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Applied Animal Behaviour Science 81 (2003) 229–244

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Clever hounds: social cognition in the domestic dog (*Canis familiaris*)

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Abstract

This paper reviews the reasons why domestic dogs make good models to investigate cognitive processes related to social living and describes experimental approaches that can be adopted to investigate such processes in dogs. Domestic dogs are suitable models for investigating social cognition skills for three broad reasons. First, dogs originated from wolves, social animals that engage in a number of co-operative behaviours, such as hunting and that may have evolved cognitive abilities that help them predict and interpret the actions of other animals. Second, during domestication dogs are likely to have been selected for mental adaptations for their roles in human society such as herding or companionship. Third, domestic dogs live in a human world and “enculturation” may facilitate the development of relevant mental skills in dogs. Studies of social cognition in animals commonly use experimental paradigms originally developed for pre-verbal human infants. Preferential gaze, for example, can be used as a measure of attention or “surprise” in studies using expectancy violation. This approach has been used to demonstrate simple numerical competence in dogs. Dogs also readily use both conspecific and human social signals (e.g. looking or pointing) as information sources to locate hidden rewards such as food or favourite toys. Such abilities make dogs particularly good models for investigating perspective-taking tasks, where animals are required to discriminate between apparently knowledgeable and apparently ignorant informants.

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Keywords: Domestic dog; Canine; Social cognition; Counting; Theory of mind; Perspective taking

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1. Introduction: the study of social cognition

The contemporary experimental paradigms used for the study of social cognition and its relationship with animal behaviour can be traced to the work of [Humphrey \(1976\)](#) and [Premack and Woodruff \(1978\)](#). In “The social function of intellect”, Humphrey argued that the primary driving forces in the evolution of human intelligence were those challenges related to the social environment, and in particular, interaction with individuals of the same species rather than those associated with the physical environment. This argument extends to the evolution of animal cognition, since the social environment contains more complex challenges than the physical environment and, consequently, highly social animals are likely to have evolved mental processing abilities to help them predict and exploit the actions of others ([Byrne and Whiten, 1990](#); [Dunbar, 1992](#)). [Premack and Woodruff \(1978\)](#) discussed “theory of mind” or the attribution of mental states (such as beliefs or desires) to others. They described this mental ability as both a mechanism for animals to predict the actions of others and a means for cognitive scientists to investigate cognitive processes in non-human animals. The ability to take the perspective of others has recently received much interest amongst comparative and evolutionary psychologists and applied to deceit and exploitation or “Machiavellian Intelligence” ([Byrne and Whiten, 1988](#); [Whiten and Byrne, 1997](#)) as well as co-operation in social animals. [Byrne and Whiten \(1988\)](#) report that, after primates, dogs are the most commonly reported species to engage in apparent tactical deception. The study of social cognition is not, however, limited to interpreting and understanding the actions of others and a wide range of mental representational abilities which would be useful to social animals, are known to have evolved in humans and may have evolved in other social species. These include: the ability to count or numerical competence; certain forms of social learning; and the communication of abstract information between individuals through language. Studies of social cognition have tended to concentrate on humans and closely related non-human primates (e.g. [Povinelli et al., 1997](#); [Heyes, 1998](#); [Call and Tomasello, 1999](#)). However, if social intelligence has functional benefits to social animals then it seems reasonable to postulate their existence in a wider range of species ([Held et al., 2001a](#)).

2. Development of social skills in the dog

Broadly, there are three reasons why we might predict that domestic dogs possess the capacity for social cognitive skills. First, they originate from wolves, a species that forms stable social bands and engages in co-operative behaviour such as hunting ([Mech, 1970](#); [Frank, 1980](#)); second, because some individuals may have been selected for such abilities during domestication and breed selection ([Coppinger and Coppinger, 2001](#)); and third, because they commonly live in a human social environment that may facilitate the development of such skills.

