

## Comprehension of Human Communicative Signs in Pet Dogs (*Canis familiaris*)

Krisztina Soproni and Ádám Miklósi  
Eötvös Loránd University

József Topál  
Hungarian Academy of Sciences

Vilmos Csányi  
Eötvös Loránd University

On the basis of a study by D. J. Povinelli, D. T. Bierschwale, and C. G. Cech (1999), the performance of family dogs (*Canis familiaris*) was examined in a 2-way food choice task in which 4 types of directional cues were given by the experimenter: pointing and gazing, head-nodding (“at target”), head turning above the correct container (“above target”), and glancing only (“eyes only”). The results showed that the performance of the dogs resembled more closely that of the children in D. J. Povinelli et al.’s study, in contrast to the chimpanzees’ performance in the same study. It seems that dogs, like children, interpret the test situation as being a form of communication. The hypothesis is that this similarity is attributable to the social experience and acquired social routines in dogs because they spend more time in close contact with humans than apes do, and as a result dogs are probably more experienced in the recognition of human gestures.

Dogs seem to represent an attractive species for understanding human communicative signs because they have been selected by humans for at least 10,000 years (Vilá et al., 1997) and live in human families, which can be regarded as their natural and social environment. Some researchers assume that this extremely long association with humans resulted in a coevolutionary process (Paxton, 2000; Schleidt, 1998) during which the behavior of dogs has changed significantly in comparison to their relatives. This coevolution hypothesis is based on the apparent temporal and geographical coincidence between the emergence of *Canis familiaris* and special forms of cooperation and communication in the modern *Homo sapiens* (Csányi, 2000). Because the adaptational demands for this species of *Canis* were similar to those of their *Homo* group mates, individuals that were able to adapt better to the human environment gained a selective advantage. It has been assumed that as a result of convergent evolutionary processes, behavioral traits emerged in dogs that are comparable to equivalents in human behavior.

This selection has led to a species that is sensitive to social reinforcers and attenuators (Frank & Frank, 1987), that is able to form an attachment relationship with their human caregiver (Topál, Miklósi, Dóka, & Csányi, 1998), that shows dependent behavior in problem-solving situations (Topál, Miklósi, & Csányi, 1997), and that is able to develop a complex communication system with humans (Miklósi, Polgárdi, Topál, & Csányi, 1998, 2000).

Recently it was shown that dogs are sensitive to human gestural communication, and they are able to use different types of human directional gestures (pointing, bowing, nodding, head turning, and glancing gestures) as cues for finding hidden food (Miklósi et al., 1998; see also Hare & Tomasello, 1999). In addition, it was revealed that dogs are also capable of intentional, functionally referential communication with their owners (Miklósi et al., 2000).

In contrast to dogs, many monkey species are very restricted in responding correctly to human communicatory visual gestures. Capuchin monkeys (*Cebus apella*) are able to comprehend human pointing gestures as discriminative cues for choosing an object, but their performance falls to chance levels if the cue is the head and eye direction of the experimenter (Anderson, Sallaberry, & Barbier, 1995; Itakura & Anderson, 1996). Similarly, rhesus monkeys (*Macaca mulatta*) also perform poorly if they are looking for food at a place indicated by human gestures. However, the same species shows a much better performance if monkeys have the opportunity to respond to visual cues displayed by conspecifics. For example, recent observations showed that rhesus monkeys are able to use the attentional cues of conspecifics to orient their own attention to objects (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello, Call, & Hare, 1998).

Comparative experiments also support the view that human influence (i.e., enculturation, see Call & Tomasello, 1996) has a

---

Krisztina Soproni, Ádám Miklósi, and Vilmos Csányi, Department of Ethology, Eötvös Loránd University, Budapest, Hungary; József Topál, Comparative Ethology Research Group, Hungarian Academy of Sciences, Budapest, Hungary.

This work was supported by Hungarian Foundation for Basic Research Grant T 029705 and by Hungarian Academy of Sciences Grant F 226/98. We are grateful to all owners and dogs for their cooperation. We would like to thank György Gergely for helpful comments on an early version of this article.

