be denotive as well.

Our definition of semanticity is limited, however, because it is based exclusively on what animals do in the wild and makes no reference to the mechanisms that underlie their behavior. From the data reviewed thus far we can conclude that vervet monkeys behave as if their calls, like some words, denote objects and events in the environment, but we cannot say whether vervets understand the referential relation that exists between their calls and features of the environment, or whether vervets, in responding to another animal's alarm call, interpret this vocalization as a representation of the caller's knowledge. As a result, we cannot say whether the parallel between vervet monkey alarm calls and human words is anything more than a superficial resemblance.

SEMANTICITY IN A STRONGER SENSE

Suppose, however, we adopt a stronger definition of semanticity and argue that an animal's vocalization is semantic only if an individual, given the opportunity to compare two calls, judges them to be the same or different on the basis not just of their acoustic properties but of what they denote. This sort of classification happens so often in language that we take it for granted. When we are asked, for example, to compare two words like "treachery" and "deceit" we judge them to be roughly the same because they refer to the same thing even though their acoustic properties are quite different. By contrast, when asked to compare two words like "treachery" and "lechery" we judge them to be different even though their acoustic properties are very similar.

The "ape language" projects provide a number of elegant cases in which animals have learned to assess and compare signs according to their meaning. To cite just one example, Premack (1970, 1976) used an artificial lexicon of plastic chips to study communication and intelligence in chimpanzees. His most famous subject was an adult female, Sarah. To test whether Sarah really understood the meaning of her symbols, Premack first asked her to describe the features of an actual apple. Was it red? Was it round? Did it have a stem? Then Sarah was asked the same questions about the symbol for apple, in this case a blue triangle. She described the blue triangle as being red, round, and having a stem. Premack then reversed the question and asked Sarah to begin with an object and describe properties of the name for that object. Shown an apple, Sarah correctly answered that the sign for this object was triangular, not round, blue, not green, and small, not big.
To test whether vervet monkeys also assess vocalizations according to the things for which they stand, we designed a series of experiments in which subjects were asked to compare two calls with different acoustic properties. In some tests the calls referred to similar objects or events; in other tests their referents were different. If vervets compare vocalizations, that is, make a same/different judgment between them, on the basis of their referents, subjects should have judged two calls as "same" even when the calls were acoustically different. By contrast, calls with different referents should always have been judged as "different".

In one series of experiments, we used as stimuli two different calls given by female and juvenile vervets to members of other groups: a short, staccato chutter and a wrr, a long, loud trilling call. Although the two calls are acoustically quite different (Figure 10.3), each occurs only in the presence of another group (Struhsaker, 1967; Cheney & Seyfarth, 1982). Wrrs are usually given when a neighboring group has first been spotted, and they seem to function to alert other animals to the proximity of another group. Roughly 45% of all intergroup encounters involve only the exchange of wrrs (Cheney, 1981). Other encounters, however, escalate into aggressive threats, chases, and even physical contact. When groups come together under these conditions, females and juveniles often give the acoustically different chutter vocalization (Cheney & Seyfarth, 1988).

Although wrrs and chutter are acoustically distinct, they have broadly similar referents. To test whether subjects compare vocalizations according to their acoustic properties or their referents, we designed experiments in which a subject would repeatedly hear animal X's wrr when there was no other group present. Under these conditions, when the subject had habituated to X's wrr, we played animal X's chutter to see if she had also habituated to this acoustically different vocalization. If the two calls have similar meanings, and if monkeys use meaning to judge the relationship between calls, habituation to X's repeated wrrs should also produce habituation to X's chutter. Alternatively, if monkeys use some other feature (like the calls' acoustic properties) to judge similarity or difference between calls, these features, and not the calls' referents, should determine whether habituation is transferred from X's wrr to X's chutter.

