

Human-like social skills in dogs?

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Domestic dogs are unusually skilled at reading human social and communicative behavior – even more so than our nearest primate relatives. For example, they use human social and communicative behavior (e.g. a pointing gesture) to find hidden food, and they know what the human can and cannot see in various situations. Recent comparisons between canid species suggest that these unusual social skills have a heritable component and initially evolved during domestication as a result of selection on systems mediating fear and aggression towards humans. Differences in chimpanzee and human temperament suggest that a similar process may have been an important catalyst leading to the evolution of unusual social skills in our own species. The study of convergent evolution provides an exciting opportunity to gain further insights into the evolutionary processes leading to human-like forms of cooperation and communication.

Almost everywhere there are people there are dogs. And although most people like dogs, very few have found them interesting from a scientific perspective. A notable exception was Charles Darwin, who found them very interesting, and indeed launched the *Origin of Species* [1] with a flurry of examples describing variability in domesticated animals, including dogs, because nowhere can descent with modification be more clearly seen than in familiar domestic species [2].

Only recently it has been discovered that dogs are interesting to science for another reason. It appears that dogs have evolved specialized skills for reading human social and communicative behavior [3,4]. These skills seem more flexible – and possibly more human-like – than those of other animals more closely related to humans phylogenetically, such as chimpanzees, bonobos and other great apes. This raises the possibility that convergent evolution has occurred: both *Canis familiaris* and *Homo sapiens* might have evolved some similar (although 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, it is possible that these similar traits arose independently via a similar evolutionary process. Indeed, recent comparative work with canids and primates supports the hypothesis that dogs' social skills represent a case of convergent evolution with humans. This

comparative work has begun to identify the selection pressures that drove the evolution of these skills, and, further, suggests that a similar process played a role in shaping human social skills as well.

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The test is simple. Hide a piece of food or an attractive object 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 task trivially easy from around 14 months of age, as they are just beginning to learn language [5]. However, perhaps surprisingly, chimpanzees, so impressive in solving so many other social problems, show little skill in using such social-communicative behaviors to solve this task (see [Box 1](#)). Meanwhile, give domestic dogs a crack at it and they show impressive flexibility in solving the same problem [6,7].

Who is the master of human behavior?

In initial studies [6–10], experimenters set up situations in which a human hid food in one of several locations and then gave a cue to the dog to indicate where the food was hidden (see [Figure 1](#)) – using control procedures to ensure that subjects could not locate the food without using the cue provided (e.g. by smell). Across all the studies, the results showed that most dogs were able to use several different behaviors to locate the hidden food at above chance levels: (i) 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); (ii) a human

Box 1. Do chimpanzees use human social-communicative cues?

All primates tested, including chimpanzees, are universally poor at finding hidden food using human social-communicative behaviors (i.e. the same tasks used with dogs), with the exception of some individuals raised with humans; [50,51]. It takes dozens of trials for primates to learn to use such information when provided by a helpful human or conspecific [52,53]. And even when one cue is mastered, chimpanzees do not generalize these skills when novel cues are available that closely resemble the one they previously learned [54,55].

This difficulty for primates and especially chimpanzees is something of a mystery. Chimpanzees, in particular, seem to have many of the requisite skills to solve such a problem, as demonstrated in other cognitive tasks. For example, in several other situations, chimpanzees appear to be capable of assessing what another individual can see – including following their gaze direction to objects hidden from their immediate view [46,56,57]. Chimpanzees also seem capable of drawing inferences from others' goal-directed actions. For example, they react differently to actions that occurred accidentally and those performed on purpose [58,59].

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Figure 1. Dogs are more skilled than chimpanzees at using human behavioral cues (e.g. pointing) to find hidden food. In the basic test an experimenter places food so that the dog sitting across from her does not know in which cup it is hidden. Then the experimenter points in the direction of the correct cup and lets the dog choose a cup.

gazing to the target location (dog sees either the head turn or a static head looking towards a location); (iii) a human bowing or nodding to the target location; and (iv) a human placing a marker in front of the target location (a totally novel communicative cue). The dogs were even able to do the task correctly when the human walked towards the wrong container while pointing in the opposite direction to the correct container. In addition, dogs performed equally well whether cues were provided by conspecifics or humans. And in all of these cases, the dogs used the behaviors effectively from their very first trials, showing that they already possessed the required skills before the experiment. In many of these tests, over two-thirds of the dogs were significantly above chance as individuals.