Correspondence concerning this article should be addressed to Krisztina Soproni, Department of Ethology, Eötvös Loránd University, Göd, Jávorka S. u. 14, 2131 Hungary. Electronic mail may be sent to lavina@ludens.elte.hu.

strong effect on animals responding to human directional cues. It has often been observed that after extensive experience with humans, apes displayed more sophisticated communicative abilities toward their caregivers. For example, although Povinelli, Bier-schwale, and Cech (1999) had to train their chimpanzees to respond appropriately to human pointing, Itakura and Tanaka (1998) reported high performance in enculturated chimpanzees and an orangutan in a similar task. A similar difference was obtained regarding the apes' response to gazing cues. Although no observable learning was reported by Povinelli et al. (1999), the chimpanzees in Itakura and Tanaka's study performed over 90% correctly in most experiments. Further contradictory results on apes' gaze-following ability can also be explained by differences in enculturation (see, e.g., chimpanzees: Itakura, 1996; Povinelli & Eddy, 1996b; gorillas: Peignot & Anderson, 1999). In summary, it is likely that differential response to human cuing in dogs, monkeys, and apes is strongly dependent on genetic or environmental factors or both.

In a recent series of experiments, Povinelli et al. (1999) tested whether juvenile chimpanzees and 3-year-old children were able to interpret the human gaze as a mental state of attention. Their aim was to dissociate two different models of chimpanzee gaze following. The so-called "low-level, nonmentalistic" model predicts that chimpanzees do not understand attention as an unobservable, internal mental state, whereas the "high-level framework" assumes that they do. Having trained chimpanzees to use the pointing of a human experimenter as a directional gesture for selecting a baited container, the animals were presented with three types of novel directional gestures (probe trials) inserted among pointing trials. Thus the experimenter was either nodding toward the correct container ("at target"), looking up above the correct container ("above target"), or glancing with eyes only toward the correct container ("eyes only").

The researchers hypothesized that if the chimpanzees understood the attentional significance of visual perception, they ought to perform well only on the trials where the experimenter was looking at the cup (at target and eyes only). In contrast, the nonmentalistic account assumes that they would respond randomly in all treatments, or they would select the correct cup in the at target and the above target probes as well. The results of the experiment supported the predictions of the low-level model of juvenile chimpanzees' understanding of seeing because they performed well both on at target and above target trials and poorly on the eyes only trials. The random selection of targets in above target trials in children was interpreted as evidence for understanding the attentional state of the other. However, as we described above, differences in rearing history (enculturation) can easily account for the relative poor performance of the chimpanzees in this study. Furthermore, it can be supposed that the chimpanzees' communicative system for comprehending directional signs is not able to react to subtle human gestures. If chimpanzees use a different behavioral gestures for such signaling, this may inhibit them from learning about human gestures relevant to this situation.

On the basis of the model by Povinelli et al. (1999), the aim of the present study was to establish the level of the comprehension of directional cues in dogs. We investigated the responses of family dogs to different types of directional human gestural cues in a procedure similar to that reported by Povinelli et al. We hypothesized that dogs would react sensitively to the attentional compo-

nent of the human gestures and that their performance would be similar to that of the children in the study by Povinelli et al. because they are not only enculturated (individually socialized) subjects but were also selected to be sensitive to certain types of human gestures.

## Method

### Subjects

Eight female and 6 male dogs (*Canis familiaris*; mean age = 51 months; range = 10–153 months) took part in this study. Except for 3 dogs, all of them had lived with human families since they were puppies; the others joined the family as adults. The dog-owner pairs were recruited from participants in our Family Dog Research Program. Seven Belgian shepherds were included: Fules (female, 62 months), Tunder (female, 16), Filip (male, 10), Fedra (female, 48), Stella (female, 14), Axel (male, 72), and Mystic (male, 24). Other dogs were of various breeds: Dugo (dachshund-like mongrel, female, 153), Szetti (setter-like mongrel, female, 48), Robin (collie, male, 26), Lili (Hungarian vizsla, female, 84), Bosko (Hungarian vizsla, male, 26), Aliz (doberman, female, 23), and Donci (Old English sheepdog, male, 108). Ten owners were women and two were men, and their ages ranged between 17 and 54 years. Owners were asked not to feed the dogs for 2 hr before the trials.

