

Behavioral Genetics of Dog Cognition: Human-like Social Skills in Dogs Are Heritable and Derived

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ALMOST EVERYWHERE THERE ARE PEOPLE THERE ARE DOGS, and although many people like dogs, very few behaviorists have found them of much scientific interest. A notable exception is Charles Darwin, who found them exceedingly interesting, and indeed launched *On the Origin of Species* (Darwin 1859) with a flurry of examples outlining variability in domestic animals, including dogs, since nowhere at the time could evidence for descent with modification be more clearly observed than in familiar domestic species (Ritvo 1998).

Recently, a number of cognitive scientists have begun to find dogs interesting as well (Cooper et al. 2003; Miklosi et al. 2004). The reason is that dogs seem to have some special skills for reading human social and communicative behavior. These skills appear to be more flexible—and possibly more human-like—than those of other animals more closely related to humans phylogenetically, such as chimpanzees. This raises the possibility that convergent evolution has occurred: Both *Canis familiaris* and *Homo sapiens* may have evolved some similar (though obviously not identical) social-communicative skills—in both cases adapted for certain kinds of social and communicative interactions with human beings. Cases of convergent evolution potentially provide a unique opportunity for making inferences regarding how heritable traits evolve. If two distantly related species share a similar trait(s), it is possible that this analogous trait(s) arose independently due to a similar evolutionary process. Moreover, it is possible that similar evolutionary processes may

have affected similar ontogenetic pathways in order to produce analogous phenotypes. Therefore, if dogs' social skills represent a case of convergent evolution with humans and conclusions are drawn about the system(s) that is affected and the selection pressure(s) that drove such evolution in dogs, it might also be possible to devise ways of testing whether a similar process played a role in shaping human cognition. We review recent research with dogs and other nonhumans which suggest that these kinds of inferences regarding the evolution of human social intelligence are possible from recent comparative studies.

HUMAN-LIKE SOCIAL SKILLS IN DOGS?

The test is necessarily simple (it must be simple, if you are to test a wide range of species). Hide a reward in one of several opaque containers, and then look at or point to that location in an attempt to help the subject find the hidden object. Human infants find this type of task trivially easy from around 14 months of age, as they are just beginning to learn language (Behne et al. 2005). However, perhaps surprisingly, chimpanzees, impressive in solving so many other social problems, show little skill in using such social and communicative cues to solve the task (Tomasello et al. 2003). Meanwhile, give domestic dogs a crack at it and they show impressive flexibility in solving the same problem (Hare et al. 1998; Miklosi et al. 1998).

The majority of results, such as these, examining the use of social and communicative behaviors across species have been obtained using the so-called object-choice paradigm (originally developed for use with primates; Anderson et al. 1995). In the object-choice paradigm a piece of food or an attractive object acts as a reward and is hidden in one of several hiding locations (usually two opaque cups spread ~1 m apart) while the subject watches. However, while the reward is hidden in one container, the other container is sham-baited so that the subject only knows the reward has been hidden, but does not know in which container it is hidden. It is only then that the human experimenter tries to help the subject by indicating the reward's location (e.g., pointing or looking at the baited cup). Once the experimenter indicates the reward's location, the subject is allowed to search in one of the two containers. If the subject chooses the baited container first, he is allowed to retrieve his reward, whereas, if he chooses the wrong container, he is only shown where the reward was hidden. This procedure is then repeated 10–20 times in order to compare the individual's performance against chance (e.g., chance is 50% when two hiding locations are used) and to give subjects an opportunity

to learn to use the experimenter's indicative behavior if they do not do so spontaneously.

All primates tested in the object-choice task, including both species of chimpanzees (*Pan troglodytes* and *Pan paniscus*) are universally poor (with the exception of some individuals raised with humans; Itakura and Tanaka 1998; Call et al. 2000) at finding hidden food rewards using human social-communicative behaviors. It takes dozens of trials for primates to learn to use such information when provided by a helpful human or conspecific (Anderson et al. 1995; Call et al. 2000). Once one type of cue is mastered, even chimpanzees do not generalize these skills when slightly modified or novel cues are available that closely resemble those they previously learned (Povinelli et al. 1997; Tomasello et al. 1997). For example, a group of chimpanzees trained to choose a container that a human was pointing to by touching it were no longer able to choose the correct cup if a human again pointed to the correct cup without touching it (Povinelli et al. 1997).

The story with dogs is very different. In all six initial studies (Hare et al. 1998; Miklosi et al. 1998, 2000; Hare and Tomasello 1999; Agnetta et al. 2000; McKinley and Sambrook 2000) conducted in three different laboratories, the majority of dogs were spontaneously able to use several different cues to locate hidden food at above chance levels: (1) a human pointing to the target location (including "distal pointing" in which the experimenter stands over a meter away from the target and points in its direction using her cross-lateral hand); (2) a human gazing to the target location (dog either sees the head turn or only a static head looking to a location); (3) a human bowing or nodding to the target location; and (4) a human placing a marker in front of the target location (a totally novel communicative cue). Some dogs were even skillful when the human walked toward the wrong container while pointing in the opposite direction toward the correct container. Similarly, dogs were capable of finding hidden food if a conspecific was oriented toward the baited container. In all of these cases, the dogs used the cues effectively from their very first trials, showing that they came to the experiment already possessing the required skills. Typically in these tests, two-thirds of the dogs were above chance as individuals. Meanwhile, control procedures were always run (i.e., forcing dogs to choose one of the hiding locations without giving any visual cues to the food's location) to ensure that subjects were not simply using olfactory cues to locate the food in all the different tests. In all cases, dogs were unable to find hidden food above chance levels when a visual cue was absent.