In a direct comparison of chimpanzees and dogs, subjects of both species were given the ‘novel block’ cue (where the human gets the animal’s attention and conspicuously places a block on the target container); the dogs performed much better than chimpanzees tested [11]. In other studies, dogs have performed well in this task even when they only see the block placed initially and it is removed before they make their choice – demonstrating that they are not just attracted to the block itself [12]. With respect to gaze cues, dogs – like human infants but unlike chimpanzees [13] – only use the human head and eye direction cue to locate hidden food if the person is gazing directly at one of two possible hiding locations; they ignore a human’s gaze if the person stares into space above the correct hiding location [14]. This suggests that dogs discriminate human communicative behaviors from other behaviors, in ways similar to human infants.

More than behavior reading?

Another line of research has demonstrated that dogs know what humans can see in 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 [6,15]. 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 [16–18] – something that chimpanzees do not do spontaneously [19]. Dogs are also more likely to avoid approaching forbidden food when a human’s eyes are open than when they are closed [20] – again, something that chimpanzees do not do spontaneously [19,21]. Moreover, dogs even avoid approaching forbidden food when they are behind a large barrier with the food in front of a small window (and the human on the other side of the barrier). 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 [22]. In addition, in the case of one particular border collie, when its owner 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) [23] – 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 only been demonstrated previously for language learning in human children [23] (although see [24]). 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 the demonstration [25–29].

A social specialization?

One of the things that makes these findings so fascinating is that, relative to other animals, dogs do not seem to show special flexibility in other, non-social domains. For example, dogs are unable to infer the location of a hidden object based on the trajectory of a hider’s movements and the results of their own previous searches [30]. When dogs are directly compared with primates in their ability to do such things as make inferences about the location of hidden food based on non-social cues – for example, seeing one board lying flat and another tilted up as if something were under it – they fail miserably in comparison with non-human great apes (Bräuer *et al.*, unpublished). Also, dogs 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 [31] – a task most primates solve easily [32]. It seems therefore that the skills dogs have shown represent a specifically social specialization.

Convergent cognitive evolution in dogs and humans?

The fact that domestic dogs possess certain human-like social skills that non-human apes do not raises the question of their origin. Could it be that the similarities between dogs and humans represent a case of convergent cognitive evolution? There are three obvious explanations, and they have been explored by comparing the use of basic human social-communicative behaviors (i.e. a pointing or gaze cue directed to the location of a hidden object; see [Figure 1](#)) both within and between various canid species.

Is good rearing everything?

The most straightforward explanation for domestic dogs’ special social skills with humans is that they grow up with humans and learn from them; that is, there is a kind of ‘enculturation’ similar to that proposed to explain the

unusual cognitive abilities of apes raised by humans [33]. This hypothesis predicts that the ability to read human social behavior should develop 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 nine weeks old were nearly perfect in the basic tests. In addition, when a group of puppies in an obedience class was compared with a group of litter-reared puppies (i.e. with relatively little exposure to humans) in their ability to use the same pointing and gazing cues, both groups were equally skilled at using the cues. These findings do not support the hypothesis that dogs need unusual amounts of exposure to humans (e.g. relative to most primates tested) to learn to read human social and communicative behavior [11].

A wolf in dog's clothing?

A second candidate hypothesis invokes the canid ancestry of dogs. Dogs evolved multiple times from Old World wolves [34–38], and as wolves are social pack hunters they need to read the social behavior of their fellow hunters as well as prey [8,38]. This hypothesis would suggest that the social skills dogs exhibit are simply inherited through common descent with the wolf. However, two independent studies have found that wolves reared by humans are not as skilled as dogs in using human social behaviors to find hidden food [11,39]. In addition, 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 directed their gaze alternately between the human and the box, whereas wolves continued to try to solve the task on their own until the test ended [39]. This is not to say that dogs are more skilled than wolves in all domains. Studies comparing wolves and dogs on simple non-social problem solving or memory tasks typically find that wolves perform as well if not better than dogs [11,40–42]. Overall, these comparisons do not support the hypothesis that dogs inherited their social skills directly from wolves.