### Procedure

The observations were carried out from May through June 1999 in the owners' flat. Only the experimenter, the owner, and the dog were present during the training and testing. All trials were conducted by the same experimenter (Krisztina Soproni). Two bowls (brown plastic flower pots: 15 cm in diameter, 15 cm in height) were used to hide the bait. Both bowls had double bottoms with one food pellet fixed under the separating panel. The bottom panels were covered with a piece of cloth to prevent any noise occurring during the baiting. Various brands of dry food were used as rewards.

**Pretraining.** The experimenter was kneeling on the floor 0.5 m back from the middle line between the two bowls, which were 1 m apart. In front of her, at a distance of 2 m the owner restrained the dog, who was facing the experimenter. The experimenter tried to make eye contact with the dog. If the dog did not pay attention within 10 s, she called it by its name. While the dog was attentive, the experimenter showed the dog a food pellet and placed it into one of the containers. Then the owner let the dog approach the bowls and choose one of them. If the dog chose the baited bowl, it could eat the reward and was also praised verbally by the owner. If the dog made an incorrect choice, the experimenter took the pellet from the other bowl and showed it to the dog. In this case, the dog did not get the food. This trial was repeated four times, but if the dog made more than one incorrect choice, two additional trials were presented. The order of baiting was previously determined by tosses of a coin, with the restriction that one side could not be baited more than twice in a row. The pretraining was necessary to ensure that the dogs knew that the bowls might contain food.

**Pointing.** The position of the participants was the same as above, but now the dog was prevented from observing the baiting. The owner gently forced the dog to a location that prohibited it from watching the baiting; for example, the owner led the dog behind folding screens or furniture. The experimenter took a piece of food in each hand and put one in each bowl simultaneously, but one was immediately removed. After the food was hidden, the owner made the dog sit facing the experimenter, who made eye contact with the dog and gave the cue, that is, pointed briefly toward the baited pot and gazed in that direction at the same time. If the dog did not set out at the first cue, the experimenter repeated the pointing gesture once again. The dog was allowed to choose only one pot. One session consisted

of 10 trials. The learning criterion was set at a minimum of 90% correct choices in two subsequent sessions.

**Testing.** The test procedure was based mainly on an experiment originally described in Povinelli et al. (1999, Experiment 2). The dogs were tested by a so-called "probe trial technique" in which novel test treatments were administered by embedding them into a background of pointing trials. Each test session consisted of 12 trials. Trials 1, 3, 4, 6, 7, 9, 10, and 12 were pointing trials, identical to those described above. Trials 2, 5, 8, and 11 served as probe trials. Three types of probe trials were used: at target, above target, and eyes only (similar to Povinelli et al., 1999, Experiment 2). The presentation and form of the cues were identical as far as possible to that described by Povinelli et al. In at target trials, the experimenter turned her head and eye gaze toward the correct bowl, with her upper torso and rest of the body aligned along the midline as in standard pointing trials. In above target trials, the experimenter oriented her head and body in the same fashion as in the at target trials, but she was looking above the baited bowl to the upper corner of the room. In the eyes only trials, the experimenter oriented her head and body to the midline facing the dog and turned only her eye gaze toward the correct bowl.

In all probe trials, the experimenter gave the particular cue continuously, while rapidly glancing back and forth from the dog's face (making direct eye contact) to the correct pot. The experimenter continued cuing until the dog responded by choosing one of the pots.

The three types of probe trials were distributed within the sessions. There were six sessions for each dog, with eight probe trials for each type of cue. The presentation of cues was balanced for right and left side. The six sessions were accomplished in 3 consecutive days. For the analysis of the number of correct choices, nonparametric statistical tests were used.

## Results

There was no significant difference in the number of correct choices on the left and the right side for any gestures displayed; thus this variable was removed from statistical analysis. In the case of the pointing trials, all but 2 dogs reached the learning criterion in two pointing sessions; for these dogs an additional training session was necessary. Regarding the three types of probe trials, there was an overall difference in dogs' performance: Friedman analysis of variance,  $\chi^2 = 18.25$ ,  $p < .01$ . During the eight test trials for each gesture, dogs performed significantly above chance on at target trials: one sample  $t$  test,  $t(13) = 5.3$ ,  $p < .01$ ; but

randomly on both above target,  $t(13) = 1.1$ ,  $ns$ ; and eyes only trials,  $t(13) = -1.0$ ,  $ns$  (Figure 1).

