and IL-21 signaling but which retain IL-7 signaling and thus B cell development, we have established in mice a phenotype that appears to closely resemble that of B cells from patients with XSCID, suggesting that defective signaling by IL-4 and IL-21 might explain the B cell defect in XSCID.

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The Domestication of Social Cognition in Dogs

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Dogs are more skillful than great apes at a number of tasks in which they must read human communicative signals indicating the location of hidden food. In this study, we found that wolves who were raised by humans do not show these same skills, whereas domestic dog puppies only a few weeks old, even those that have had little human contact, do show these skills. These findings suggest that during the process of domestication, dogs have been selected for a set of social-cognitive abilities that enable them to communicate with humans in unique ways.

Recent research has shown that primates possess a number of sophisticated social-cognitive skills, with some theories of cognitive evolution predicting that highly social primates are special in this regard (*1*, *2*). For example, many species of nonhuman primate follow the gaze direction of conspecifics and humans to outside objects—an adaptive social-cognitive skill for vicariously detecting food, predators, and important social interactions among group mates (*3*). Chimpanzees even follow the gaze direction of humans past distracting stimuli and behind barriers to a specific target, and they also understand that another individual cannot see something if its perspective is occluded by a barrier, thus demonstrating a fairly sophisticated understanding of how the visual perception of others works (*4–6*).

Curiously, however, there is one task involving gaze-following at which chimpanzees and other primates perform poorly. In the so-called object choice task, an experimenter hides a piece of food in one of two opaque containers, and the subject, who did not see where the food was hidden, is allowed to choose only one. Before presenting the subject with the choice, the experimenter gives a communicative cue indicating the food's location, for example, by looking at, pointing to, tapping on, or placing a marker on the correct container. The majority of primates, as individuals, do not spontaneously perform above chance levels on this task, no matter what the cue [although for possible exceptions, see (*7*, *8*)], and those who eventually perform well typically take dozens of trials or more to learn (*9–17*). In addition, when primates have been tested in more difficult tests that require them to show flexible use of social cues (such as with novel or arbitrary social cues), without exception they do not use the cues provided (*10*, *11*, *15*).

In contrast, the majority of domestic dogs (*Canis familiaris*) tested in the object choice paradigm effectively use many different visual cues presented by humans (such as looking at, pointing to, or touching the correct container). Dogs have even shown the ability to use novel social cues to find hidden food; for example, a human placing a physical marker on the correct container. They also are successful in more difficult tests, when a human moves toward the incorrect choice while giving the cue or when the cues are presented statically (for example, the dog enters the room to see a human or conspecific already looking at or pointing at the correct food location). Many dogs are skillful from the first trial, with no learning effects being observed within the experiment. Controls have ruled out the possibility that dogs use olfactory cues to find the hidden food (*18–22*). Although it seems from these studies that dogs are more skillful than primates in using human social cues to find hidden food, there has yet to be a direct comparison between the ability of dogs and that of any primate species in their use of human social cues. Thus, in the first experiment, we compared chimpanzees (*Pan troglodytes*) and dogs (*C. familiaris*) in an object choice task using a common methodology.

Another obvious question is how domestic dogs have acquired their skill in using human social cues. One hypothesis is that canids in general are unusually flexible in the types of social information they are capable of exploiting. For example, wolves, the closest relative of dogs (*23*), typically live in cooperatively hunting social groups, making it likely that they need to exploit the behavior of conspecifics and quarry alike, and this ability may then generalize to humans (*19*). The canid generalization hypothesis predicts that many canids (especially wolves) should perform at least as well as dogs on social tasks, as has been found previously with nonsocial tasks (*24*, *25*). Another hypothesis is that domestic dogs have much more experi-

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ence with humans than do most primates, and so they have learned their skills during their individual ontogenies (*19*). The human exposure hypothesis predicts that variation in individual dogs' experience with humans will be associated with variation in task performance; and, as a corollary, that young dogs should have relatively poor skills. Finally, a third hypothesis suggests that there has been selection pressure on dogs during the process of domestication for specific skills of social cognition and communication with humans (*20*). The domestication hypothesis predicts both that dogs should be more skillful than wolves and that variations in experience with humans should not affect the performance of either species (and that past a certain age, dog puppies should be as skillful as older dogs).

Therefore, in experiments 1 to 4, we test among the three hypotheses for the origin of dogs' ability to use human social cues by comparing the performance of (i) adult dogs and wolves (both reared by humans) in an object choice task and a nonsocial memory task and (ii) puppies of various ages and amounts of exposure to humans in an object choice task.

In the first experiment, 11 dogs and 11 chimpanzees were tested for their ability to use a conspicuous social cue to locate food hidden in one of two containers. An experimenter reached toward, gazed at, and marked the baited container with a wooden block (*26*). Nine of 11 dogs used the social information to find the hidden food, whereas only 2 of 11 chimpanzees effectively used the same social cue ($P < 0.05$, binomial tests, one-tailed). In addition, the dogs as a group chose correctly significantly more often than the chimpanzees, $t(18.244) = 3.98$, $P < 0.001$ [Welch independent sample t test (Fig. 1)].