A domestic product?

This leaves the possibility that dogs' social skills evolved during the process of domestication; that is, during the tens of thousands of years that our two species have lived together. But if such evolution took place, how would one test for such a possibility – and, most importantly, what might have been the selection pressures that drove such evolutionary change? Luckily, dogs are not the only domesticated canids. A unique population of foxes has also been experimentally domesticated (see Box 2). During the process of domestication individual foxes were selected for breeding based solely on their tendency to approach humans fearlessly and non-aggressively. When fox kits from this 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, when compared with a population of control foxes that were bred randomly in respect to their approach towards humans, the domestic

foxes were more skilled than the controls at using human social cues (although there was no difference between the two populations in a non-social task). Crucially, neither population of foxes was bred or tested for their ability to use human communicative gestures or behaviors. Therefore, these findings confirm the likelihood that dogs' unusual ability to read human social-communicative behaviors evolved during the process of domestication, and in addition identify a selection pressure that is likely to have played a role in driving the evolution: selection against fear and aggression towards humans [43]. Such selection probably occurred as, for example, wolves began exploiting the niche created by refuse in and around human settlements [38].

Emotional evolution

Taken together, these comparative findings suggest that the unusual social skills of dogs arose as a result of domestication and represent a case of convergent evolution with humans (i.e. similar derived traits in distantly related species; see Figure 2). Perhaps most surprisingly, research with domesticated foxes suggests that dogs' skills for reading human social-communicative behavior might have initially evolved as an incidental by-product of selection for tame behavior (i.e. just like floppy ears, etc.). That is, it may be that dogs' specialized social problem-solving skills first appeared after systems mediating fear and aggression evolved, systems that are typically not thought of as cognitive systems at all (see Box 2). Once this initial evolution occurred so that dogs were motivated to apply inherited cognitive abilities (i.e. 'reading' conspecific behavior; [6]) to solve a new set of social problems involving humans, the variance in these cognitive abilities might have come under direct selection,

Box 2. The Siberian domestication experiments

In 1959, Dr Dmitry Balyaev and his colleagues in Siberia began one of the longest running experiments in history with the goal of studying the behavioral genetics of domestication [60]. Since the start of the experiment two separate populations of foxes (*Vulpes vulpes*) have been maintained (and the same was done for rats, mink and otters). An experimental population was selectively bred based on a single criterion – whether they fearlessly and non-aggressively approached a human. The second population was maintained as a control and has been bred randomly in respect to their behavior towards humans [61,62].

Based on this single selection criterion, behavioral, physiological and morphological changes were observed in the experimental fox population that were not observed in control foxes (see fox photos in Figure 2). As would be predicted, experimental foxes show little fear and aggression towards humans [63]. This reduction in aggressiveness and fear is probably due to attenuated activity of the pituitary-adrenal axis. The common pool of circulating glucocorticoids, their *in vitro* production, the basal level of the adrenocorticotropic hormone (ACTH), and the adrenal response to stress were all reduced in the experimental foxes relative to the controls [64]. 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 altered in the experimental foxes [65,66]. Finally, and perhaps most surprising, the domesticated foxes have a higher frequency of floppy ears, short or curly tails, depigmentation of hair, extended reproductive seasons, as well as changes in the size and shape of the crania and dentition [61,62,67].