2.1. Ancestral influences from the wolf

There has been considerable debate amongst anthropologists and biologists about the ancestry of the domestic dog and the process of its domestication, though it is generally

accepted that the majority of dogs evolved from wolves (*Canis lupis*); albeit over different time periods across the world and involving a number of sub-species of wolf (Fox, 1978; Clutton-Brock, 1995; Vila et al., 1997). Wolves commonly live in tightly knit groups or packs, consisting of related individuals of varying age, and with clear dominance hierarchies amongst males and females (Mech, 1970). Packs engage in co-operative hunting, involving the co-ordinated tracking, chasing, catching and killing of prey (Mech, 1970; Fox, 1971). Wolves may, therefore, benefit functionally from the ability to predict the behaviour of other wolves or their prey (Frank and Frank, 1982; Gagnon and Dore, 1994). The wolf also forms strong stable bonds between individuals and therefore meets another important criterion underlying the selective advantage of social cognitive skills. The majority of species, in which some form of social cognition has been claimed form relatively long-lived stable social groups. These include humans and other apes (e.g. Povinelli et al., 1990; Tomasello et al., 1997), dolphins (e.g. Tschudin, 2001), parrots (Pepperberg, 1994) and pigs (Held et al., 2000, 2001b).

2.2. *Effects of domestication and breed diversification*

Domestic dogs have undergone two selective processes related to their association with human societies. The first is domestication, which involves biological and cultural changes in both the domestic animal and the domesticators (Clutton-Brock, 1995). The second is breed diversification where dogs have been selected for specific traits to suit specific roles in human society (Coppinger and Schneider, 1995). Both these processes may have involved selection for social intelligence (by accident or design) in dogs.

A process commonly seen in domesticated species is neotenisation, which means the process whereby juvenile characteristics are retained into adulthood. It has been suggested that this is a general effect of domestication (Fox, 1968), since sub-adults exhibit greater behavioural plasticity and may be more manageable as a result in the domestic environment (Hediger, 1938). The mechanism by which neotenisation is achieved is uncertain (Price, 1984), but there is evidence for its occurrence in the dog at both the physical and behavioural level (Ginsburg and Schotte, 1978; Frank and Frank, 1982; Coppinger and Coppinger, 2001). It has also been suggested that humans exhibit many features comparable to a neotenisated wild ape species (Bolk, 1926) and Gould (1978) has argued that this may be adaptive for humans by increasing their capacity to learn. Thus, it may be that through neoteny both humans and dogs retain and develop a range of cognitive processes into adulthood, which are not retained in their phylogenetic relatives.

Frank (1980) has argued that the domestication of the dog has selected against cognitive processes, which may exist in the wolf. Experimental support for this is weak, as it is based on limited samples with different developmental backgrounds. Behavioural changes are notoriously difficult to track over evolutionary time-scales as they leave little direct evidence in the form of fossil records. Behavioural changes may nevertheless be inferred from changes in anatomical features such as the skull. Domestic dogs have a smaller cranial capacity and consequently smaller brain size than the wolf (Wayne, 1986; Coppinger and Schneider, 1995), which would appear to support Frank's hypothesis. A smaller brain does not, however, necessarily preclude cognitive abilities in animals and the social aspects of cognition in mammals are more closely related to the size and complexity

of the neocortex size rather than whole brain size (Kruska, 1988; Dunbar, 1992). Wolves have a relatively large neocortex, which in carnivores is only exceeded by lions and hyenas (Dunbar and Bever, 1998) and thus have a large area of the brain devoted to processing cognitive information. No such comparative data have, however, been calculated for dogs, either using fossil records, or comparing breeds and it would be worthwhile to do so to relate changes in brain size during domestication and breed selection to the changing roles of dogs in human society.

In addition to indirect selection, there may have been direct selection for social skills to suit the needs of people and dogs, such as companionship and trainability. Dogs/wolves have co-existed with humans for millennia as, for example, scavengers of human refuse or as food resources themselves, but the actual use of dogs in work such as co-operative hunting appears to be a relatively recent development (Clutton-Brock, 1995). In the later diversification of breeds, dogs have been artificially selected for specific tasks such as hunting or herding, which involve co-operation with humans or other dogs (McConnell and Bayliss, 1985; Slabbert and Rasa, 1997). Social cognitive skills, such as observational learning, would be useful in traditional roles for dogs (Slabbert and Rasa, 1997) and are potentially advantageous in some of the new roles for dogs in human society such as guiding the blind (Naderi et al., 2001). Without further study of, for example, breed differences in brain morphology or task completion in rigorous experimental paradigms it is perhaps unwise to comment further on the role of selection of behavioural traits in the development of social skills in dogs.