In the second experiment, seven adult wolves (*Canis lupus*) and seven adult dogs were tested in a series of object choice tasks. The following social cues were used to indicate the food's location: (i) Gaze + Point + Tap cue (GPT): The experimenter looked toward the baited bowl while extending his/her cross-lateral arm and tapping on the bowl for 3 to 5 s, which made a small noise. (ii) Gaze + Point cue (GP): identical to GPT, except that the tapping was replaced with pointing at the baited bowl (the index finger was 10 to 15 cm from the bowl). (iii) Point cue (P): identical to GP, except that no gaze cue was given (the experimenter looked at the subject). (iv) Control cue (C): the experimenter gave no cue (looked straight ahead) (*26*).

Dogs found more food than the wolves with all three visual cues, but not in the control condition (Fig. 2) [GPT: $t(9.77) = 7$, $P < 0.001$; GP: $t(7.14) = 2.54$, $P < 0.04$; P: $t(7.33) = 2.78$, $P < 0.03$ (Welch independent sample t test)]. As a group, the performance of the dogs was significantly above chance for each of the cues [for the GPT cue, $t(6) = 8.44$, $P < 0.001$; for the GP cue, $t(6) = 3.41$, $P < 0.02$; and for the P cue, $t(6) = 3.7$, $P < 0.01$ (one-sample t tests)]; however, their performance was not above chance in the control condition. As a group, the performance of the wolves was above chance for one cue: the GP cue, $t(6) = 2.45$, $P = 0.05$ (and not above chance for the GPT cue, the P cue, or in the control condition). In addition, as a group, both species found the food at above chance levels when their performance with all three social cues was combined [dogs: $t(6) = 5.28$, $P = 0.002$; wolves: $t(6) = 3.43$, $P = 0.013$ (one-sample t test)]. No effect of learning across trials was detected in either species (*26*). Individually, all dogs performed above chance on at least one cue, whereas no wolf performed above chance on any cue. Seven dogs used the GPT cue, five used the GP cue, and four used the P cue to find the food at a rate above chance ($P < 0.05$, binomial test, one-tailed). Three dogs used all three cues, three dogs used two cues (two used GPT and GP, and one used GPT and P), and one dog used only one cue (GPT). No subject of either species performed above chance in the control condition.

In the third experiment, we tested whether five dogs and five wolves differed in performance in a nonsocial food-finding game. The goal of this study was to test whether dogs perform better than wolves in all human-guided tasks. In this game, there was a delay betweeen the time when subjects saw food hidden (in a canister held in the hand) and when they chose a location (*26*). As a group, both species performed above chance in the memory task [wolves: $t(4) = 8.23$, $P = 0.001$; dogs: $t(4) = 11.23$, $P < 0.001$ (one-sample t test)]. There was no difference between species [$t(8) = -0.866$, P = NS (independent t test) (Fig. 3)]. As individuals, four of the five subjects of both species performed at above chance levels in the memory task. In addition, all subjects tested in a control task (they did not see the food hidden) performed at chance levels, ruling out the possibility that they were using olfaction to locate the food in the test condition.

In a fourth experiment, the same basic methodology was used as in studies 1 and 2, with a set of 32 dog puppies varying in age from 9 to 26 weeks. The puppies were tested with two cues: GP (same as for adult dogs in experiment 1) and G (the experimenter turned his head in the direction of and stared at the bowl where the food was hidden). Some of the puppies had lived with human families (being adopted between birth and 8 weeks of life) throughout their lives (family-reared), whereas others had lived their entire lives with littermates in a kennel and so had been exposed to humans for only a few minutes each day for husbandry purposes (litter-reared) (*26*).

There was no difference between the rearing groups in their use of either cue [independent t tests (Fig. 4)]. Individually, three of six family-reared and five of six litter-reared puppies used the GP cue to find food, and one family-reared puppy used the G cue ($P < 0.05$, binomial tests, one-tailed). No effect of learning across trials was detected in either rearing group. To test the effect of age on performance, an analysis was conducted in

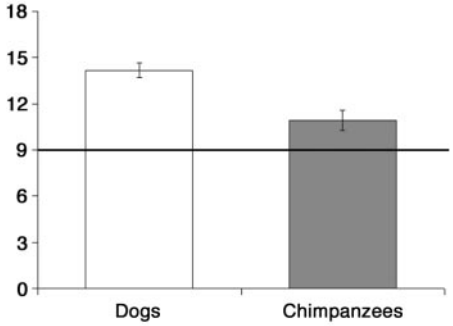

Fig. 1. Mean number of correct choices (±SEM) by dogs and chimpanzees when a social cue is provided by a human experimenter in study 1. Chance performance equals nine correct choices.