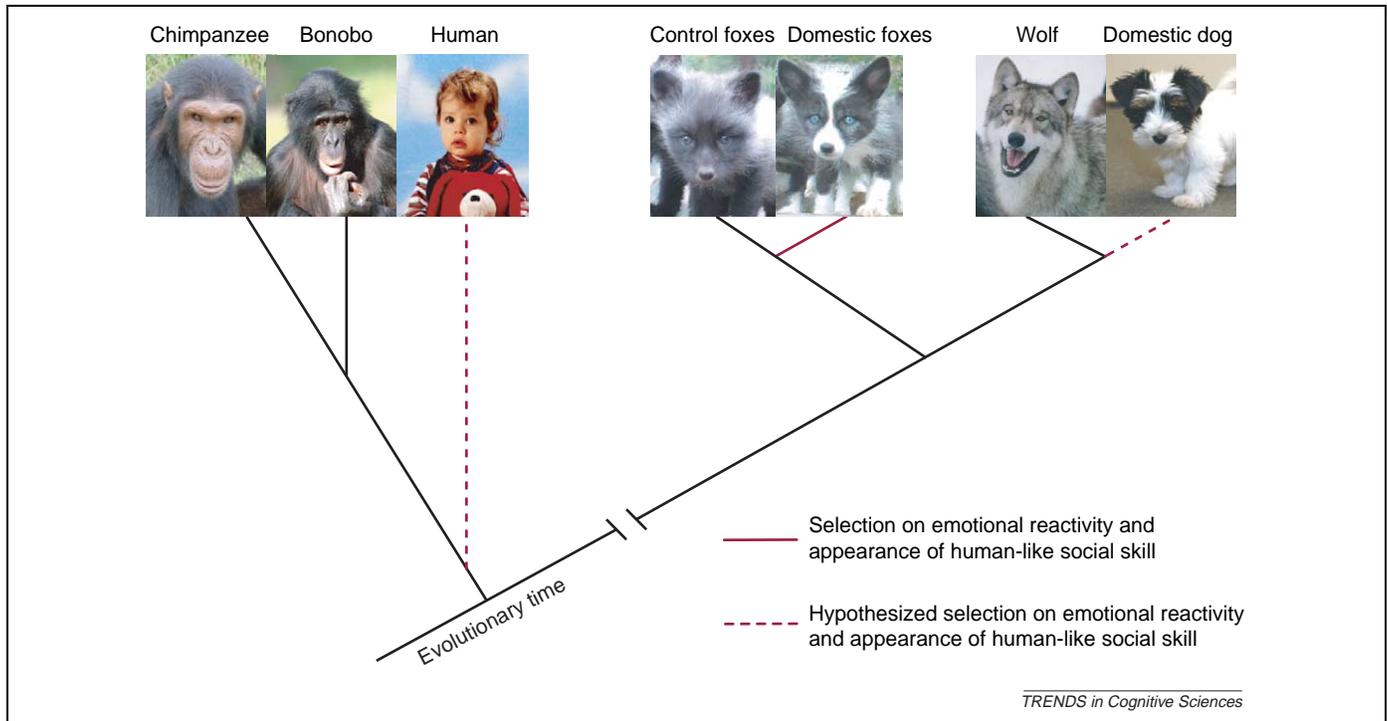


Figure 2. Comparative studies suggest that a set of derived social skills in domesticated canids and in humans are convergent and initially evolved by selection on systems mediating fear and aggression (figure not drawn to scale).

for example, in contexts such as herding or hunting that require cooperation and communication with humans (although currently there is little evidence for this second selection event). However, if such cognitive evolution occurred, it would not have been possible without the initial selection on systems controlling emotional reactivity, which placed dogs in a new adaptive space in which they were able to interact with humans as comfortably as with conspecifics.

Implications for human cognitive evolution

This recent comparative work suggests that human-like social intelligence could initially have evolved, not as an adaptation, but rather as a by-product of selection on seemingly unrelated social-emotional systems – perhaps supported primarily by limbic and endocrine systems rather than the neocortex. Is there any evidence to suggest that humans' social and communicative abilities might have begun to evolve in this way? One prediction of this 'emotional reactivity' hypothesis is that the social problem-solving of non-human great apes should be highly constrained by their temperament.

Can temperament constrain problem solving?

Support for the hypothesis that changes in temperament paved the way for further social-cognitive evolution in humans comes from studies of chimpanzee cooperation. The basic finding is that cooperation among chimpanzees is highly constrained by levels of inter-individual tolerance (i.e. probably controlled by systems mediating fear and aggression). For example, without any training chimpanzees will cooperate to pull ropes together to retrieve a heavy box of food. However, chimpanzees are only willing to do this if: (i) the food is sharable, (ii) the

partners are out of each others' reach, and (iii) the partners have shared food previously in a similar context. If such social criteria are not met, then chimpanzees will not cooperate [44]. It seems from such tests that unless the conditions are right subordinate chimpanzees are simply not willing to risk being attacked by intolerant dominants, and dominants are not able to control their aggression towards subordinates trying to obtain food – even if it means they will never receive any food.