Perhaps most surprisingly, when dogs are directly compared to chimpanzees on identical object-choice tasks, they are much more skilled at

using a novel social cue to find hidden food (i.e., a human places a block on the correct container conspicuously while the subject watches) (Hare et al. 2002). In other studies, dogs have performed well when they see the block placed but then it is removed before their choice—demonstrating that they are not just attracted to the block itself (Reidel et al. 2005). With respect to gaze cues, dogs—like human infants and unlike chimpanzees (Povinelli et al. 1999)—only use the direction someone is looking (head and eye direction) to locate hidden food if the human is gazing directly at one of two possible hiding locations; they ignore a human's gaze if the human stares into space above the correct hiding location (Soproni et al. 2001). This suggests that dogs identify human communicative behaviors, as opposed to other behaviors, in ways more similarly to human infants than do chimpanzees.

Another line of research has also demonstrated that dogs can assess what a human can or cannot see in a number of other contexts. For example, if a human throws a ball for the dog to fetch and then turns his back, the dog almost always brings the ball back around his body to drop it in front of his face (Hare et al. 1998; Miklosi et al. 2000). In addition, when dogs are forced to choose between two humans with food, they prefer to beg from a human whose head and eyes are visible and are not covered with either a blindfold or a bucket (Gasci et al. 2004; Viranyi et al. 2004; Bishop and Young 2005), something that chimpanzees do not do spontaneously (Povinelli and Eddy 1996). Dogs are also more likely to avoid approaching forbidden food when a human's eyes are open than when they are closed (Call et al. 2003), again, something that chimpanzees do not do spontaneously (Povinelli and Eddy 1996; Kaminski et al. 2004b). Moreover, dogs also avoid approaching forbidden food when it is visible to the forbidding human through a transparent window in a barrier between the dog and the human. That is, in this situation dogs make the decision not to approach the food at a moment when they cannot see the human and the human cannot see them, apparently projecting what the human can see through the small window (they do approach in the absence of the window) (Brauer et al. 2004).

Finally, it seems that dogs can learn about their environment from humans in a variety of surprising ways that can be either highly communicative or even noncommunicative. For example, when the owner of a particular Border collie tells him to fetch using a novel word ("The dax!"), he reliably retrieves a novel toy instead of a familiar one whose name he already knows (e.g., a ball)—a kind of reasoning by exclusion (if she had wanted the ball she would have asked for "The ball," so the dax must be the other one). Such social inferences have previously been

demonstrated only for language-learning human children (Kaminski et al. 2004a; but see Markman and Abelev 2004). Finally, dogs who witness a human or conspecific demonstrator solving simple instrumental and detour tasks are quicker and more successful at those tasks than other dogs who have not witnessed a demonstration (Slabbart and Rasa 1997; Pongracz et al. 2001, 2003; Kubinyi et al. 2003a,b).

One thing that makes the human-like social skills of dogs so fascinating is that dogs do not seem to show unusual flexibility in other, nonsocial domains. For example, dogs are unable to infer the location of a hidden object based on the trajectory of a hider's movements and as the result of their own previous searches (Watson et al. 2001; Bräuer et al. 2004), whereas great apes are capable of such inferences in a number of situations (Call and Carpenter 2001). When dogs have been directly compared to primates in their ability to do such things as make inferences about the location of hidden food based on nonsocial cues—for example, seeing one board lying flat versus another board tilted up as if food could be under it—dogs fail miserably as compared with nonhuman great apes (J. Bräuer et al., unpubl.). Dogs also fail means-end tasks that require them to avoid pulling a string that is not connected to food in favor of one that is connected to the food (Osthaus et al. 2005), a task most primates easily solve (Tomasello and Call 1997). The fact that dogs are so skilled in the social domain but unremarkable in solving physical tasks leads one to wonder how and why dogs have acquired a social specialization for solving problems involving humans.

CONVERGENT COGNITIVE EVOLUTION IN DOGS AND HUMANS?

Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly unconsciously modify other parts of the structure, owing to the mysterious laws of the correlation of growth.

DARWIN 1859

The fact that domestic dogs, but not nonhuman apes, possess such human-like social-cognitive skills begs the question of the origin of these abilities. Could it be that the similarities between dogs and humans represent a case of convergent cognitive evolution? There are three obvious explanations for the origin of such specialized social skills in dogs, and they have been explored by comparing the use of basic human social-communicative behaviors (i.e., a point or gaze cues) in the object-choice task both within and between various canid species.

