Social Cognitive Evolution in Captive Foxes Is a Correlated By-Product of Experimental Domestication

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Summary

Dogs have an unusual ability for reading human communicative gestures (e.g., pointing) in comparison to either nonhuman primates (including chimpanzees) or wolves [1–8]. Although this unusual communicative ability seems to have evolved during domestication [6, 8], it is unclear whether this evolution occurred as a result of direct selection for this ability, as previously hypothesized [8], or as a correlated by-product of selection against fear and aggression toward humans [9]—as is the case with a number of morphological and physiological changes associated with domestication [11–18]. We show here that fox kits from an experimental population selectively bred over 45 years to approach humans fearlessly and nonaggressively (i.e., experimentally domesticated) are not only as skillful as dog puppies in using human gestures but are also more skilled than fox kits from a second, control population not bred for tame behavior (critically, neither population of foxes was ever bred or tested for their ability to use human gestures) [11, 12]. These results suggest that sociocognitive evolution has occurred in the experimental foxes, and possibly domestic dogs, as a correlated by-product of selection on systems mediating fear and aggression, and it is likely the observed social cognitive evolution did not require direct selection for improved social cognitive ability.

Results and Discussion

In experiment one, both experimental fox kits and the dog puppies found the hidden food significantly above chance with the point-and-gaze (PG) cue (experimental foxes: $t[10] = 9.04$, $p < 0.001$, one-sample t test; dog puppies: $t[9] = 7.3$, $p < 0.001$, one-sample t test; Figure 1). Comparisons between species reveal that the experimental fox kits and dog puppies were equally successful in finding the hidden food with the PG cue ($t[19.7] = 0.51$, $p =$ not significant [NS], Welch independent sample t

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test; Figure 1). The ten foxes tested in the control condition were unable to find the hidden food when no visual cue was provided ($t[9] = 0.318$, $p =$ NS, one-sample t test). In addition, when the foxes' number of correct choices from their first nine trials is compared to that of their second nine trials, there is no evidence that their performance improved with experience during the test session ($t = 0.76$, $df = 10$, $p =$ NS, one-sample t test). Similarly, it has been repeatedly shown that dogs, even as adults, are unable to find hidden food with olfactory cues in this same setting, and there is no evidence that performance improves within a test session [5–8].

In experiment two, 13 experimental foxes and 13 control foxes approached the experimenter (E) within the 3 min introduction trial. In addition, 17 experimental foxes and 16 control foxes approached the novel object within the introduction trial. However, the experimental fox kits' time to first approach (7.2 s) was significantly shorter than that of the control fox kits' (37.6 s) when a human was present ($t[13.47] = 2.7$, $p = 0.009$, Welch independent sample t test). In addition, the experimental fox kits' time to first approach (mean 6.7 s) was significantly shorter than the control foxes' (29.2 s) when the novel object was presented ($t[19.64] = 2.19$, $p = 0.021$, Welch independent sample t test).

In the human cue test of experiment two, there was no difference between the number of trials in which the experimental and control foxes participated by manipulating one of the two toys ($t[31.98] = 0.9$, $p =$ NS, Welch independent sample t test). In fact, all of the subjects in both groups touched one of the two toys on their very first trial. However, across the session the experimental foxes touched the same toy as E significantly above chance, whereas the control foxes did not (experimental foxes: $t[16] = 3.69$, $p = 0.001$; control foxes: $t[16] = 0.22$, $p =$ NS, one-sample t test; Figure 2; note that control foxes chose at chance levels and did not have an aversion to touching the toy E touched). In addition, the experimental foxes touched the same toy the experimenter had manipulated significantly more than the control foxes ($t[28.98] = 2.3$, $p = 0.014$, Welch independent sample t test; Figure 2). Even on the very first trial, the experimental foxes tended to touch the same toy more than the control foxes ($X^2[1, n = 34] = 2.94$, $p = 0.086$, chi-square test of independence).