In conducting our experiments, we borrowed a method that has been used successfully in research on preverbal human infants (e.g., Eimas, Siqueland, Jusczyk, & Vigorito, 1971). On day 1, as a control, a subject was played a particular female's chutter in order to establish the baseline strength of the subject's response to this vocalization. Then, on day 2, the subject heard the same female's wrr repeated eight times at roughly 20-min intervals. We measured subjects' responses and found that they did, in fact, habituate. Finally, roughly 20 min after the last playback in the habituation series, the subject heard the same female's chutter again (the test condition). The magnitude of the decrement in response between control and test conditions measured the extent
Meaning reference and intentionality

Figure 10.4. Results of habituation tests using wrrs and chutters given by the same individual. Histograms show the duration, in seconds (mean + SD) of 10 subjects' responses to playback of a given individual's intergroup chutter following repeated exposure to the same individual's wrr (test) compared with subjects' responses to the same chutter in the absence of such exposure (control). Mean duration of subjects' responses during habituation trials is also shown. Subjects responded for significantly shorter durations to test than to control calls.

Baseline data on the strength of a subject's response to individual Y's chutter. Then, on day 2, we played X's wrr to the subject eight times. After the subject had habituated to X's wrr we then tested to see if she had also habituated to Y's chutter.

A third test examined whether vervets would also transfer habituation if the identity of the signaler remained the same but the call's referent was changed. We therefore repeated the procedure described for the first set of experiments but now, instead of wrrs and chutters, we used leopard and eagle alarm calls as stimuli.

Results provided clear evidence that vervet monkeys compare different calls on the basis of their meaning and not just their acoustic properties. In all experiments, subjects rapidly habituated to repeated presentation of the same vocalization. When they were presented with the same individual's wrr and chutter, two acoustically different calls with roughly the same referent, they transferred habituation across different call types (Figure 10.4). In other words, if a subject had habituated to animal X's wrr, she also ceased responding to X's intergroup chutter.

By contrast, when subjects were asked to compare two calls whose referents were different, they did not transfer habituation across call types (Figure 10.5). If a subject had ceased responding to X's leopard alarm call, she nevertheless still responded at normal strength to X's eagle alarm.

Habituation was also not transferred when the calls had the same referent but were given by two different individuals. Even if a subject had ceased responding to individual X's wrr, individual Y's chutter still elicited the same response as it had under normal conditions (see Cheney & Seyfarth, 1988, for details of this and further experiments).

Compared with our earlier research on the vervets' alarm calls, these tests address the question of meaning and reference more directly, by asking animals to compare two vocalizations and to reveal the criteria they use in making their comparison. Like humans (e.g., Yates & Tule, 1979), vervet monkeys appear to process vocalizations according to an abstraction—their meaning—and not just according to acoustic similarity. The fact that subjects failed to transfer habituation when played the calls of two different individuals suggests that they took into account both the signal's meaning and the signaler's identity when attending to a call.
Figure 10.5. As in Figure 10.4, except results shown are for 10 subjects tested with one individual's leopard (or eagle) alarm after repeated exposure to the same individual's eagle (or leopard) alarm.

For further evidence that vervet monkeys make judgments about vocalizations according to the objects and events they denote, consider the monkeys' responses to the alarm calls of a sympatric bird, the superb starling (Spreo superbus). Like vervets, starlings have at least two distinct alarm calls, neither of which bears any acoustic resemblance to the vervets' own alarms. One starling alarm, a harsh, noisy chatter, is given to a variety of terrestrial predators. The second, a clear rising or falling tone, is given to hawks and eagles that attack from the air.

Vervet monkeys appear to recognize the difference between these calls, because they respond differently to each. When we carried out playback experiments using starling terrestrial predator alarms, starling raptor alarms, and starling song as stimuli, monkeys responded by running toward trees when they heard terrestrial predator alarms and looking up when they heard raptor alarms. By contrast, the monkeys showed no particular response when they heard the starlings' song (Cheney & Seyfarth, 1985).

Figure 10.6. Results of habituation tests using vervet and starling eagle alarm calls. Histograms show the duration, in seconds (mean + SD) of eight subjects' responses to playback of a vervet eagle (or starling raptor) alarm followed by repeated exposure to a starling raptor (or vervet eagle) alarm (test) compared with subjects' responses to the same alarm call in the absence of such exposure (control). Subjects responded for significantly shorter durations to test calls than to control calls. VE = vervet eagle alarm; ST R = starling raptor alarm; VL = vervet leopard alarm; ST T = starling terrestrial predator alarm.