To observe any effect of learning during the testing, we compared the performance of dogs in Sessions 1 through 3 and 4 through 6 for each type of gesture separately (Figure 2). In at target trials, the performance level did not change: Wilcoxon matched paired signed-ranks test,  $T(N = 10) = 12$ ,  $p = .13$ . Dogs had already chosen the baited bowl significantly over chance during the first three sessions,  $t(13) = 3.3$ ,  $p < .01$ , and the rate of correct choices remained at a high level,  $t(13) = 5.3$ ,  $p < .01$ . In the case of above target trials, there was no change during the experiment:  $T(N = 6) = 7.5$ ,  $p = .625$ . The performance of dogs remained at chance level in both the first,  $t(13) = 0.4$ ,  $ns$ ; and the last,  $t(13) = 1.2$ ,  $ns$ , three sessions of the experiment. In contrast, the performance of dogs in response to the gazing gestures (eyes only trials) changed considerably over time:  $T(N = 10) = 3$ ,  $p = .01$ . During Sessions 1 through 3, dogs performed significantly below chance,  $t(13) = -3$ ,  $p = .01$ ; but in the last three sessions, performance was at the chance level,  $t(13) = 1.9$ ,  $ns$ .

## Discussion

Our overall results demonstrate that dogs perform well in a two-way food choice task originally developed by Povinelli et al. (1999). Except for pointing, all gestures were introduced in the test phase to study the spontaneous interpretation of these human signs by the dogs.

At target gestures in our experiment can be considered a complex sign that consists of a referential component (i.e., the orientation of the head at the target) and an accompanying attentional cue (i.e., gazing at the baited bowl). A similar informative role can be attributed to gazing (eyes only) gestures with the difference that successful performance in eyes only trials may reflect the subject's ability to recognize the informational significance of changes in visual attention as signaled by eye direction only. In contrast, the above target gesture can be thought of as having only a discriminative function because it consists of an inadequate referential component (orienting at the ceiling), which could have also been interpreted by the subjects as signaling inattention with regard to

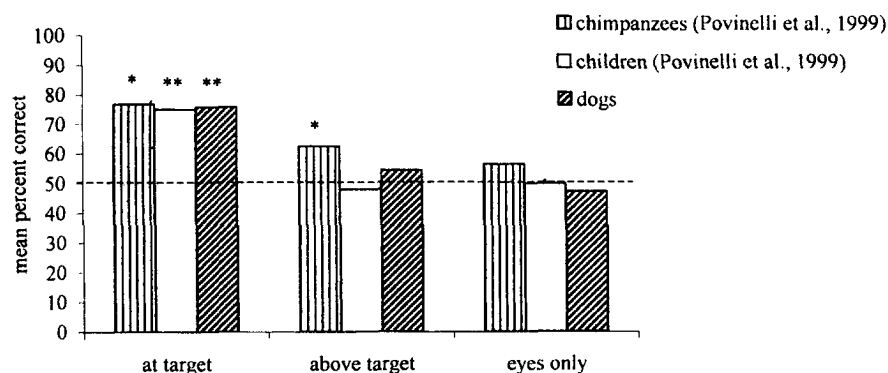


Figure 1. Mean percentage of correct choices for target locations in at target, above target, and eyes only probe trials. The data of chimpanzees and children are taken from the study of Povinelli et al. (1999). The dashed line indicates chance performance level (50%). \* $p < .05$ . \*\* $p < .01$ .

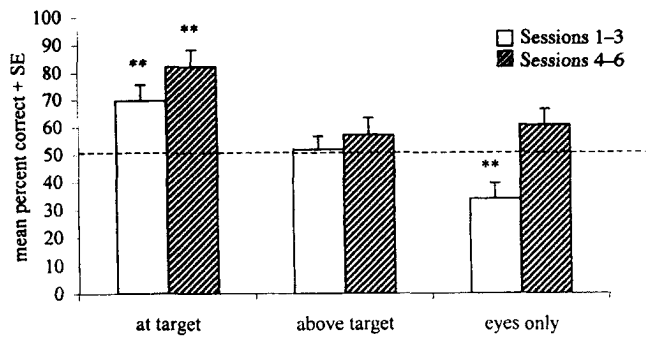


Figure 2. A comparison of the dogs' performance in Sessions 1-3 and 4-6 showing the mean percentage of correct choices (+SE) in at target, above target, and eyes only probe trials. The dashed line indicates chance performance level (50%).  $**p < .01$ .

the present situation or attention being directed to something or somewhere else.