In experiment three, there was again no difference between the two groups in the number of trials in which they chose to participate by touching one of the two toys ($t[12.54] = 1.37$, $p =$ NS, Welch independent sample t test). However, unlike experiment two, the experimental foxes did not differ significantly from the control foxes. The two groups did not differ in their preference for playing with a toy that was manipulated by an object ($t[15.23] = 1.57$, $p =$ NS, Welch independent sample t test; Figure 3). In fact, whereas the domesticated foxes did not have a preference for touching the same toy an object touched ($t[8] = 0.035$, $p =$ NS, one-sample t test; Figure 3), the control foxes did have a preference for
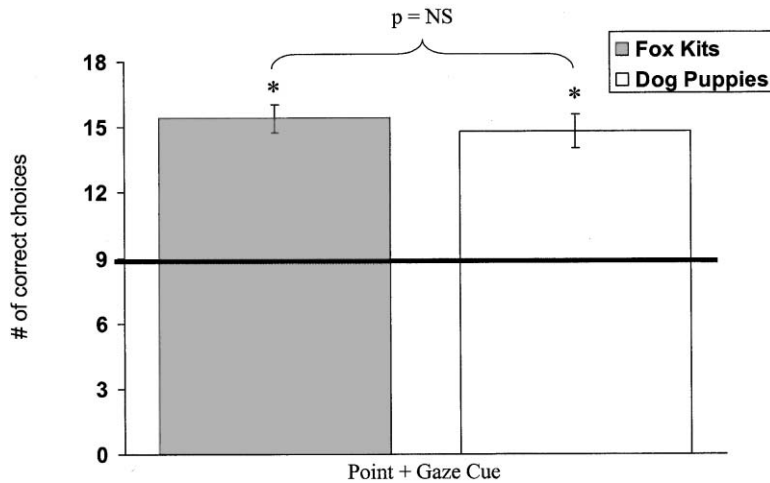
Figure 1. Number of Correct Choices (i.e., Food Located) Made by Experimental Fox Kits and Dog Puppies when the Point-and-Gaze Cue Was Provided by a Human

touching the toy the object had touched (t[8] = 2.47, p = 0.02, one-sample t test; Figure 3).

In experiment four, both the control and experimental foxes used the PG cue to find the hidden food at above-chance levels (experimental foxes: t[5] = 5.65, p = 0.001; control foxes: t[5] = 2.78, p = 0.02; Figure 4). However, the experimental foxes used the human communicative cue significantly more than the control foxes (t[9.9] = 2.06, p = 0.03, Welch independent t test; Figure 4). When the number of correct choices in the first nine trials of the test session was compared to that of the second set of nine trials, there was no evidence that either the experimental or control foxes improved their ability to locate the hidden food during the test session (experimental foxes: t = 0.415, df = 5, p = NS; control foxes: t = 0.745, df = 5, p = NS, paired t test).

Discussion

Before the current study, it has only been possible to speculate on what selection pressure(s) led to the observed change in social cognitive ability in dogs since the split from their last common wolf ancestor. The "selection for communication" hypothesis suggests that predicting and manipulating human behavior by reading various human communicative signals (e.g., visual gestures) was a direct target of selection during domestication. Therefore, those dogs that were most skilled at utilizing human gestures (e.g., to locate things in their environment or to go where directed) were more likely to survive and reproduce [6, 8]. Alternatively, the "correlated by-product" hypothesis suggests that the ability to read human communicative gestures was not a target of selection during domestication. Instead, this hypothesis proposes that such an ability evolved in dogs as a correlated by-product of selection for tame behavior (selection against fear and aggression and in favor of interspecific social contact) toward humans. Specifically, those individuals living without stress and behaving prosocially toward humans (because of high fear-aggression thresholds) had the highest fitness [9]. These same individuals, because of heritable changes responsible for high levels of tameness (i.e., physiological changes associated with domestication), were no longer constrained (e.g., by fear or disinterest) in applying previously existing social problem-solving skills to humans in interspecific interactions [10].
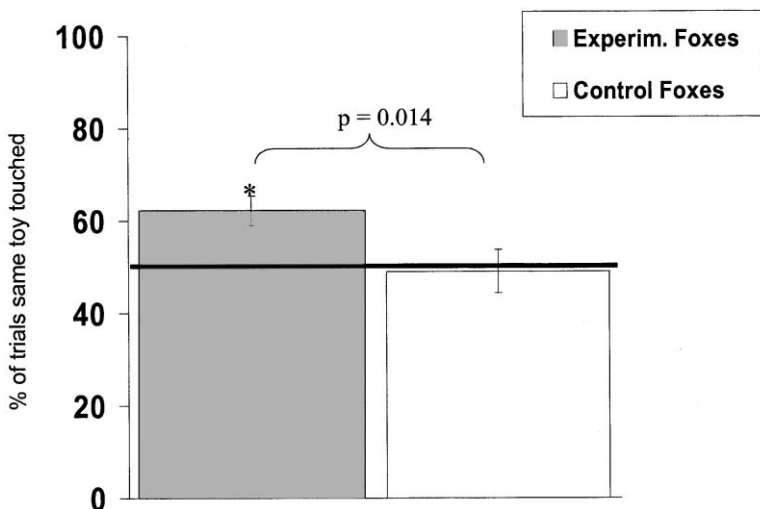