The most straightforward explanation for dogs' special social-cognitive skills with humans is that dogs grow up with unusual exposure to humans and so have an unusual opportunity to learn from them; that is, there is a kind of "enculturation" similar to the kind proposed to explain the unusual problem-solving abilities of apes raised by humans (Call and Tomasello 1996). For example, two different studies have found that two different pairs of adult chimpanzees, who were all raised as infants by humans, spontaneously use a number of social cues when tested in the object-choice task (Itakura and Tanaka 1998; Call et al. 2000). Given that all the tests described thus far were on adult dogs, it is entirely possible that, like human-reared apes, all the observed skill is acquired. This hypothesis predicts that the ability to read human social cues should improve over a dog's lifetime and should vary depending on the amount of exposure a dog has had to humans. However, a cross-sectional comparison of puppies found that different age groups did not differ in their ability to use a human pointing or gaze cue; even puppies as young as 9 weeks old were nearly perfect in the basic tests. In addition, when a group of puppies in an obedience class were compared in their ability to use pointing and gazing cues to a group of litter-reared puppies (who had relatively little exposure to humans), both groups were skilled at using the cues and there was no difference between them (Hare et al. 2002). This is, of course, not to say that learning cannot occur during a dog's life. For example, there is evidence for learning from a comparison between active and pet working dogs. Although both groups of dogs were quite skilled at using human social cues, active working dogs were more successful than pet working dogs at using a pointing cue in the object-choice task (McKinley and Sambrook 2000). However, taken together, these findings do not support the hypothesis that dogs require unusual amounts of exposure to humans (i.e., relative to most primates tested) in order to learn to read human social and communicative behavior, although, at the same time, they do not rule out that such exposure can shape such abilities.

A second candidate hypothesis invokes the canid ancestry of dogs. Amazingly, a convergence of genetic comparisons shows that all the phenotypic variance observed in dogs is inherited from a single species: the wolf (*Lupus lupus*). Comparisons between wolf and dog mitochondrial control regions suggest that dogs arose through multiple domestication events within multiple wolf populations (Vila et al. 1997; Savolainen et al. 2002). A comparison of mitochondrial DNA in a worldwide sample of dogs suggests that initial domestication events may have occurred in East Asia. In particular, Chinese wolves that are relatively small and docile

(compared to their larger European and American relatives) may have been repeatedly domesticated in a number of locations throughout East Asia (Savolainen et al. 2002). Perhaps then dogs, as direct ancestors of wolves, simply inherited their skill for reading the behavior of others from wolves. Indeed, wolves are social pack hunters and likely need to read the social cues of their fellow hunters as well as prey in order to effectively cooperate while hunting, providing a plausible explanation for the skill observed in their dog descendants (Clutton-Brock 1999; Coppinger and Coppinger 2001). This hypothesis predicts that the social skills dogs exhibit should also be seen if the same types of tests are used to examine wolves (Hare and Tomasello 1999). However, the wolves tested thus far are not particularly skilled at reading human social cues; they are much more like chimpanzees than dogs in this respect. Two independent studies have found that captive wolves reared by humans (and tested by the humans who reared them) are not as skilled as dogs in using human social cues to find hidden food (Hare et al. 2002; Miklosi et al. 2003). Importantly, this difference is unlikely due to the wolves' being poor in all such human-led cognitive tasks. Indeed, studies comparing wolves and dogs in simple nonsocial problem-solving or memory tasks typically find that wolves perform as well if not better than dogs (in some cases these were the same wolves and dogs compared in the social tasks; Frank 1980, 1982; Frank et al. 1989; Hare et al. 2002). Instead, it seems that for some reason wolves just relate to people very differently than do dogs. For example, when human-reared dogs and wolves were both presented with an impossible task (opening a locked box with food inside) the dogs almost immediately gave up and gazed alternately at the human and the box, whereas the wolves continued to try to solve the task on their own until the test ended (Miklosi et al. 2003). Therefore, it seems that, when uncertain, dogs want or expect human help, whereas wolves behave as if they do not want human help or realize that a human might help them. Overall then, the comparisons made thus far do not provide any support for the idea that dogs inherited their social-cognitive skills directly from wolves.

This leaves the possibility that dogs' social-cognitive skills evolved during the process of domestication: that is, these skills evolved during the tens of thousands of years that our two species have lived together. In some sense, this seems an unlikely explanation. Is it really plausible that during the same period that dogs underwent a 25% reduction in cranial capacity (as compared to wolves) they also became more skilled at solving social problems involving humans? In fact, it has often been suggested that if domestication has any effect on the cognitive abilities of

domesticates it is to dull their problem-solving abilities (for review, see Kruska 2004). Perhaps most problematic is that even if such evolution took place during domestication, how would one test for such a possibility and how could any test determine with any precision or certainty the selection pressure(s) that drove such evolution during domestication? Unfortunately, until very recently, there was no way to systematically compare different dog breeds in order to test such a hypothesis. We just knew too little about the breeding history of dogs over the past millennia to have any confidence in within-species comparisons. Luckily, dogs are not the only domesticated canids.