As noted earlier, however, such playbacks say nothing about the mechanisms that underlie the vervets' discrimination among different alarm call types. To investigate such mechanisms in more detail, we once again used a habituation/dishabituation paradigm that asked subjects to compare two vocalizations. We reasoned that if vervet monkeys not only distinguish between the starling's different alarm calls but also classify starling alarms according to the types of predator they denote, then subjects should transfer habituation from the alarm calls of one species to the alarm calls of another provided the calls have the same referent. For example, vervets who have habituated to the raptor
alarm calls of starlings should cease responding to the raptor alarms of vervets, and vice versa. By contrast, subjects who have habituated to one species' terrestrial predator alarm should not transfer habituation to the other species' raptor alarm.

Once again, results suggested that vervet monkeys assess and compare vocalizations according to the calls' meaning and not just their acoustic properties. For example, when subjects had habituated to repeated presentation of a vervet's (or starling's) raptor alarm call, they transferred habituation to the raptor alarm of the other species (Figure 10.6). The monkeys behaved as if vervet eagle alarms and starling raptor alarms, despite their different acoustic properties, were in at least one respect similar to one another. In contrast, when subjects were asked to compare starling raptor alarm calls with vervet leopard alarms (Figure 10.7), no transfer of habituation occurred (for further details and results of other tests, see Seyfarth & Cheney, 1990).

This, of course, makes perfectly good biological sense. Given the high rates of predation in the vervets' environment (Cheney & Seyfarth, 1990a), there is every reason for them to have learned that sympatric species like starlings can be just as effective as other vervets in warning of an imminent attack. At the same time, it is interesting to note that when the monkeys were asked to compare two of their own species' vocalizations (wrrs and chutters), caller identity played an important role in the assessment of call meaning. By contrast, when the monkeys made a comparison that involved the calls of another species, caller identity seemed less important.

Taken together, the results of experiments using wrrs, chutters, vervet alarm calls, and starling alarm calls are difficult to explain without assuming that monkeys have some representation of the objects and events denoted by different call types and that they compare and respond to vocalizations on the basis of these representations. Apparently, when one monkey hears another monkey (or even a nearby bird) vocalize, the monkey forms a representation of what that call means. And if, shortly thereafter, the monkey hears a second vocalization, the two calls are compared on the basis of their representations, not just their physical similarity.

This is not to say that monkeys are necessarily aware of the distinction between signs and the objects they denote, or aware of their ability to compare vocalizations according to their referents. We cannot assume that an individual who can make same/different judgments about two calls on a habituation test will be able to make conscious use of this distinction in his daily life. Indeed,

![Figure 10.7](image-url)

Figure 10.7. As in Figure 10.6, except results shown are for 7 subjects tested with a vervet leopard (or starling raptor) alarm after repeated exposure to a starling raptor (or vervet leopard) alarm.

there is evidence that infant chimpanzees that can perceive a relational distinction when tested with an habituation procedure are nevertheless unable to apply their apparent knowledge of this distinction in a match-to-sample test (Oden, Thompson, & Premack, 1988). Habituation data alone, therefore, do not prove that monkeys understand the relation wrr denotes another group or eagle alarm denotes an eagle in the same way that a chimpanzee understands the relation blue triangle means apple.

**SEMANTICITY IN THE STRONGEST SENSE**

Human language involves more than just a recognition of the referential relation between words and the objects or events they denote. When communicating with one another we also attribute mental states like knowledge, beliefs, or desires to others, and we recognize that there is a causal relation between mental states and behavior: what an individual thinks influences what he does. Similarly, as listeners we interpret words not only as signs for things but also as representations of the speaker's knowledge. We are, moreover, acutely sensitive to the relation between words and the mental states that underlie them. If we detect a mismatch between what another person says and what he thinks, we immediately consider the possibility that he is trying to deceive us.
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Human language thus provides us with a definition of semanticity in its strongest sense. Having shown that monkeys make judgments about vocalizations based on their referents, we now consider whether animals ever attribute mental states to one another, know that these mental states can affect behavior, and as a result vocalize not only to influence what other animals do but also to influence what they think.