Further support for a role for emotional reactivity comes from the fact that chimpanzees spontaneously exploit the social behaviors of others when competing for food [45,46] – a context in which chimpanzees seem particularly engaged (i.e. it is motivating when someone else might eat my food!). For example, chimpanzees demonstrate spontaneous food-finding behavior when they see a human who has previously established a competitive relationship with them, reaching unsuccessfully towards a potential food location in an apparent attempt to obtain hidden food. However, if the same chimpanzees see a helpful human pointing to the hidden location (i.e. morphologically similar to reaching towards it), they do not use the gesture to locate the food [45]. Therefore, it could be that chimpanzees do not demonstrate human-like skills in using communicative gestures because they lack a human-like temperament for sharing information (see [Box 1](#)).

Human intelligence requires human temperament

Recent research with chimpanzees seems to suggest that a prerequisite for flexible forms of human cooperation and communication is a human-like temperament ([Figure 2](#)). In fact, the evolution of the human temperament might necessarily have preceded the evolution of more complex

Box 3. Questions for future research

- What, if anything, do dogs understand about the unobservable mental life of others? There is evidence that dogs are capable of making some simple social inferences, but are they making these inferences based on an understanding of others psychological states (i.e. perceptual, desire or belief states)? For example, what do dogs really understand about the individual helping them to find food? Do they understand these communicative behaviors as intentional?
- There is currently no direct evidence for the emotional reactivity hypothesis from experiments with dogs (i.e. it is the work with foxes that suggests the hypothesis). In addition, there is no evidence that selection acted directly on social problem-solving skills in dogs. How can this be tested? One potential test would be a comparison of social skills in domestic dog breeds found to be more genetically wolf-like and those shown to be genetically less wolf-like [37]. Less genetically wolf-like dogs (especially working breeds) should have different temperaments and use human communicative behaviors more flexibly than more genetically wolf-like dogs (i.e. both groups are domesticated but the genetic difference between the two groups could be partially due to direct selection on the social cognition of the less wolf-like breeds).
- In humans, did temperament evolve before more sophisticated forms of social cognition? One further way to test this hypothesis is to examine individual differences in social problem-solving with respect to temperament. Are individuals with certain types of temperaments (in both humans and dogs) more or less skilled than others at solving social problems?

forms of human social cognition (e.g. a more sophisticated theory of others' behavior or mental states would be of little use when cooperating if individuals are rarely able to share the rewards of joint effort). It is only after the human temperament evolved that variation in more complex forms of communicative and cooperative behaviors could have been shaped by evolution into the unique forms of cooperative cognition present in our species today. 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 within a social group either killed or ostracized those who were over-aggressive or despotic; [47–49]). Thus, like domestic dogs, this selection for tamer emotional reactivity put our hominid ancestors in a new adaptive space within which modern human-like forms of social interaction and communication could be selected for [49].

Summary

It would seem that our canine companions have come to join in the human conversation in some unique and telling ways. The abilities that enable them to do this – particularly those relating to 'reading' human communicative behavior – evolved, at least initially, as a by-product of domestication and converge with those found in our own species. Further investigations into the ways in which dogs do and do not communicate with humans – and how they come to have their special social skills – provide us with an exciting opportunity to gain further insight into the evolutionary processes leading to human-style cooperative interactions and communication (see also Box 3). These insights should then continue to inform comparisons between humans and our nearest primate relatives

that aim to identify not only unique forms of human communication, cooperation and culture but also the processes by which they evolved.