In 1959, Dr. Dmitry Belyaev and his colleagues in Siberia, Russia, began one of the longest-running experiments in history with the goal of studying the behavioral genetics of domestication (Belyaev 1979). Since the start of the experiment, two separate populations of foxes (*Vulpes vulpes*) have been maintained. An experimental population was selectively bred based on a single criterion—whether they fearlessly and nonaggressively approached a human. The second population was maintained as a control and has been bred randomly with respect to their behavior toward humans (Trut 1999, 2001).

Based on the single selection criterion the Russians used, behavioral, physiological, and morphological changes were observed in the experimental fox population that were either not found in control foxes or were expressed at a significantly higher frequency in the experimental population (a number of these differences appeared after only 20 generations of selection). First, not surprisingly, the individuals in the experimental population were observed from 1 month of age onward to show little fear or aggression toward humans. Subsequent experiments have demonstrated that selection for tameness retarded the development of fear responses to novelty while enhancing exploratory behavior in unfamiliar situations (Plyusnina et al. 1991). 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 relative to controls (Oskina 1996). 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 (Popova et al. 1991; Trut et al. 2000). Finally, and perhaps most surprising, the domesticated foxes manifested a number of correlated changes that are commonly

found in a number of other domesticated species. A higher frequency of domesticated foxes have 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 (Trut 1999, 2001; Trut et al. 2000)—traits commonly found in other domesticated mammals (Kruska 2005). Thus, the results of the fox farm experiment demonstrate with unprecedented certainty that selection against aggressive and fearful behavior likely has been the driving force behind the heritable changes observed in domesticated mammals. In addition, the two populations of foxes provide a perfect test of the hypothesis that dogs evolved their unusual social skills not only during domestication, but also as a direct result of domestication. If the process of domesticating dogs is responsible for the evolution of their social-cognitive specialization, then the experimentally domesticated foxes should perform much like dogs when tested in the object-choice task, whereas the control foxes should perform more like wolves (and nonhuman primates).

Indeed, when fox kits from the domesticated population were compared with age-matched dog puppies on the basic pointing and gaze-following tests, the foxes were as skilled as the dogs in using the human social cues. In addition, to test whether the experimental foxes' skill was a result of the selection regime, a group of experimental fox kits were compared to an age-matched group of control foxes in two different social tasks. One of the tasks compared their ability to find hidden food using a human pointing cue in a standard object-choice task, and the other task compared their preferences for playing with a toy a human gestured toward and touched as opposed to a toy the human ignored (no food reward was given in the second test regardless of a subject's response). Not only were the experimental kits more skilled than control kits at using a human gesture to find hidden food, but they also were more likely to play with the toy a human had gestured toward than were control kits. As in the case of the comparisons between wolves and dogs, these differences are unlikely to be due to differences in rearing histories between the two populations or an inability of the control foxes to be skillful in any human-led task. First, both groups of foxes were reared in an identical manner in which they had negligible contact with humans before testing. Second, the control foxes were as skillful (if not more so) as the experimental foxes on a nonsocial task even though a human experimenter was present throughout the testing (Hare et al. 2005).

These findings with this special population of foxes seem to confirm the likelihood that dogs' unusual ability to read human social-communicative behaviors evolved not only during the process of domestication, but also

as a result of domestication—a process of selecting against individuals with fear and aggression toward humans while selecting for those individuals with interest in humans. Perhaps most surprisingly, however, the research with domesticated foxes also suggests that dogs' skills for reading human social-communicative behavior may have initially evolved as an incidental by-product of selection for tame behavior. It is important to note that neither population of foxes was ever bred or tested on the basis of their ability to use human communicative gestures or behaviors; the single selection criterion was simply based on their approach behavior toward a human in a totally noncommunicative context (i.e., there was nothing to find or choose between and thus nothing about which to communicate during the selection trials).

In addition, the fox results raise the possibility that the unusual social skills of dogs may have evolved in stages. It may have been that dogs' special social-cognitive skills, like the foxes', first appeared after systems mediating fear and aggression were altered, systems which normally are not thought of as cognitive systems at all. Once this initial evolution occurred so that dogs were able to solve a new set of social problems involving humans (i.e., exapted), it may have been then that variance in social cognitive abilities came under direct selection. However, such evolution (if it indeed happened at all) would not have been possible without the initial selection on systems controlling emotional reactivity that allowed dogs to enter an entirely new adaptive space, one in which they interacted with humans in similar ways as they do with conspecifics. An exciting evolutionary scenario, indeed, and one that might even be implicated more broadly than the current case of observed cognitive evolution in canids, but once again, we are left with the task of coming up with a way to test this stage model. How are we to test such an idea using dogs, if we remain without any solid evidence about the selective history of the different dog breeds?