Figure 2. Percentage of Trials the 17 Experimental and Control Subjects Touched the Same Toy the Experimenter Gestured Toward and Manipulated
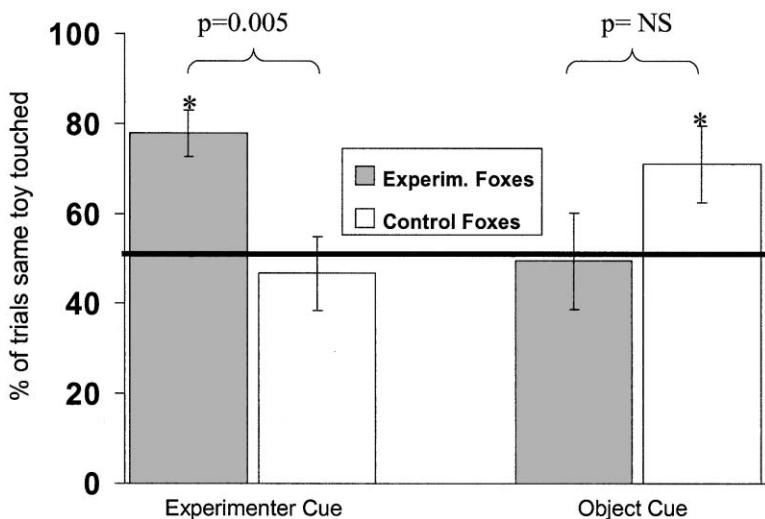
Figure 3. Percentage of Trials Nine Experimental Fox Kits and Nine Control Fox Kits Touched the Same Toy an Experimenter or Object Manipulated

*Note: These 18 subjects were the subjects from experiment two with the highest levels of participation from each group. Thus, nine subjects were tested from each of the two groups from experiment two (therefore, the data illustrated concerning subject's preference for touching the toy the experimenter manipulated are from experiment two).

The current findings demonstrate that: (1) experimentally domesticated foxes with almost no experience with humans are as skilled at using human communicative gestures (i.e., a point-and-gaze cue) as domestic dogs when searching for hidden food (and therefore more skilled than primates), with no evidence that such skills are learned within the test; (2) although experimentally domesticated foxes are no more likely than control foxes to approach a strange human or novel object, they do approach strange humans and novel objects more quickly [14]; (3) even when no food is provided as reinforcement, experimentally domesticated foxes are spontaneously more interested in playing with a toy that a human has recently gestured toward and touched than control foxes, but they are no more interested in playing with a toy an object has recently manipulated than control foxes; and (4) although control foxes are capable of using human communicative gestures after weeks of exposure to humans, experimentally domesticated foxes (with far less experience with humans) are still more skilled at using the same communicative gestures than control foxes. Therefore, the findings of these studies do not support the selection for communication hypoth-

esis, whereas they do support the correlated by-product hypothesis. (Note that the selection for communication hypothesis simply mirrors the adaptive hypothesis previously proposed as driving social cognitive evolution in primates. The "social intelligence" hypothesis suggests that primate [and human] cognitive evolution was largely driven by an ever-increasing need to predict and manipulate the behavior of other group members by reading subtle cues in their behavior [19].) The experimental fox kits were as skillful in using human communicative gestures as age-matched dog puppies and were more skilled at using such cues than age-matched control fox kits.