We found that similar to the chimpanzees and children, dogs seemed to have understood the significance of the head orientation during at target trials from the outset (see Figure 1). This observation can be explained by the fact that dogs living in a human family might have had some previous experience with this type of gestural sign. In the case of above target trials, the dogs' behavior was comparable to that of children, neither of whom comprehended this gesture as referring to the place of the reward. Interestingly, this does not mean that dogs cannot be trained to use this gesture as a directional cue. Miklósi et al. (1998) demonstrated that dogs are able to find food on the basis of head-turning gestures, but they needed considerable amounts of training to achieve a reliable level of performance. In our case, the eight trials with this gesture were clearly not enough for such learning to take place. In contrast, there was no difference in at target and above target trials in the chimpanzees (Povinelli et al., 1999). In both cases, they seemed to select the baited container significantly over chance from the beginning of testing.

Regarding the eyes only trials, Povinelli et al. (1999) found that instances of gazing were not recognized as informing gestures. Both children and chimpanzees performed at chance level, and it was hypothesized that the direction of the experimenter's eyes was too inconspicuous a sign for them. In our study, the dogs clearly recognized the gazing gesture from the beginning as was demonstrated by the significant avoidance of the baited bowls during eyes only trials in Sessions 1 through 3. This avoidance, however, ceased for the last three sessions (4 through 6), supporting the view that under appropriate circumstances, some dogs are able to show rapid learning.

It is worth noting that in most canids, the eyes play an important part in communicative exchanges between conspecifics; however, the duration of eye contact might be crucial. Dominant members of the pack use wide-open eyes during agonistic stares at low-ranking individuals (Fox, 1971). Behavioral observations suggest that enduring direct stare by humans can evoke either submissive lateral recumbency in subordinate dogs, or it can provoke an attack or threat in adult dogs on their home territory (Fox, 1971). Much shorter eye contact could lead to initialization of play (Fox, 1971). It might have been the case that in eyes only trials, the extended

duration of eye contact or the exaggerated gesture (i.e., small changes in the size of the signaling eye) might have been misinterpreted by some of the dogs at the beginning of the test trials. It should also be noted that in contrast to our earlier study (in which the dogs were able to interpret glancing gestures of humans; Miklósi et al., 1998), the experimenter was not the owner but a familiar stranger.

These conclusions suggest that the dogs' reluctance to respond to the above target gesture cannot be explained on an attentional or motivational basis or by their inability to learn in such situations. The strong contrast between their response to eyes only and above target gestures underlines that there is a fundamental difference in how dogs interpret these signs. One possibility is that according to the above-mentioned hypothesis put forward by Povinelli et al. (1999), dogs use a high-level model in comprehending gestural signs. This would imply that similar to children, in the above target condition dogs interpreted the experimenter's gesture as signaling inattention. We should note, however, that it is possible that recognition of the behavioral signs of other's attentive status evolved independently of the ability to attribute the mental state of attention to others (see Povinelli & Eddy, 1996a). That is, a subject could be able to categorize behavioral changes of another subject as attentive or inattentive without the abstract mental representation of attention as a specific mental state (Gómez, 1997). The plausibility of this hypothesis is supported by human infant studies in which it was found that infants are able to get involved in joint attention tasks well before the full development of their mental capacities related to understanding the nature of attention (Corkum & Moore, 1995).

We should also mention that the negative results obtained for the chimpanzees do not necessarily reflect real species-specific differences in the interpretation of directional signs. Because both dogs and children spend more time in close contact with humans than apes do, they are probably more experienced in recognizing human gestures. Comparing the social-cognitive abilities of wild and captive apes, Call and Tomasello (1996) suggested that enculturation may have a determining effect. We can also suppose, however, that during domestication, dogs have become selectively sensitive to human communicative gestures as the basis of discriminative learning or as the basis of higher mentalistic processes. Therefore we suspect that the chimpanzees' poorer performance in comparison with children (Povinelli et al., 1999) and dogs can be explained by the lack of social routines or differences in evolutionary preadaptations or both.