Timing is on our side. Thanks to a brand-new phylogenetics study that provides the first reliable data for mapping out the relationship among 85 breeds of domestic dogs, we have conducted an initial test of the two-stage model of cognitive evolution in canids (Parker et al. 2004). Indeed, these new phylogenetics data seem to provide tentative support for the stage theory of dog evolution in that nine dog breeds (chow chow, husky, malamute, shar-pei, Shibu-Inu, Akita, Afghan hound, saluki, and basenji) were identified as being more genetically wolf-like than the remaining breeds examined. This raises the specter that these breeds remain more wolf-like because they were "left behind" and did not undergo a second wave of selection as did the rest of the dog breeds sampled. Perhaps then, the first stage of dog domestication occurred due to natural selection as the least

fearful East Asian wolves were at a selective advantage in exploiting a new niche created by garbage left near human settlements—a domestication event that would be highly similar to that observed in experimental populations of foxes. Then a second stage possibly occurred within the last millennium as humans began intensively and intentionally selecting individuals for their appearance or working ability—with those dogs best at reading human social-communicative behaviors having a fitness advantage when being bred to actively work with humans (Coppinger and Coppinger 2001). This stage hypothesis for selection during domestication predicts that whereas all domestic dogs will likely be skilled at reading social cues relative to wolves, dogs that are thought to have been bred for the ability to communicate with humans for the purpose of cooperating (after controlling for the degree to which they are genetically wolf-like) should be more flexible in their ability to use human communicative cues (i.e., selection on communicative ability leads to increases of skills and this ability segregates independently of other heritable traits under selection).

To test this hypothesis, we recently compared the ability of four groups of dog breeds for their ability to use human social-communicative behaviors in the ubiquitous object-choice task. We chose our breed groups based on whether they were considered working or nonworking breeds (according to the American Kennel Club) and whether they had been determined to be more or less wolf-like genetically: (1) nonworking more genetically wolf-like: basenji and New Guinea singing dogs, (2) working more genetically wolf-like: huskies, (3) nonworking less genetically wolf-like: a variety of toy dogs, and (4) working less genetically wolf-like: golden and Labrador retrievers. As the two-stage hypothesis predicts, although all the groups of dog breeds were skilled at using human social-communicative cues to find hidden food, the dogs—regardless of the genetic relation with wolves—thought to be bred in order to communicate in cooperative interactions with humans (retrievers and huskies) were the most skilled overall at using all the social cues when tested. These findings suggest that the ability to read human communicative behavior may have been under direct selection in these breeds. In addition, this finding is consistent with the idea that there is a heritable component to this phenotypic trait that may segregate independently of other traits that have been under selection. As increasingly sensitive phylogenetic comparisons are made between differing dog breeds, behaviorists will increasingly be able to compare breeds in a meaningful way to test various hypotheses for how genetic differences may code for meaningful behavioral and even cognitive differences.

In summary, comparative studies within and between canid species seem to suggest that dogs have evolved a social-cognitive specialization

not only during domestication, but as a result of domestication. Initial comparisons between dog breeds seem to support the idea that an initial wave of selection on emotional reactivity may have been followed by further selection and heritable change resulting in a further specialized ability to use human communicative gestures in non-wolf-like working dogs. Future studies will be needed to test such an idea more fully. Finally, because domestication has resulted in the evolution of unusual social-cognitive skills in dogs, it now seems fair to characterize such skills as being convergent with those that seem to have evolved in our own lineage (i.e., skills that among primates are only robustly expressed in humans). Are there then lessons to be learned about human evolution from research on dog cognition?

IMPLICATIONS FOR HUMAN COGNITIVE EVOLUTION

These findings with dogs and their close relatives suggest that some aspects of human-like social intelligence may potentially evolve not as adaptations specifically, but rather as a result of selection on seemingly unrelated social-emotional systems—underlain not by the neocortex but by the limbic and endocrine systems. These findings suggest the further possibility that some of humans' social-cognitive and communicative abilities may have begun evolving in a similar way. That is, following this line of reasoning, one might seriously entertain the hypothesis that an important first step in the evolution of modern human societies was a kind of self-domestication (selection on systems controlling emotional reactivity) in which a human-like temperament was selected (e.g., individuals of a social group either killed or ostracized those who were overaggressive or despotic; [Boehm 1999; Leach 2003; Wrangham 2005]). Thus, much like domestic dogs, this selection for more tame forms of emotional reactivity put our hominid ancestors in a new adaptive space (where new human-like forms of social interaction and communication came into existence), enabling subsequent selection to favor variance that allowed for complex forms of these new social interactions and communication that characterize human cultural life today.

In support of the hypothesis that human temperament evolution preceded significant social cognitive evolution in our species is the fact that forms of potential cooperative behavior in chimpanzees are highly constrained by their levels of inter-individual tolerance (i.e., likely controlled by systems mediating levels of emotional reactivity). Whereas humans (including young infants) are quite helpful and tolerant of other unfamiliar humans when having to work together to accomplish a com-

mon goal (Tomasello et al. 2005; F. Warneken et al., in prep.), even familiar chimpanzees are unable to work together in the simplest of cooperative tasks except in a very constrained set of social situations. For example, chimpanzees are only able to work together successfully in an instrumental task (i.e., pulling two ropes simultaneously to retrieve a box full of food that is too heavy for any single individual to obtain) if they are (1) paired with another chimpanzee with whom they have previously shared food, (2) the food is sharable, and (3) there is enough working space so individuals are out of each other's reach (A. Melis et al., in prep.). If such social criteria are not met, then chimpanzees (subordinate individuals of any pair in particular) will refuse to ever cooperate even over a span of dozens of trials. It seems from such tests that subordinate chimpanzees are simply not willing to risk being physically attacked by intolerant dominants, and dominants are not able to control their aggression toward subordinates trying to obtain food—even if it means they will never receive any food. Chimpanzees, it seems, just do not have the temperament for human-like flexibility in their cooperative repertoire.