2.3. *Effects of lifetime developmental experience*

There is considerable anecdotal evidence for the expression of social intelligence by dogs within the context of the human–animal relationship (Byrne and Whiten, 1988). More recently, Topal et al. (1997, 1998) have investigated the influence of the type of attachment between people and their pet dogs on the dog's behaviour, including problem-solving abilities. They found that dogs performed better at solving novel problems in the presence of their owners than in the presence of strangers or when isolated, even when their owners had no actual knowledge of the task to be solved (Topal et al., 1998). During these tests they noted frequent glancing toward the owner as if the dog was monitoring the owner's behaviour or even soliciting help with the task. Topal et al. (1997) argue that the formation of strong social bonds are important in the behavioural development of the dog, resulting in a form of imprinting which can be seen both in situations where dogs are naturally protective of family members, and in the enthusiasm with which dogs greet familiar people.

Evaluating the significance of enculturation in the domestic environment on social cognition is extremely difficult. Animals with close associations with humans will have plenty of opportunity to learn to use our behaviour, both intentional and unintentional, to predict future events as a result of simple learned contingencies. However, exposure to the human world may also facilitate the development of the more complex social cognitive skills. If exposure to the human environment itself is an important factor in the expression of these skills, then it becomes difficult to compare the findings of laboratory studies involving enculturated animals with those of their wild cousins (Heyes, 1993; Povinelli, 1994). In other words, wild animals may only rarely use their potential cognitive abilities to

solve problems, as most challenges in the natural environment could be solved by other means such as species-specific responses, trial and error learning or observational learning. The effects of exposure to our culture on dogs' behavioural development and of breeding and other selective pressures on their cognitive abilities are both important areas for future investigation, but first it is important to establish reliable methodologies for testing for these abilities in dogs. We review some of our own experiences in the following section.

3. Experimental methodologies to investigate cognitive processes in dogs

One of the principal difficulties with investigating mental representation in animals is finding irrefutable evidence that they have used a cognitive process to change their behaviour (that is, differentiating simple associative learning from true cognitive learning). In humans this is partly solved by language, as we can articulate how we solved problems, or our feelings at the time. In dogs, as in many other species, changes due to mental representation can only be inferred from changes in behaviour. Behaviourists recognised at an early stage that the majority of such changes in behaviour need only be explained by the re-enforcing properties of the consequences of the behaviour's action on the environment, and that there was no need to infer unmeasurable changes in mental state as an intervening variable. In the face of this logical argument, comparative psychologists have often limited themselves to the tools employed by developmental psychologists to investigate cognitive processes in pre-verbal infants (Piaget, 1952). These tools have, however, proved exceedingly powerful. For example, *expectancy violation* is used to investigate the ability to hold mental information and use it to predict future events. This approach can be used to investigate object permanence, or the ability to maintain a representation of an object when it is not in view in animals and pre-verbal infants (Hauser, 2000).

3.1. *Expectancy violation*

An example of expectancy violation in animals was reported by Tinkelpaugh (1928) in an experiment similar to the cup and ball illusion. In this experiment, a food item was shown to a rhesus monkey, then covered by an upside-down cup. At the same time similar cups were placed upside down but not covering food. If rewarded by receiving whatever was underneath the cup, the monkey rapidly learned to indicate the food-covering cup even if the positions of the cups were changed or briefly hidden from view by a screen. In itself, this is quite impressive, but the monkey may have only formed a simple association that lifting the appropriate cup leads to a food reward, rather than a mental concept of what lies beneath each cup. If, however, the food item was highly prized (e.g. item of fruit) and was secretly exchanged for a less desirable food item after it was covered (e.g. swap fruit for lettuce), Tinkelpaugh described the monkey's response as "surprised and angry" when the lettuce leaf was revealed in the place of the fruit. As Hauser (2000) argues, it is not possible to verify these interpretations of the monkey's feelings, but the study seems to demonstrate that the monkey detected a violation of an expectation based on a stored memory. These behavioural changes are, however, difficult to objectively measure and quantify. Hence, psychologists have developed additional tools in their armoury that may quantify the

degree of surprise. One such tool is gaze duration, as we tend to look for longer at situations that differ from our expectations.