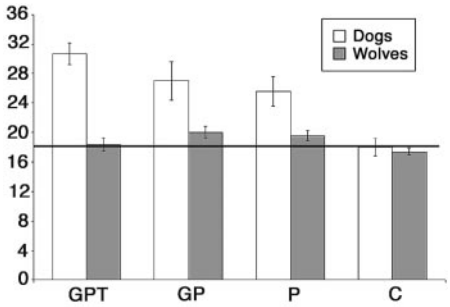

Fig. 2. Mean number (±SEM) of correct responses by the seven dogs and seven wolves in each of four conditions in study 2. Chance perfomance equals 18 correct choices.

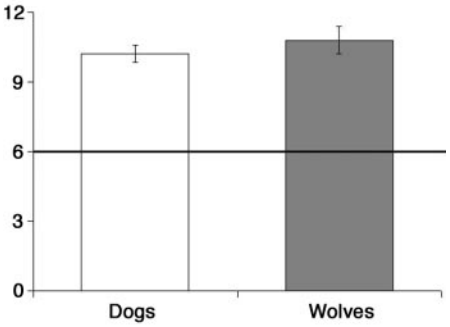

Fig. 3. Mean number of correct choices (±SEM) by dogs and wolves in the experimental condition of the nonsocial memory task in study 3. Chance performance equals six correct choices.

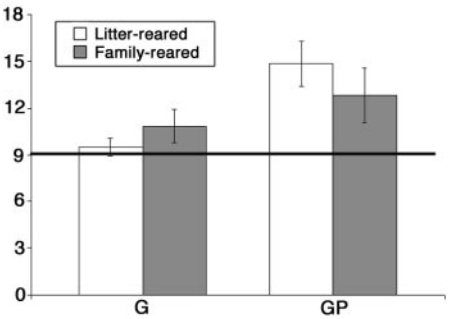

Fig. 4. Mean number (±SEM) of correct responses for each rearing group with both cues in study 4. Chance performance equals nine correct choices.

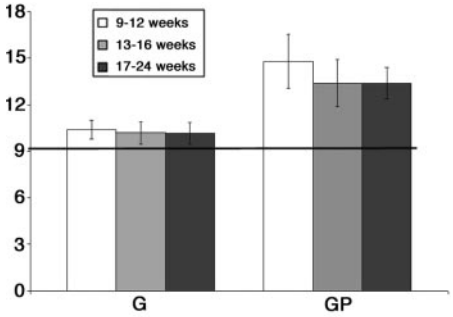

Fig. 5. Mean number (±SEM) of correct responses for each age group of puppies with both cues in study 4. Chance performance equals nine correct choices.

which subjects were separated into three age groups (9 to 12 weeks, 13 to 16 weeks, and 17 to 24 weeks). When a two-way analysis of variance with age and cue as factors was used, no effect of age was detected (Fig. 5), although there was a group difference in that the GP cue was used more effectively than the G cue [F (1, 26) = 16.15, $P < 0.001$]. However, as a group, puppies used both cues to find the food at above chance levels [GP cue: $t(14) = 6.10$, $P < 0.001$; G cue: $t(16) = 3.26$, $P < 0.005$ (one-sample t tests)]. Again, no effect of learning across trials was detected (*26*).

These studies demonstrate that (i) domestic dogs are more skillful than chimpanzees (one of humans' two closest extant primate relatives) at using human social cues to find hidden food in the object choice paradigm; (ii) domestic dogs are also more skillful than wolves, their closest extant relative, at using human social cues to find hidden food in the object choice paradigm; and (iii) dog puppies' use of human social cues in the object choice paradigm is quite skillful and does not vary by age or by their rearing history with humans. We also found that dogs and wolves do not perform differently in a nonsocial memory task, ruling out the possibility that dogs outperform wolves in all human-guided tasks. Taken together, these results do not support the predictions of either the canid generalization hypothesis (dogs have inherited their skills from wolves) or the human exposure hypothesis (dogs are skillful because they experience intense exposure to humans through their lives). Instead, these results provide the strongest support for the domestication hypothesis: that dogs' social-communicative skills with humans were acquired during the process of domestication.

Given that dogs' abilities to use human social cues originated during the process of domestication, it is likely that individual dogs that were able to use social cues to predict the behavior of humans more flexibly than could their last common wolf ancestor (which was only capable of using human social cues at low levels, like primates) were at a selective advantage. Potentially, this adaptive hypothesis can be tested further by replicating experiments two and three with another domesticated canid species, Belyaev's silver foxes, who were experimentally domesticated without any direct selection for their social-cognitive or communicative abilities (*27*).

These findings demonstrate a signficant social-cognitive difference between two closely related nonhuman species (dogs and wolves) and also provide evidence for the adaptive context—in this case, a unique context—in which this difference evolved. Our conclusion is that as a result of the process of domestication, some aspects of the social-cognitive abilities of dogs have converged, within the phylogenetic constraints of the species, with those of humans through a phylogenetic process of enculturation, perhaps similar in some ways to the ontogenetic process of enculturation experienced by some nonhuman primate individuals raised by humans (*28*).

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Materials and Methods
Tables S1 to S4

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