Additionally, we should emphasize that although associative processes cannot be ruled out entirely, their contribution to this type of communicative exchange is limited. Similar to Hare, Call, Agnetta, and Tomasello (2000) and many others (see also Tomasello & Call, 1997), we are of the opinion that post hoc explanations of complex associations do not actually correspond with the fast adaptability of the behavior to a new behavioral situation in a new context. Despite their appealing simplicity and parsimonious value, the supposed associative processes would entail a more complex system than would follow from cognitive accounts.

In summary, it seems that dogs' behavior in this test situation is similar to that observed with children, in contrast to chimpanzees' behavior. As discussed above, we hypothesize that, like children, dogs interpret the situation as being communicative. The adequate responses given by the dogs to human gestures may reflect both

evolutionary preadaptation to the human environment and the individuals' extensive experiences in interpreting human signs. This suggests that the method proposed by Povinelli et al. (1999) for distinguishing high- or low-level mentalistic comprehension of human gazing does not account for species-specific preadaptations and rearing conditions.

### References

- Anderson, J. R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, *49*, 201–208.
- Call, J., & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371–403). Cambridge, England: Cambridge University Press.
- Corkum, V., & Moore, C. (1995). Development of joint visual attention in infants. In C. Moore & P. J. Durham (Eds.), *Joint attention: Its origins and role in development* (pp. 61–83). Hillsdale, NJ: Erlbaum.
- Csányi, V. (2000). The “human behavior complex” and the compulsion of communication: Key factors of human evolution. *Semiotica*, *128*, 45–60.
- Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., & Baker, C. I. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *111*, 286–293.
- Fox, M. W. (1971). *Behaviour of wolves, dogs and related canids*. London: Jonathan Cape.
- Frank, H., & Frank, M. G. (1987). The University of Michigan canine information processing project. In H. Frank (Ed.), *Man and wolf: Advances, issues and problems in captive wolf research* (pp. 143–167). Dordrecht, The Netherlands: Dr W. Junk Publishers.
- Gómez, J. C. (1997). Do concepts of intersubjectivity apply to nonhuman primates? In S. Braten (Ed.), *Intersubjective communication and emotion in ontogeny: A source book* (pp. 137–152). Cambridge, England: Cambridge University Press.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*, 771–785.
- Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, *113*, 1–5.
- Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research*, *38*, 174–180.
- Itakura, S., & Anderson, J. R. (1996). Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Current Psychological Cognition*, *15*, 103–112.
- Itakura, S., & Tanaka, M. (1998). Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology*, *112*, 119–126.
- Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, *1*, 113–121.
- Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (2000). Intentional behaviour in dog–human communication: Experimental analysis of “showing” behaviour in the dog. *Animal Cognition*, *3*, 159–166.
- Paxton, D. W. (2000). A case for a naturalistic perspective. *Anthrozoös*, *31*, 5–8.
- Peignot, P., & Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology*, *113*, 253–260.
- Povinelli, D. J., Bierschwale, D. T., & Cech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, *17*, 37–60.
- Povinelli, D. J., & Eddy, T. J. (1996a). Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *Journal of Comparative Psychology*, *110*, 336–345.
- Povinelli, D. J., & Eddy, T. J. (1996b). What young chimpanzees know about seeing. *Monographs for the Society for Research in Child Development*, *61*(3, Serial No. 247).
- Schleidt, W. M. (1998). Is humaneness canine? *Human Ethology Bulletin*, *13*, 1–4.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Call, J., & Hare, B. (1998). Five species of nonhuman primates follow the visual gaze of conspecifics. *Animal Behaviour*, *55*, 1063–1069.
- Topál, J., Miklósi, Á., & Csányi, V. (1997). Dog–human relationship affects problem solving behaviour in the dog. *Anthrozoös*, *10*, 214–224.
- Topál, J., Miklósi, Á., Dóka, A., & Csányi, V. (1998). Attachment behavior in dogs: A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, *112*, 219–229.
- Vilá, C., Savolainen, P., Maldonado, J. E., Amorim, I. E., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., & Wayne, R. K. (1997, June 13). Multiple and ancient origins of the domestic dog. *Science*, *276*, 1687–1689.

Received April 26, 2000

Revision received September 26, 2000

Accepted September 28, 2000 ■