To attribute beliefs, knowledge, or ignorance to another individual is to have what Premack and Woodruff (1978) term a theory of mind. A theory of mind is a theory because, unlike behavior, mental states are not directly observable, although they can be used to make predictions about behavior. Many animals are adept at monitoring each other’s behavior. What is not known is whether they are equally adept at monitoring each other’s states of mind (see discussion by Dennett, 1987). To cite just one example, the alarm calls of many birds and mammals are not obligatory, but depend on social context. Individuals often fail to give alarm calls when there is no functional advantage to be gained by alerting others—for instance, when they are alone or in the presence of unrelated individuals (e.g., ground squirrels, Sherman, 1977; downy woodpeckers, Sullivan, 1985; vervet monkeys, Cheney & Seyfarth, 1985; roosters, Gyger, Karakashian, & Marler, 1986). However, while this audience effect clearly requires that a signaler monitor the presence and behavior of group companions, it does not demand that the signaler also distinguish between ignorance and knowledge on the part of his audience. Indeed, in all species studied thus far, signalers call regardless of whether or not their audience is already aware of danger. Vervet monkeys, for example, will continue to give alarm calls long after everyone in their group has seen the predator and retreated to safety (for further discussion see Cheney & Seyfarth, 1990a).

According to Grice (1957), true communication does not occur unless both signaler and recipient take into account each other’s states of mind. By this criterion (from which we derive the definition of semanticity in its strongest sense), it is highly doubtful that any animal signal could ever be described as truly communicative. Does this matter, though? It could easily be argued that there is little selective advantage to be gained from determining whether or not one’s audience is ignorant or knowledgeable before uttering an alarm call; as long as the call functions to inform others of danger, the audience’s state of mind is irrelevant. In at least some species, however, individuals who give alarm calls put themselves at greater risk than those who remain silent, because their alarm calls attract the attention of predators (see, e.g., Sherman, 1977, 1985 for ground squirrels). Under these conditions, an individual would be at an advantage if he could determine whether or not an alarm call was necessary before giving a vocalization.

Pedagogy as Evidence for a Theory of Mind

An individual who cannot recognize the difference between his own and another individual’s knowledge and beliefs will be incapable of selectively teaching or informing others of information that he possesses, simply because he will be unable to recognize ignorance in others. There is very little evidence, however, that the behavior of monkeys is ever influenced by other individuals’ states of mind. Consider, for example, the development of antipredator behavior in young vervet monkeys. As noted earlier, when infant vervets first begin giving alarm calls they often make “mistakes,” giving alarm calls to species like vultures or storks that pose no danger to them. Adults nonetheless respond to infant alarm calls, albeit in some cases quite briefly. For example, if an infant gives an eagle alarm in response to a pigeon, adults will look up and then quickly go back to what they were doing. By contrast, if an infant is the first member of his group to give an eagle alarm in response to a genuine predator (a martial or crowned eagle), adults will look up and then give an alarm call themselves (Seyfarth & Cheney, 1986). At first glance these “second alarms” by adults seem to be explicitly instructive, because they reinforce the infant’s behavior when it is correct. Adults, however, are no more likely to give second alarms after correct alarm calls by infants than they are after correct alarm calls by other adults. Even though infants make many more errors than adults, adults make no special effort to reward them when they are correct. We would expect such special efforts if adults attributed ignorance to infants.

A similar picture emerges when we consider infants’ responses to alarm calls. Here again, young infants make many mistakes. When we played tape-recorded alarm calls to infants younger than 6-months of age, adult-like responses were rare. Instead, infants either ran toward their mothers or responded in a way that actually increased their vulnerability to predation. An infant, for example, might look up when he heard a snake alarm or run into a bush when he heard a leopard alarm (Seyfarth & Cheney, 1986). In analyzing the responses of infants and mothers to playbacks of alarm calls, we looked carefully to see whether an infant’s behavior affected what his mother did—whether, in this respect, mothers ever corrected their infants’ errors. We found no such evidence.