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References

- 1 Darwin, C. (1859) *On the Origin of Species*, John Murray
- 2 Ritvo, H. (1998) Foreword. In *The Variation of Animals and Plants under Domestication*. Charles Darwin, John Hopkins University
- 3 Miklosi, A. et al. (2004) Comparative social cognition: what can dogs teach us? *Anim. Behav.* 67, 995–1004
- 4 Cooper, J. et al. (2003) Clever hounds: social cognition in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 81, 229–244
- 5 Behne, T. et al. One-year-olds comprehend the communicative intentions behind gestures in a hiding game. *Dev. Sci.* (in press)
- 6 Hare, B. et al. (1998) Communication of food location between human and dog (*Canis familiaris*). *Evolution of Communication* 2, 137–159
- 7 Miklosi, A. et al. (1998) Use of experimenter-given cues in dogs. *Anim. Cogn.* 1, 113–121
- 8 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
- 9 Agnetta, B. et al. (2000) Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Anim. Cogn.* 3, 107–112
- 10 McKinley, J. and Sambrook, T. (2000) Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Anim. Cogn.* 3, 13–22
- 11 Hare, B. et al. (2002) The domestication of social cognition in dogs. *Science* 298, 1634–1636
- 12 Reidel, J. et al. Novel cues that dogs do and do not use. *Anim. Cogn.* (in press)
- 13 Povinelli, D. et al. (1999) Comprehension of seeing as a referential act in young children but not juvenile chimpanzees. *Br. J. Dev. Psychol.* 17, 37–60
- 14 Soproni, K. et al. (2001) Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J. Comp. Psychol.* 115, 122–126
- 15 Miklosi, A. et al. (2000) Intentional behavior in dog-human communication: an experimental analysis of "showing" behavior in the dog. *Anim. Cogn.* 3, 159–166
- 16 Bishop, S. and Young, R. Do domestic dogs understand the importance of eye contact with humans? *Anim. Cogn.* (in press)
- 17 Viranyi, Zs. et al. (2004) Dogs respond appropriately to cues of humans' attentional focus. *Behav. Processes* 66, 161–172
- 18 Gacsi, M. et al. (2004) Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim. Cogn.* 7, 144–153
- 19 Povinelli, D.J. and Eddy, T.J. (1996) What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* 61, 1–152
- 20 Call, J. et al. (2003) Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *J. Comp. Psychol.* 117, 257–263
- 21 Kaminski, J. et al. (2004) Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Anim. Cogn.* 7, 216–223
- 22 Brauer, J. et al. (2004) Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Appl. Anim. Behav. Sci.* 88, 299–317
- 23 Kaminski, J. et al. (2004) Word learning in a domestic dog: evidence for 'fast mapping'. *Science* 304, 1682–1683
- 24 Markman, E. and Abelev, M. (2004) Word learning in dogs? *Trends Cogn. Sci.* 8, 479–481