These findings are relevant to both those studying domestication's effect on dog social cognition and those studying social cognitive evolution more generally. First, the finding that domestication has led to an improved ability to use human communicative gestures in the experimental foxes supports the role of domestication in altering domestic dogs' social cognitive skills after splitting from their last wolf ancestor. Second, the current findings suggest the possibility that selection against fear and aggression and for interspecific social contact with humans during domestication may have
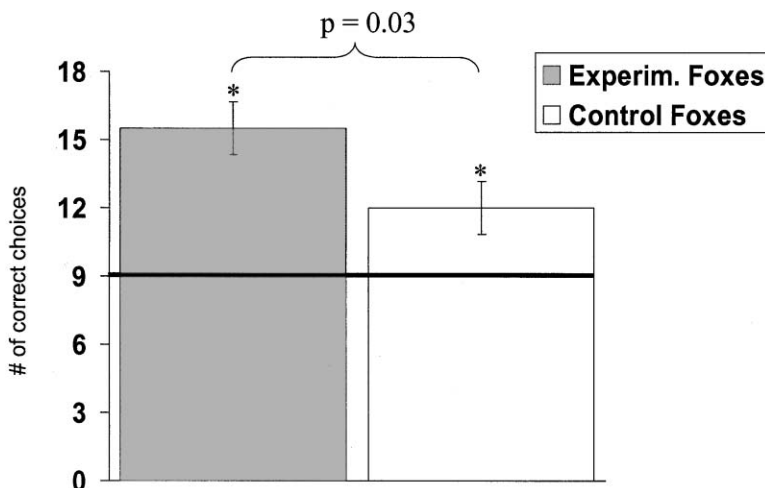

Figure 4. Number of Correct Choices (i.e., Food Located) Made by Experimental and Control Foxes when the Point-and-Gaze Cue Was Provided by a Human

been sufficient to produce the unusual ability of dogs to use human communicative gestures (for example, natural selection that likely occurred as wolves began exploiting the niche created by refuse in and around human settlements [9]). Such an "emotional reactivity" hypothesis is further supported by the gene-expression differences observed between adult wolves and dogs in brain areas, such as the hypothalamus, that are involved in emotional control [20]. However, a longitudinal study with wolves will be especially useful in testing the prediction of this hypothesis that their ability to use human gestures decreases with the development of adult-like stress responses (as would be predicted with adult control foxes as well).

At the same time, it is important to note that the current findings do not rule out the possibility that multiple selection pressures acted in concert to shape dog social cognition during domestication. It remains possible, even likely, that selection acted directly on dogs' ability to read human communicative cues either before or after primitive dogs began cohabiting with humans. The results of this experiment only suggest that selection for tameness is enough on its own to produce a change in canid social problem-solving ability.

Finally, these results suggest more precisely than any other previous experiment exactly what type of selection pressure might lead to a heritable change in social cognitive ability. Given the level of certainty for which the selection pressure that led to sociocognitive evolution is known in the experimental foxes, future evolutionary models will also have to account for the probability that other cases of cognitive evolution (including those observed in humans) may have occurred as a correlated by-product of selection on other seemingly unrelated phenotypic traits [21, 22]. As an example, it has been suggested that selection on systems mediating fear and aggression in humans (and perhaps other primates) may have led to prosocial behavior changes that in turn altered the expression of social cognitive abilities that were inherited from our last common ape ancestor [4, 23].