Such an emotional reactivity hypothesis should then also apply to a wide range of social problems. For example, such a hypothesis would seem to predict that chimpanzees should be more skillful at using social-communicative cues in the object-choice task if the task can be made more emotionally engaging. Indeed, chimpanzees demonstrate spontaneous skill at finding food when they see a human, who has previously established a competitive relation with them, reaching unsuccessfully toward a potential food location in an apparent attempt to obtain hidden food. However, if the same chimpanzees see a helpful human pointing (i.e., morphologically similar to reaching) toward the hiding location, they do not use the cue (Hare and Tomasello 2004). This finding suggests that chimpanzees only view humans as relevant to their success when competing—a context in which chimpanzees seem particularly engaged emotionally (i.e., the human might eat the food!). Otherwise it seems, in any other context, chimpanzees view their potential social partner as largely irrelevant to their success in the object-choice task. Therefore, it may be that chimpanzees do not demonstrate human-like skills at using social-communicative behaviors in the object-choice task because they lack a human-like temperament for sharing information—especially when a prized piece of food is on the line. Arguably then, the production and comprehension of cooperative communicative intentions—intended merely to inform others of things, with no direct benefit to oneself—is one of the species-specific social-cognitive abilities of human beings (the one possible exception being that of dogs). In addition, it would seem

that the evolution of this unique ability must have been preceded by temperament evolution.

Therefore, taken together, comparisons between chimpanzees and humans seem to suggest that prerequisite for flexible forms of human cooperation and communication is a human-like temperament. In fact, the evolution of the human temperament may have necessarily preceded the evolution of more complex forms of social cognition that make us uniquely human (e.g., a more sophisticated theory of others' behavior or mental states would be of little use when cooperating if individuals are unable to share the rewards of their joint effort). It is then only once the human temperament evolved that variance in more complex forms of communicative and cooperative behaviors could have been shaped by evolution into unique forms of cognition present in our species today.

It seems then, based on these comparative findings between humans and chimpanzees, that careful behavioral and physiological studies are now needed to understand more precisely how humans and chimpanzees may differ in the systems that mediate their emotional reactivity, if we are to understand more precisely what it is about the human temperament that might have made such evolution possible. However, at this early stage of this research it is important to recognize that it was the comparative studies of canid social cognition which made this model of human cognitive evolution seem not only plausible, but worth pursuing further.

SUMMARY: DOGS AND THE FUTURE OF BEHAVIORAL GENETICS

In this chapter, we have reviewed a fast-growing literature on dog cognition and an area of research that promises to be an exciting avenue for gaining not only a better understanding about what the animal mind is capable of, but also more about the process by which intelligence evolves in mammals. The work thus far leads to the conclusion that dogs have evolved a social-cognitive specialization that allows them unusual skill in cooperating and communicating with humans. In addition, the latest research suggests that this specialization evolved not only during the process of domestication, but also as an incidental result of domestication (i.e., the specialization is an unintentional and unselected by-product of selection for tame behavior). However, there are now some data possibly implicating direct selection on communicative ability in dogs. Comparisons between different breed groups (determined by phylogenetic analysis) suggest that there may have been intentional selection by humans on social-communicative skills during the last millennia on certain breeds of working dogs. Taken together, this work with dogs has had important

implications for thinking about how the cognitive abilities of our own species may have evolved.

Overall then, it would seem that our canine companions have come to join into the human conversation in some unusually human-like ways. It is hoped that further investigation of the ways in which dogs do and do not do this—and how they come to have their special skills—will provide us with further insights into the evolutionary processes leading to human-style cooperative interactions and communication. For example, future research with canids should potentially provide behavioral geneticists with the opportunity of identifying and exploring fully the ontogenetic pathway(s) that has been under selection and allow for social cognitive evolution—perhaps even those that are in some way involved in making our own species human.

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REFERENCES

- Agnetta B., Hare B., and Tomasello M. 2000. Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Anim. Cognition* 3: 107–112.
- Anderson J.R., Sallaberry P., and Barbier H. 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Anim. Behav.* 49: 201–208.
- Behne T., Carpenter M., and Tomasello M. 2005. One-year-olds comprehend the communicative intentions behind gestures in a hiding game. *Dev. Sci.* (in press).
- Belyaev D. 1979. Destabilizing selection as a factor in domestication. *J. Hered.* 70: 301–308.
- Bishop S. and Young R. 2005. Do domestic dogs understand the importance of eye contact with humans? *Anim. Cognition* (in press).
- Boehm C. 1999. *Hierarchy in the forest: The evolution of egalitarian behavior*. Harvard University Press, Cambridge, Massachusetts.
- Bräuer J., Call J., and Tomasello M. 2004. Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Appl. Anim. Behav. Sci.* 88: 299–317.
- Call J. and Carpenter M. 2001. Do apes and children know what they have seen? *Anim. Cognition* 4: 207–220.
- Call J. and Tomasello M. 1996. The effect of humans on the cognitive development of apes. In *Reaching into thought* (ed. A.E. Russon et al.), pp. 371–403. Cambridge University Press, Cambridge, United Kingdom.
- Call J., Agneta B., and Tomasello M. 2000. Cues that chimpanzees do and do not use to find hidden objects. *Anim. Cognition* 3: 23–34.
- Call J., Brauer J., Kaminski J., and Tomasello M. 2003. Domestic dogs (*Canis familiaris*)