In both of these cases, the vervets’ behavior draws our attention to the distinction between active pedagogy and more passive observational learning.
Perhaps because adult monkeys do not recognize the difference between what they know and what an infant knows, adults do not go out of their way to instruct infants about predators and the proper response to alarm calls. As a result, infants are left to learn by observation, which is a much slower and less efficient way to transmit information.

In a second set of trials, mothers were presented with a "predator" in the form of a technician wearing a surgical mask and brandishing a net as if to capture her. After 10 s of exposure, the technician hid behind a barrier next to the test arena. In the "knowledgeable" condition the mother was seated next to her offspring so that both mother and offspring saw the technician. In the ignorant condition, as before, the offspring was seated some distance from the mother, visually isolated and physically separated from her by a steel partition. Now only the mother could see the apple slices being placed in the food bin. After the food had been placed in the bin, the offspring, but not the mother, was released into the test arena where it had access to the food bin.

In both experiments the mothers' behavior seemed unaffected by their offspring's knowledge. In the food experiments, mothers and offspring did exchange vocalizations at low rates, but there was no difference in calling rate between mothers whose offspring were knowledgeable and those whose offspring were ignorant. In the predator experiments, mothers did not alarm call at higher rates when their offspring were ignorant, nor did they orient toward or look at their offspring more when the offspring were ignorant than when the offspring had also observed the predator (Cheney & Seyfarth, 1990b).

In each experiment, the mothers' apparent failure to communicate information to their ignorant offspring had measurable consequences. In the food experiments, the mean latency for finding and eating food was significantly shorter for knowledgeable offspring than for ignorant ones (Figure 10.8). In other words, even though mothers had ample opportunity to recognize a mismatch between their own knowledge and that of their offspring, they took no apparent steps to redress this imbalance—for example, by giving coo vocalizations while looking at the food bin. In the predator experiments, offspring who knew the technician was present spent significantly more time sitting huddled near the barrier separating them from their mothers than did ignorant offspring, who were more likely to wander around the cage (Figure 10.9). Once again, the primary factor in the amount of anxiety shown by offspring was their own knowledge, and not their mothers'.

Of course, these negative results do not allow us to distinguish between the inability to attribute states of mind to others and the failure of this ability to alter behavior. It is certainly possible that monkeys do recognize the difference between their own knowledge and the knowledge of others, but that their behavior is simply unaffected by this knowledge. Whenever knowledge in another species is defined operationally, through behavior, there is a danger of concluding that an ability is absent when it is simply not manifested. Negative results are of interest, however, when compared with information transmission in humans. Although human cultures vary in their emphasis on active informing and pedagogy (see, e.g., Boyd & Richerson, 1985), in no culture are these
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modes of transmission absent. In contrast, pedagogy has yet to be documented conclusively in any nonhuman primate species, including chimpanzees (for reviews see Cheney & Seyfarth, 1990a; Visalberghi & Fragaszy, 1990). Even if nonhuman primates are capable of distinguishing ignorance and false beliefs in others, therefore, their apparent failure to act on this knowledge is striking.

SUMMARY

Vervet monkey vocalizations qualify as semantic signals in the weak sense that they provide listeners with information about objects and events in the environment. Vervet calls are also semantic in the stronger sense that their production and interpretation depend on the mental states of both signaler and recipient. For example, when monkeys in habituation experiments are asked to compare two vocalizations, they do so not just according to the calls' acoustic properties but also according to their referents. To a vervet, the world is composed of two fundamentally different sorts of things: objects, such as leopards, snakes, or other groups; and vocalizations, which serve as representations of these objects. Monkeys respond to objects according to their physical features; they respond to vocalizations according to the things for which they stand.

Although vocalizations are semantic in this stronger sense, the calls of vervets and other monkeys seem not to be semantic in the strongest sense of being given with an intent to modify the mental states of listeners, or to draw listeners' attention to the signaler's own mental state. Adult monkeys, for
example, make no special effort to correct infants that use and respond to vocalizations incorrectly. Similarly, there is no evidence that adults distinguish between juveniles that are unaware of food or danger and those that already know that food and danger are present. We suggest that monkeys cannot communicate with an intent to modify the mental states of others because they do not recognize that such mental states exist.

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