Gaze duration and expectancy violation have been used to investigate numerical competence in pre-verbal children (Wynn, 1992). Five-month-old infants were trained to gaze at a screen behind which objects (Mickey Mouse dolls) were placed. Once the screens were removed there were either the same or a different number of dolls as they had seen placed. For example, two dolls may have been placed behind the screen, but upon screen removal there were either one, two or three dolls in view. Wynn (1992) found that infants would stare for longer at the dolls' location if there were one more or one less than should be expected. Thus, infants appeared to have some degree of numerical competence or representation of number of objects even though they could not report the difference with words or place semantic labels to what they have seen.

Numerical competence would be a valuable skill for both social and non-social animals, for example in predator or prey detection, or estimation of the number of animals in rival groups (McComb et al., 1994). In principle, a concept of number of predators could be adaptive for prey species particularly those that are preyed upon by co-operative hunters. Similarly co-operative hunters, when co-ordinating an attack would benefit from a concept of where and how many of their fellows there were even when not all of the pack are in view. A concept of number can take a number of forms (Hauser, 2000). At its simplest, this could be just an ability to judge relative numerosness (i.e. X is greater than Y). More complex processes may include some reference to mental representation of number such as subitising (i.e. assigning an exact numerical tag to a small quantity of items) and estimation (i.e. the process of approximating when the array contains six or more items). Finally, counting itself implies some rather complex representational information. For example, using a label (e.g. two) to indicate the number of objects and recognising that this label is independent of the objects it applies to (i.e. two bananas is the same number as two apples or even the same number as 2 days, a concept you cannot physically see or touch).

These latter processes are difficult to demonstrate without language (Pepperberg, 1994), but some forms of numerical competency may be investigated using Wynn's methods in non-verbal animals. This has been done by Hauser (2000), who found that rhesus monkeys appeared to be able to add up to three eggplants (aubergines), but no more. Similar studies have been conducted by our own group in domestic dogs (West and Young, 2002). In this experiment, pet dogs were tested using large bone-shaped biscuits instead of dolls. During training, single biscuits were placed behind an opaque screen. The screen was then removed to reveal the same biscuit as had been placed (Fig. 1A–C). Once each dog had attained a stable gaze duration (approximately 6 s between screen removal and looking away), they were presented with three simple calculations: $1 + 1 = 2$ (correct), $1 + 1 = 1$ (incorrect), $1 + 1 = 3$ (incorrect) and gaze duration was recorded from videos from the time of screen removal to the time of looking away (preferential looking method). With expected outcomes (i.e. $1 + 1 = 2$), dogs spent the same amount of time looking at the result of the calculation as they did upon the presentation of a single biscuit (Table 1). When the result was unexpected (i.e. $1 + 1 = 1$ or $1 + 1 = 3$) dogs spent significantly longer looking at the outcome of the calculation than they did with a single biscuit control.

These results show that dogs gazed for longer if there were either more or fewer biscuits than they expected. The dogs may have been solving this task by actual counting or simple