Experimental Procedures

To discriminate between our two hypotheses for the evolution of dog social cognition, we used tests previously designed for comparing dogs and wolves [6, 8], with a population of recently domesticated silver foxes (*Vulpes vulpes*) and a population of control foxes maintained in Siberia, Russia [11, 12]. Because of physiological changes observed in the experimental foxes' pituitary-adrenal axis and in their altered levels of neurotransmitters (e.g., serotonin)—all of which are involved in modulating stress responses—the experimental foxes readily initiate interactions with humans [12–17]. These behavioral and physiological changes are accompanied by a suite of correlated (unselected) morphological changes that are associated with domestication in other mammals [12, 13] in experimental foxes. These changes include higher rates of shortened or curly tails, floppy ears, depigmentation of hair, and changes in the shape and size of the skull [12, 18].

We first compared the ability of the experimental foxes to that of domesticated dogs in their use of human communicative cues to find hidden food. Second, we compared the experimental foxes to the control foxes in their use of communicative cues provided by a human or cues provided by an interesting object. Because the foxes from the experimental population were never selected on the basis of their comprehension of human communicative signals, the selection for communication hypothesis predicts that (1) dogs will be

more skillful using human gestures to find hidden food than the experimental foxes and (2) there will be no differences between the experimental and control foxes in their use of cues provided by a human or an object. The correlated by-product hypothesis, in contrast, predicts that the experimental foxes (1) will match domestic dogs in their skill at using human social cues in locating hidden food and (2) will attend to human gestures, but not object cues, more than control foxes.

In the first experiment, 11 experimental fox kits were compared to 11 age-matched dog puppies for their ability to use human communicative cues when searching for hidden food. Subjects were first introduced to and then tested in a novel testing room. When tested, food was hidden in one of two cups that were placed 1.7 meters from each other and 1.5 meters from the subject on the floor of the testing room. Once the food was hidden, the experimenter (E) indicated the location of the hidden food to the subject by pointing and gazing toward the correct location (PG cue). The experimenter extended her arm and index finger in the direction of the hidden food while also gazing at the baited bowl. The experimental foxes were also tested in a control condition to assess whether they were capable of finding the hidden food with olfactory cues alone. Therefore, they were tested in a session of 18 trials in which the experimenter hid the food, as before, in one of the two cups but did not provide a cue to the food's location (E only stared directly at the subject).

In a second experiment, 17 experimental and 17 control foxes were first introduced for 3 min to (1) a novel E and (2) a novel object (i.e., a testing table with two identical toys placed at either end) while in their home room. After this introduction, a test was conducted in which E assessed the subjects' preference for playing with a toy that she had recently manipulated (no food reward was given, regardless of a subject's response). E sat behind the testing table, which was placed in front of the subjects' home room. Once seated, E then gestured toward and touched one of the two toys that were attached to either side of the table. Then E pushed both toys within reach of the subject simultaneously.

In a third experiment, E tested the preference of nine experimental and nine control foxes for playing with a toy that was recently manipulated by an object. The subjects for experiment three were chosen on the basis of their participation levels in experiment two (see the Supplemental Data available with this article online for details of selection). This test was designed to assess whether experimental foxes simply perform better than control foxes in all human-led tasks. This experiment was almost identical to experiment two, except that once seated behind the testing table, E touched one of the two toys with a feather attached to a long stick (although subjects could see E, they could not see that E was moving the stick and feather because an occluder blocked their view of his hands, arms, and chest—only the stick and feather protruded from the occluder). Then E pushed both toys within reach of the subject simultaneously.

In a fourth experiment six experimental and six control foxes were directly compared for their ability to find hidden food with the PG cue from experiment one. Before testing, the control foxes had interacted with E for twice as long as the experimental foxes. For the test, as in experiment one, food was hidden in one of two bowls, and then E indicated its location with the PG cue.

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Supplemental Experimental Procedures

Details of Selection on Experimental and Control Foxes

The experimental and control populations were founded from commercial stock in 1959 and have subsequently been maintained in identical conditions. However, the experimental population of foxes was selected for breeding based on standardized behavioral measures since 1959 [S1, S2]. Starting at 1 month old, each experimental subject was tested for its reaction to an experimenter. Once a month during infancy, an experimenter would attempt to stroke and handle each kit while offering it food. In addition, it was observed whether kits preferred to associate with other kits or the experimenter. Once the kits reached sexual maturity, at 7–8 months old, each subject was tested for a final time and was assigned an overall tameness score based on a strict set of behavioral criteria. First, experimenters independently rated each subject's tendency to approach them while they were standing in front of their home pen. Second, experimenters independently rated each subject's tendency to bite at them if they tried to touch it. Within the experimentally selected population, only those individuals who were least fearful and aggressive toward a human (evidenced by their approach behavior and attempts to initiate human contact) were selected for breeding. Less than 20% of each successive generation in the experimental population were allowed to breed each year [S1, S2].