- are sensitive to the attentional state of humans. *J. Comp. Psychol.* 117: 257–263.
- Clutton-Brock A. 1999. *A natural history of domesticated mammals*. Cambridge University Press, Cambridge, United Kingdom.
- Cooper J.J., Ashton C., Bishop S., West R., Mills D.S., and Young R. J. 2003. Clever hounds: Social cognition in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 81: 229–244.
- Coppinger R. and Coppinger L. 2001. *Dogs: A startling new understanding of canine origin, behavior and evolution*. Scribner Press, New York.
- Darwin C. 1859. *On the origin of species*. John Murray, London.
- Frank H. 1980. Evolution of canine information processing under conditions of natural and artificial selection. *Tierpsychologica* 59: 389–399.
- . 1982. On the effects of domestication on canine social development and behaviour. *Appl. Anim. Ethol.* 8: 507–525.
- Frank H., Frank M.G., Hasselbach L.M., and Littleton D.M. 1989. Motivation and insight in wolf (*Canis lupus*) and Alaskan Malamute (*Canis familiaris*): Visual discrimination and learning. *Bull. Psychonomic Soc.* 27: 455–458.
- Gasci M., Miklósi A., Varga O., Topál J., and Csányi V. 2004. Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim. Cognition* 7: 144–153.
- Hare B. and Tomasello M. 1999. Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *J. Comp. Psychol.* 113: 173–177.
- . 2004. Chimpanzees are more skillful at competitive than cooperative cognitive tasks. *Anim. Behav.* 68: 571–581.
- Hare B., Call J., and Tomasello M. 1998. Communication of food location between human and dog (*Canis familiaris*). *Evol. Commun.* 2: 137–159.
- Hare B., Brown M., Williamson C., and Tomasello M. 2002. The domestication of social cognition in dogs. *Science* 298: 1634–1636.
- Hare B., Plyusnina I., Ignacio N., Schepina O., Stepika A., Wrangham R., and Trut L. 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Curr. Biol.* 15: 226–230.
- Itakura S. and 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*). *J. Comp. Psychol.* 112: 119–126.
- Kaminski J., Call J., and Fischer J. 2004a. Word learning in a domestic dog: Evidence for “fast mapping”. *Science* 304: 1682–1683.
- Kaminski J., Call J., and Tomasello M. 2004b. Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Anim. Cognition* 7: 216–223.
- Kruska D.C. 2005. On the evolutionary significance of encephalization in some eutherian mammals: Effects of adaptive radiation, domestication and feralization. *Brain Behav. Evol.* 65: 73–108.
- Kubinyi E., Miklósi A., Topál J., and Csányi V. 2003a. Social mimetic behaviour and social anticipation in dogs: Preliminary results. *Anim. Cognition* 6: 57–63.
- Kubinyi E., Topál J., Miklósi A., and Csányi V. 2003b. Dogs (*Canis familiaris*) learn from their owners via observation in a manipulation task. *J. Comp. Psychol.* 117: 156–165.
- Leach H. 2003. Human domestication reconsidered. *Curr. Anthropol.* 44: 349–368.
- Markman E. and Abelev M. 2004. Word learning in dogs? *Trends Cognit. Sci.* 8: 479–481.
- McKinley J. and Sambrook T. 2000. Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Anim. Cognition* 3: 13–22.
- Miklósi A., Topál J., and Csányi V. 2004. Comparative social cognition: What can dogs teach us? *Anim. Behav.* 67: 995–1004.
- Miklósi A., Polgárdi R., Topál J., and Csányi V. 1998. Use of experimenter-given cues in dogs. *Anim. Cognition* 1: 113–121.
- . 2000. Intentional behavior in dog-human communication: An experimental analysis of “showing” behavior in the dog. *Anim. Cognition* 3: 159–166.
- Miklósi A., Kubinyi E., Topál J., Gácsi M., Virányi Z., and Csányi V. 2003. A simple reason for a big difference: Wolves do not look back at humans, dogs do. *Curr. Biol.* 13: 763–766.
- Oskina I. 1996. Analysis of the function state of the pituitary-adrenal axis during post-natal development of domesticated silver foxes (*Vulpes vulpes*). *Scientific* 20: 159–161.
- Osthaus B., Lea S.E.G., and Slater A.M. 2005. Dogs (*Canis familiaris*) fail to show understanding of means end connections in a string pulling task. *Anim. Cognition* 8: 37–47.
- Parker H.G., Kim L.V., Sutter N.B., Carlson S., Lorentzen T.D., Malek T.B., Johnson G.S., DeFrance H.B., Ostrander E.A., and Kruglyak L. 2004. Genetic structure of the purebred domestic dog. *Science* 304: 1160–1164.
- Plyusnina I.Z., Oskina I.N., and Trut L.N. 1991. An analysis of fear and aggression during early development of behavior in silver foxes (*Vulpes vulpes*). *Appl. Anim. Behav. Sci.* 32: 253–268.
- Pongracz P., Miklósi A., Kubinyi E., Topál J., and Csányi V. 2003. Interaction between individual experience and social learning in dogs. *Anim. Behav.* 65: 595–603.
- Pongracz P., Miklósi A., Kubinyi E., Gurobi K., Topál J., and Csányi V. 2001. Social learning in dogs: The effect of a human demonstrator on the performance of dogs in a detour task. *Anim. Behav.* 62: 1109–1117.
- Popova N., Voitenko N.N., Kulikov A.V., and Avgustinovich D.F. 1991. Evidence for the involvement of central serotonin in the mechanism of domestication of silver foxes. *Pharmacol. Biochem. Behav.* 40: 751–756.
- Povinelli D.J. and Eddy T.J. 1996. What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* 61: 1–152.
- Povinelli D., Bierschwale D.T., and Cech C.G. 1999. Comprehension of seeing as a referential act in young children but not juvenile chimpanzees. *Br. J. Dev. Psychol.* 17: 37–60.
- Povinelli D. J., Reaux J.E., Bierschwale D.T., Allain A.D., and Simon B.B. 1997. Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cogn. Dev.* 12: 423–461.
- Reidel J., Buttelmann D., Call J., and Tomasello M. 2005. Domestic dogs (*Canis familiaris*) use a physical marker to find hidden food. *Anim. Cognition* (in press).
- Ritvo H. 1998. Foreword. In *The variation of animals and plants under domestication* (ed. C. Darwin), pp. v–xiii. John Hopkins University Press, Baltimore, Maryland.
- Savolainen P., Zhang Y-P., Luo J., Lundeberg J., and Leitner T. 2002. Genetic evidence for an East Asian origin of domestic dogs. *Science* 298: 1610–1613.
- Slabbart J. and Rasa O. 1997. Observational learning of an acquired maternal behaviour pattern by working dog pups: An alternative training technique. *Appl. Anim. Behav. Sci.* 53: 309–316.
- Soproni K., Miklósi A., Topál J., and Csányi V. 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J. Comp. Psychol.* 115: 122–126.
- Tomasello M. and Call J. 1997. *Primate cognition*. Oxford University Press, New York.

