

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

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

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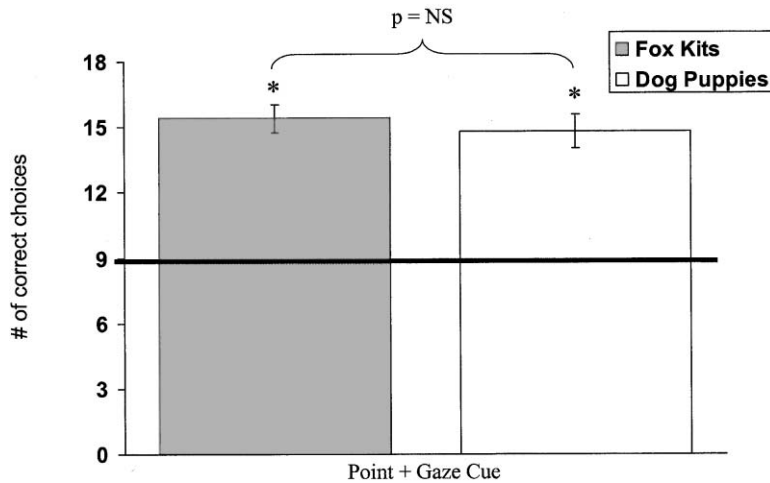


Figure 1. Number of Correct Choices (i.e., Food Located) Made by Experimental Fox Kits and Dog Puppies when the Point-and-Gaze Cue Was Provided by a Human

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].

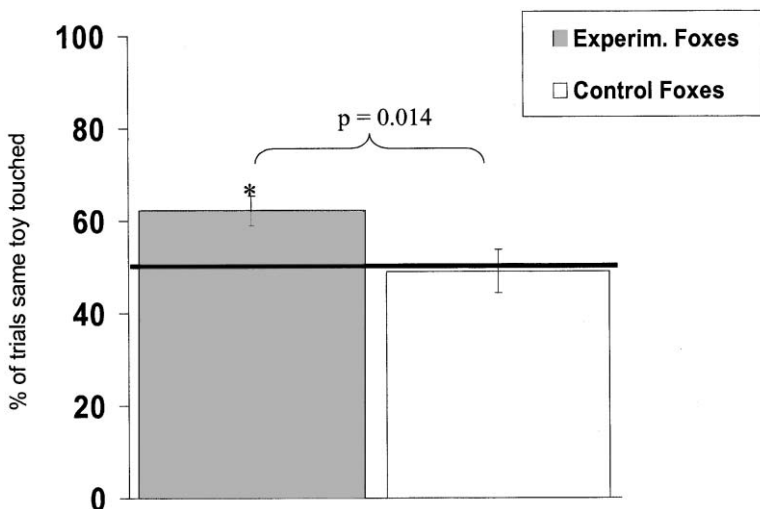


Figure 2. Percentage of Trials the 17 Experimental and Control Subjects Touched the Same Toy the Experimenter Gestured Toward and Manipulated

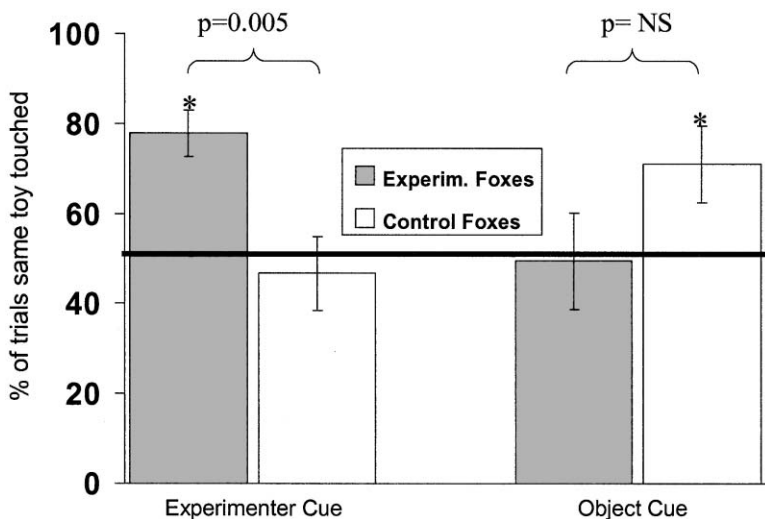


Figure 3. Percentage of Trials Nine Experimental Fox Kits and Nine Control Fox Kits Touched the Same Toy an Experimenter or Object Manipulated

*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

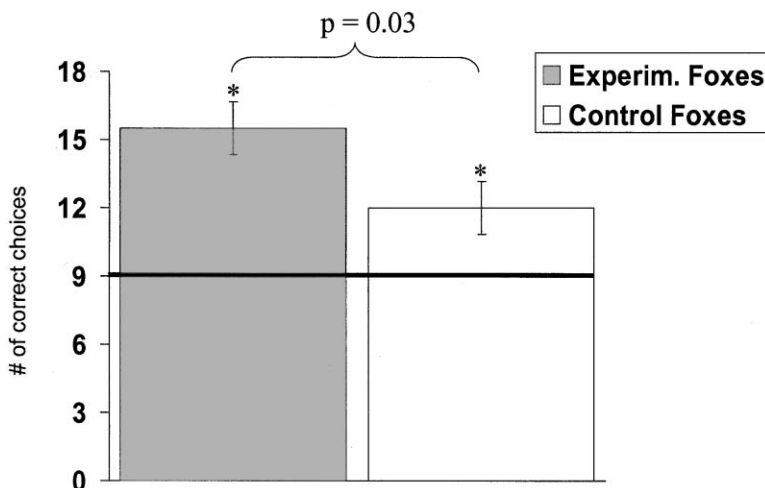


Figure 4. Number of Correct Choices (i.e., Food Located) Made by Experimental and Control Foxes when the Point-and-Gaze Cue Was Provided by a Human

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.

Supplemental Data

Detailed Experimental Procedures are available at <http://www.current-biology.com/cgi/content/full/15/3/226/DC1/>.

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