On the basis of this single selection criterion, behavioral, physiological, and morphological changes that were either not found in control foxes or were expressed at a significantly higher frequency in the experimental population were observed in the experimental fox population. First, the individuals in the experimental population were observed from 1 month of age onward to show little fear or aggression toward humans in that they were more "eager to establish human contact, whimpering to attract attention and sniffing and licking the experimenters like dogs" (page 163 in [S2]). Subsequent experiments have demonstrated that selection for tameness retarded the development of fear responses to novelty and enhanced exploratory behavior in unfamiliar situations [S3]. Second, physiological changes were observed after several generations of selection. The first change detected was attenuated activity of the pituitary-adrenal axis. The common pool of circulating glucocorticoids, their in vitro production, the basal level of the adrenocorticotrophic hormone (ACTH), and the adrenal response to stress were all reduced in the experimental foxes in relation to controls [S4]. Subsequently, the activities of the serotonin, noradrenaline, and dopamine transmitter systems in specific brain regions that are implicated in the regulation of emotional-defensive responses have also been found to be altered in the experimental foxes [S5, S6]. Finally, and perhaps most surprising, the domesticated foxes manifested a number of morphological changes that are commonly found in a number of other domesticated species. A higher frequency of domesticated foxes had floppy ears, short or curly tails, depigmentation of hair, extended reproductive seasons, and even changes in the size and shape of the crania and dentition [S1, S2, S7].

The results of the fox farm experiment demonstrate that selection against aggressive and fearful behavior not only leads to changes in behavior, but also results in a number of other correlated or unselected modifications in the mammalian phenotype (similar effects of selection against aggression and fear have been shown in mink and rats [S2]). The presence of such correlated by-products raises the possibility that selection for tame behavior may also have correlated effects on the cognitive abilities of domesticated canids.

Experiment One: Do Experimental Foxes Use Human Communicative Cues to Find Food?

Subjects

Eleven experimentally domesticated foxes (six females and five males) and eleven dog puppies (four females and seven males) were compared. All of the foxes tested in this and subsequent studies were born and raised at the experimental farm of the Institute for Cytology and Genetics in Siberia, Russia. Subjects were selected to be tested during an initial screening in which the boldest individuals between 2 and 4 months old (the youngest available at the time) were chosen to participate. All of the foxes tested were born between April and May, 2003. Until they were 6–8 weeks old, the subjects lived with their mother and littermates. Subjects were then housed with their littermates until they were approximately 12 weeks old. After this period, they were singly housed in a wire mesh pen (90 × 75 × 70 cm). While living in their pen, subjects could interact at anytime with neighboring foxes in adjacent pens. In addition, each subject was fed a fresh mixture of meat, fish, corn, vegetables, and vitamin supplements in a metal bowl twice daily. Before participating in the current investigation, the subjects were only handled for management purposes (approximately twice a month). Therefore, subjects had minimal interactions with humans, typically only seeing someone briefly when their food and water bowls were refilled each day (this is the same for the control foxes used in later studies). On testing days, subjects were given their morning meal immediately after completing the test session. The 11 domestic dog puppies had previously been tested [S8]. As with the foxes, all of the puppies in this sample were 2–4 months of age when they were tested.