- Tomasello M., Call J., and Gluckman A. 1997. Comprehension of novel communicative signs by apes and human children. *Child Dev.* 68: 1067–1080.
- Tomasello M., Call J., and Hare B. 2003. Chimpanzees understand the psychological states of others—the question is which ones and to what extent. *Trends Cogn. Sci.* 7: 153–157.
- Tomasello M., Carpenter M., Call J., and Moll H. 2005. Understanding and sharing intentions: The origins of cultural cognition. *Behav. Brain Sci.* (in press).
- Trut L. 1991. Intracranial allometry and morphological changes in silver foxes (*Vulpes vulpes*) under domestication. *Genetika* 27: 1605–1611.
- . 1999. Early canid domestication: The farm-fox experiment. *Am. Sci.* 87: 160–169.
- . 2001. Experimental studies of early canid domestication. In *The genetics of the dog* (ed. A. Ruvinsky and J. Sampson), pp. 15–43. CABI Publishing, New York.
- Trut, L., Plyusina I.Z., Kolesnikova L.A., and Kozlova O.N., 2000. Interhemispherical neurochemical differences in brains of silver foxes selected for behavior and the problem of directional asymmetry. *Genetika* 36: 942–946.
- Vila C., Savolainen P., Maldonado J.E., Amorim I.R., Rice J.E., Honeycutt R.L., Crandall K.A., Lundeberg J., and Wayne R.K. 1997. Multiple and ancient origins of the domestic dog. *Science* 276: 1687–1689.
- Viranyi Z., Topál J., Gacsi M., Miklósi A., and Csányi V. 2004. Dogs respond appropriately to cues of humans' attentional focus. *Behav. Processes* 66: 161–172.
- Watson J.S., Gergely G., Csányi V., Topál J., Gacsi M., and Sarkozi Z. 2001. Distinguishing logic from association in the solution of an invisible displacement task by children (*Homo sapiens*) and dogs (*Canis familiaris*): Using negation of disjunction. *J. Comp. Psychol.* 115: 219–226.
- Wrangham R. 2005. *The cooking ape*. Harvard University Press, Cambridge, Massachusetts. (In press.)

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The Genetics of Domesticated Behavior in Canids: What Can Dogs and Silver Foxes Tell Us about Each Other?

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DOMESTICATED ANIMALS DISPLAY DISTINCT DIFFERENCES in behavior, morphology, and physiology from their wild counterparts. They usually exhibit reduced aggressiveness, increased social tolerance among conspecifics, and reduced sensitivity to environmental changes (for review,