- 25 Pongracz, P. *et al.* (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
- 26 Pongracz, P. *et al.* (2003) Interaction between individual experience and social learning in dogs. *Anim. Behav.* 65, 595–603
- 27 Slabbar, 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
- 28 Kubinyi, E. *et al.* (2003) Social mimetic behaviour and social anticipation in dogs: preliminary results. *Anim. Cogn.* 6, 57–63
- 29 Kubinyi, E. *et al.* (2003) Dogs (*Canis familiaris*) learn from their owners via observation in a manipulation task. *J. Comp. Psychol.* 117, 156–165
- 30 Watson, J. *et al.* (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
- 31 Osthaus, B. *et al.* (2005) Dogs (*Canis familiaris*) fail to show understanding of means end connections in a string pulling task. *Anim. Cogn.* 8, 37–47
- 32 Tomasello, M. and Call, J. (1997) *Primate Cognition*, Oxford University Press
- 33 Call, J. and Tomasello, M. (1996) The effect of humans on the cognitive development of apes. In *Reaching into Thought* (Russon, A.E. *et al.*, eds), pp. 371–403, Cambridge University Press
- 34 Vila, C. *et al.* (1997) Multiple and ancient origins of the domestic dog. *Science* 276, 1687–1689
- 35 Savalain, P. *et al.* (2002) Genetic evidence for an East Asian origin of domestic dogs. *Science* 298, 1610–1613
- 36 Clutton-Brock, A. (1999) *A Natural History of Domesticated Mammals*, Cambridge University Press
- 37 Parker, H. *et al.* (2004) Genetic structure of the purebred domestic dog. *Science* 304, 1160–1164
- 38 Coppinger, R. and Coppinger, L. (2001) *Dogs: A Startling New Understanding of Canine Origin, Behavior and Evolution*, Scriber Press
- 39 Miklosi, A. *et al.* (2003) A simple reason for a big difference: wolves do not look back at humans, dogs do. *Curr. Biol.* 13, 763–766
- 40 Frank, H. (1980) Evolution of canine information processing under conditions of natural and artificial selection. *Z. Tierpsychol.* 59, 389–399
- 41 Frank, H. (1982) On the effects of domestication on canine social development and behaviour. *Applied Animal Ethology* 8, 507–525
- 42 Frank, H. *et al.* (1989) Motivation and insight in wolf (*Canis lupus*) and Alaskan Malamute (*Canis familiaris*): visual discrimination and learning. *Bull. Psychon. Soc.* 27, 455–458
- 43 Hare, B. *et al.* (2005) Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Curr. Biol.* 15, 226–230
- 44 Melis, A. *et al.* Engineering chimpanzees cooperation: levels of tolerance constrain cooperation. *Anim. Behav.* (in press)
- 45 Hare, B. and Tomasello, M. (2004) Chimpanzees are more skillful at competitive than cooperative cognitive tasks. *Anim. Behav.* 68, 571–581
- 46 Hare, B. *et al.* Chimpanzees deceive a human competitor by hiding. *Cognition* (in press)
- 47 Boehm, C. (1999) *Hierarchy in the Forest*, Harvard University Press
- 48 Leach, H. (2003) Human domestication reconsidered. *Curr. Anthropol.* 44, 349–368
- 49 Wrangham, R. *The Cooking Ape* (in press)
- 50 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
- 51 Call, J. *et al.* (2000) Social cues that chimpanzees do and do not use to find hidden objects. *Anim. Cogn.* 3, 23–34
- 52 Anderson, J.R. *et al.* (1995) Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Anim. Behav.* 49, 201–208
- 53 Itakura, S. *et al.* (1999) Chimpanzee use of human and conspecific social cues to locate hidden food. *Dev. Sci.* 2, 448–456
- 54 Tomasello, M. *et al.* (1997) Comprehension of novel communicative signs by apes and human children. *Child Dev.* 68, 1067–1080
- 55 Povinelli, D.J. *et al.* (1997) Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cogn. Dev.* 12, 327–365
- 56 Tomasello, M. *et al.* (2003) Chimpanzees understand the psychological states of others – the question is which ones and to what extent. *Trends Cogn. Sci.* 7, 153–157
- 57 Povinelli, D.J. and Vonk, J. (2003) Chimpanzee minds: suspiciously human? *Trends Cogn. Sci.* 7, 157–160
- 58 Call, J. and Tomasello, M. (1998) Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *J. Comp. Psychol.* 112, 192–206
- 59 Call, J. *et al.* (2004) Unwilling versus unable: chimpanzees understanding of human intentional action. *Dev. Sci.* 7, 488–498
- 60 Belyaev, D. (1979) Destabilizing selection as a factor in domestication. *J. Hered.* 70, 301–308
- 61 Trut, L. (2001) Experimental studies of early canid domestication. In *The Genetics of the Dog* (Ruvinsky, A. and Sampson, J., eds), pp. 15–42, CABI Publishing
- 62 Trut, L. (1999) Early canid domestication: the farm-fox experiment. *Am. Sci.* 87, 160–169
- 63 Plyusnina, I. *et al.* (1991) An analysis of fear and aggression during early development of behavior in silver foxes (*Vulpes vulpes*). *Appl. Anim. Behav. Sci.* 32, 253–268
- 64 Oskina, I. (1996) Analysis of the function state of the pituitary-adrenal axis during postnatal development of domesticated silver foxes (*Vulpes vulpes*). *Scientificur* 20, 159–161
- 65 Popova, N. *et al.* (1991) Evidence for the involvement of central serotonin in the mechanism of domestication of silver foxes. *Pharmacol. Biochem. Behav.* 40, 751–756
- 66 Trut, L. *et al.* (2000) Interhemispheric biochemical differences in brains of silver foxes selected for behavior, and the problem of directional asymmetry. *Genetika* 36, 940–946
- 67 Trut, L. (1991) Intracranial allometry and morphological changes in silver foxes (*Vulpes vulpes*) under domestication. *Genetika* 27, 1605–1611

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