Procedure

Each subject was brought into the testing room (3 × 4 m) for three to four play sessions in which they were free to interact with the experimenter for 45 min to ensure that the subjects were accustomed to the experimenter and testing room (the experimenter sat on the floor and waited for the subject to initiate interactions). After each subject readily took food from the experimenter's hand and out of the bowls to be used in the test, it was introduced to the general testing procedure [S8]. Each subject was taken from its home pen to the familiar testing room, where two hemispherical bowls (20 cm diameter and 8 cm tall) had been placed 1.7 meters apart in the middle of the room. A line that was equidistant between the two bowls was drawn in the middle of the room. Then, a subject was shown that food could potentially be found in both hiding locations. One experimenter (E1) placed a small piece of food (i.e., fresh cheese) in one of the two bowls while the subject watched while being held by a second experiment (E2) 1.5 m away from each bowl. Once the food was hidden in one of the bowls, the subject was released by E2 to retrieve the food (E2's eyes remained closed throughout a trial so that they did not know where the food was baited). If the subject first touched the bowl where the food was hidden, it received the reward, whereas if it touched the empty bowl first, it was shown the location of the food but did not receive the reward. Subjects only entered the testing phase after successfully finding the hidden food in four out of five consecutive trials during this introduction phase.

The experimental session was similar to the introduction and occurred on a separate day. E1 placed the two bowls 1.7 m apart while E2 held the subject approximately 1.5 m away from the bowls. After showing the subject a piece of food, E1 then sham-baited both bowls, only leaving food in one of the two bowls. Therefore, the subjects knew food was hidden, but did not know in which bowl. Once the food was hidden, E1 attracted the attention of the subject (i.e., by snapping), and then, while lying on the ground (to ensure

that the subject would see E), indicated the location of the food by pointing and gazing toward it. The experimenter extended her arm and index finger in the direction of the hidden food while also gazing at the baited bowl.

Once E was pointing and gazing at the correct bowl, E2 released the subject to retrieve the food while E1 continued giving the cue as the subject approached one of the bowls. If the subject chose the correct container, it was rewarded. If it chose the wrong container, it was shown where the food was hidden but did not receive the treat. In addition, after the completion of all testing, the experimental foxes were given a control test. This condition was identical to that just described, with the exception that the experimenter did not provide a cue to the food's location after it was hidden. Instead, the experimenter only stared directly at the subject until it made its choice.

Subjects received 18 trials in each condition in separate sessions. Food was never hidden in one of the bowls for more than two trials in a row, and the food placement was counterbalanced within and across subjects. Subjects' choices were scored live during testing. Subjects were tested in no more than one session per day, and all trials were videotaped from behind E1. Within groups, performance was assessed by comparing overall number of correct choices to chance with a one-sample t test. Between group performances were compared with Welch independent sample t tests. Because of our a priori and directional predictions (see Introduction), all tests were one-tailed unless otherwise noted (this is true throughout all four experiments).

Experiment Two: Do Experimental or Control Foxes Use Human Gestures More?
Subjects
Seventeen experimentally domesticated (nine females and eight males) and seventeen control-line foxes participated (nine females and eight males). None of these subjects participated in experiment one. All of the fox kits were born in April, 2003 and were between 3 and 4 months old when tested.
Apparatus
Subjects were tested in their home pens, which were rectangular and made of wire mesh (90 × 75 × 70 cm). During testing, the neighboring foxes, living in pens on either side of the subject's pen, were removed, and opaque barriers were placed inside these pens, making it impossible for the subject to see any other conspecific during testing. A rectangular board (80 × 30 cm) with a line down the middle was placed in the center of the floor of the subject's home cage; subjects quickly developed a preference for sitting upon it. A table was built that could be placed against the front of a fox's home cage. Attached to the table top (70 × 50 cm) was a board (70 × 20 cm) that could slide across the table top 40 cm. Attached to either end of the board were two wooden cubes (10 cm³), each of which had a long, thin piece of flexible metal (15 × 1 cm) that extended 10 cm in front of the sliding board (the metal was cut from a retractable ruler or tape measure). When pressed down and then released, the flexible metal (i.e., the toy) would return to its original position and make a small noise in the process. There was 60 cm between the two metal toys. Wooden sticks (75 cm × 2 cm) were placed on the pen's mesh front to aid the experimenter with coding. One stick was placed vertically on the center of the mesh front, whereas the remaining two sticks were placed 20 cm from the center.
Procedure
Introduction: On their first day, all subjects participated in an introduction. In this introduction, the experimenter conducted three manipulations, including (1) approaching the subject's pen until she was standing an arm's length away and could touch the wire mesh with one hand, (2) placing the apparatus against the front of the subject's pen before leaving, or (3) not placing herself or the apparatus near the subject's pen. Each manipulation lasted 3 min. Half of the subjects within each group were presented with the experimenter first, and half with the apparatus first. Subsequently, the remaining two manipulations were completed and also counterbalanced within each group.