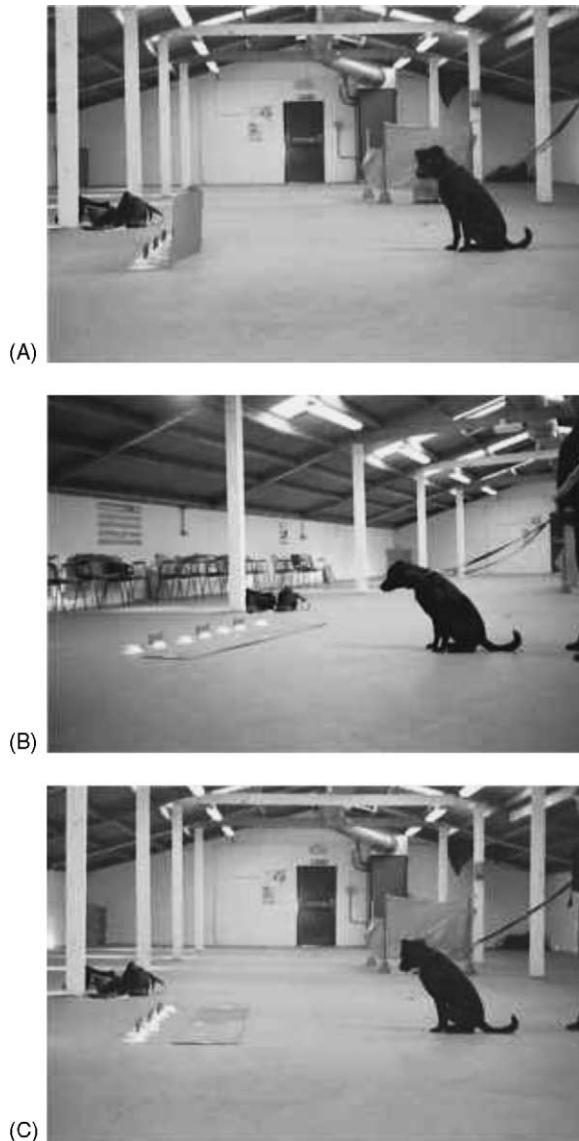


Fig. 1. Preferential gaze in the dog as used by [West and Young \(2002\)](#). (A) Three bone-shaped biscuits have been placed behind the screen. (B) The screen is removed and the time taken between screen removal and the dog's looking away (C) recorded. Photos courtesy of Rebecca West, De Montfort University.

arithmetic, though there is little evidence to support this conclusion from their overt behaviour. They did not, for example, appear to linger on each biscuit then move on. Alternatively, the results may be interpreted as a simple form of object permanence or delayed matching to sample, which at least shows a representation of object not in view, though not representing this as a number of objects. This interpretation may be fair except

Table 1
 Preferential looking times (s) for dogs in three tests

Bones	Control 1 (one bone)	Test 1 (two bones)	Control 2 (one bone)	Test 2 (one bone)	Control 3 (one bone)	Test 3 (three bones)
Dog						
1	5.69	5.28	6.72	8.19	5.12	6.72
2	5.53	6.69	6.84	8.15	5.29	6.88
3	4.62	5.03	3.38	4.50	–	–
4	4.97	3.76	4.14	4.56	–	–
5	6.60	7.96	6.62	9.41	–	–
6	6.24	6.68	5.12	5.94	–	–
7	5.03	4.48	5.34	5.61	–	–
8	4.73	5.26	5.41	6.75	–	–
9	11.03	11.63	9.38	15.59	9.57	13.07
10	5.25	4.52	4.38	5.59	4.25	4.79
11	9.71	11.75	9.57	11.94	8.81	11.4
Mean	6.31	6.64	6.08	7.84**	6.61	8.57*

In the first test ($n = 11$) two bones were placed behind screen and both remained when screen was removed ($1 + 1 = 2$). In the second test ($n = 11$) two bones were placed behind screen and only one remained when the screen was removed ($1 + 1 = 1$) and in the third test ($n = 5$) two bones were placed behind the screen but three were present when the screen was removed ($1 + 1 = 3$). Before each test there was a control where a single bone was placed behind the screen, which was still there when the screen was removed. Dogs gazed for longer when the number of bones differed from their “expectation”. Data from [West and Young \(2002\)](#).

* $P < 0.05$.