Test: Each subject was tested at least 1 day after its introduction. The apparatus was again placed in front of the subject's home cage

while the experimenter sat behind it. Once a subject was seated in the center of the pen, the experimenter gazed at, gestured toward, and touched one of the two metal toys with her contralateral arm so that it moved and made a small noise.

Once the experimenter gave the cue, the sliding board was pushed forward so that the metal toys were within reach of the subject (10 cm inside its cage). The subjects were then observed for 30 s. If they did not touch one of the toys in this time, the sliding board was moved so that both toys were again removed from the subjects' reach. If the subject did touch one of the toys, the experimenter recorded which of the toys the subject touched first. Subjects were allowed to play with the toys regardless of whether they touched the same toy as the experimenter. The toys were then removed after 5–10 s of play. Each subject participated in a single 18-trial session. The same metal toy was never manipulated for more than two trials in a row, and the order of the toy manipulation by the experimenter in each session was counterbalanced within and between subjects.

Scoring and Analysis
Within the introduction, the subject's time to first approach was coded in the manipulations involving either the experimenter or apparatus. A first approach was scored from videotape as the time between the start of a trial (when the human or apparatus first touched the pen) and the time at which a subject first touched the experimenter or apparatus with its mouth or paw. Within the test session, the experimenter coded live which of the two toys the subject first touched with its mouth or paw. All introduction and test trials were videotaped so that both the subject and the experimenter were visible.

Experiment Three: Are Experimental Foxes More Skilled than Controls in All Human-Led Tasks?
The method used in the current experiment was identical to experiment two, except for the following changes: First, only a subsample of subjects were tested from experiment one (experimental: three females, six males; control: five females, four males), on the basis of their level of participation in experiment two. In each group, the nine subjects who participated at the highest level in experiment two were chosen for testing in experiment three. Once chosen, an analysis comparing the overall level of participation between this subset of experimental and control foxes showed that this subset from each group also did not differ in their level of participation in experiment two (t[13.14] = 1.24, p = NS, Welch independent sample t test). Yet even when compared on their first five trials, the nine experimental foxes touched the toy the experimenter manipulated significantly more than the nine control foxes (t[12.57] = 3.11, p < 0.005, Welch independent t test; Figure 2). Therefore, in experiment three each subject participated in a five-trial session to test its preference for touching a toy an object had manipulated. Second, two additional pieces of equipment were added to the apparatus: (1) an opaque occluder (80 × 30 cm) and (2) a feather attached to a wooden stick (50 cm). The opaque occluder could be placed on the table top, thus shielding the movements of the experimenter's arms and hands from the subject's view. The feather was then used to manipulate one of the two metal toys and made a small noise from behind the occluder in each trial. Therefore, although the subject could see the human experimenter's face, shoulders, and legs, it could not see that the experimenter moved the feather from behind the occluder with the aid of the stick. Third, there was no introduction session. Fourth, subjects only received five trials with the object cue.

Experiment Four: Are Experimental Foxes More Skillful with Human Communicative Cues than Controls?
The same method was used in this experiment as was used in experiment one, with a few exceptions. First, the performance of six 2–3-month-old control fox kits (the youngest available; four females and two males) was compared to the previous performance from experiment one of six age-matched experimental fox kits (four females and two males). Second, unlike the experimental foxes, these six control foxes were brought into the testing room every

day for several weeks so that they could play and interact with the experimenters for 1–2 hr a day (these play periods were carried out as experiments one to three were being conducted). Third, the control foxes were only tested with the point-and-gaze cue.

Supplemental References

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