** $P < 0.001$.

that the dogs never actually saw the biscuits in their precise locations behind the screen, but rather the placing of the biscuits. Consequently, they would have had to transfer observed information involving movement to a position behind the screen to location information once the screen was removed, rather than actually having seen where the bones were placed. This transfer of information implies, at the very least, some concept of number of objects, though it would not be fair to infer anymore than simple subitising of number. It may therefore be that dogs only represent numbers of objects as “one”, “two”, and “lots”. Preferential looking technique may be extended to larger numbers, though in rhesus monkeys, the technique has only been used successfully up to four, which may represent a limitation on the animal’s numerical competence or a limitation of the technique ([Hauser, 2000](#)).

3.2. Mental state attribution

Other important tools for investigating cognitive processes are problem-solving paradigms involving the acquisition or expression of novel, behavioural responses. The aim of such paradigms is to be able to eliminate simpler or more parsimonious explanations of apparent problem-solving ability, which may be based on evolutionary rules of thumb, trial and error learning or prior experience. This positivist, scientific requirement to ascribe the most parsimonious explanation of observed events is just as important today as in the time

of Lloyd-Morgan and has recently been reviewed by, amongst others, Dawkins (1993) and Heyes (1994).

Such approaches can also be used to investigate object permanence in animals. One example is selective search behaviour for objects out of view (Gagnon and Dore, 1994) but a more interesting paradigm for investigating social cognition is based on perspective taking. An example of such a paradigm is the false believe task originally created by Wimmer and Perner (1983) and modified by Baron-Cohen et al. (1985), who called it the “Sally-Anne” task. In Wimmer and Perner’s original method two children see an experimenter place a toy in a location A. One child leaves the room and the experimenter moves the toy to another location B. The remaining child is asked to indicate where the absent child would look for the toy on their return. A child able to take the perspective of others would indicate location A, as they will realise that the other child has not seen the toy being moved. A child unable to take the perspective of others would indicate location B. As children age, they shift from consistently choosing the box in which the object is actually located to indicating the box in which the object was originally placed (Wimmer and Perner, 1983). Co-incidentally children with impaired social skills perform poorly on this task (Baron-Cohen et al., 1985; Pilowsky et al., 2000). This task, however, involves fairly sophisticated linguistic abilities, which may explain why younger children perform poorly. A non-verbal form of this location change task involving marking the locations has been developed by Call and Tomasello (1999) for use with pre-verbal humans and animals, which was successfully completed by most 5-year-old children, some 4-year olds, but not by orang-utans or chimpanzees.

An alternative approach to investigating perspective taking is the Knower:Guesser paradigm that has been developed by Povinelli and colleagues and originally involving chimpanzees (e.g. Povinelli et al., 1990, 1997; Povinelli and Eddy, 1996). In this paradigm, the ability to distinguish between an apparently knowledgeable social cue (the Knower) and an apparently ignorant social cue (the Guesser) is used to demonstrate that animals can see the world from the perspective of others. Povinelli’s group developed two methods to investigate this ability using non-human primates as test species and humans as the Knower and the Guesser.

3.2.1. *Choice of target when begging*

The first method is based on food soliciting (begging) from a human provider/helper (Povinelli and Eddy, 1996). The chimps are first trained to solicit food from a human provider, and then they are asked to discriminate between an apparently knowledgeable provider and an apparently unknowledgeable provider with, for example, a blindfold over their eyes. As a control for presence of blindfold alone, they are also offered choices between provider with blindfold over eyes and providers with blindfold over mouth or over hair. In this paradigm, three out of four chimpanzees consistently preferred to beg from the provider that could see, whereas no rhesus monkeys made this discrimination (Povinelli and Eddy, 1996). This approach has been adapted for dogs by our own group using a range of vision obstructers including blindfolds over eyes, buckets on heads and books obscuring eyes (Bishop and Young, *in press*). Overall, dogs preferred to solicit food from a human who could see the reward, or whose eyes the dog could clearly see (Table 2), though this finding was strongest when vision was obscured by a book (Friedmann test; $P < 0.01$).

Table 2

Number of times (out of 10) each dog begged from the “seeing” person in each experimental condition

Dog	Blind 1	Blind 2	Blind 3	Bucket	Hands	Book	Total (%)
A	7	8	8	6	6	8	43 (72)
B	5	7	8	7	5	9 ^a	41 (68)
C	7	7	9 ^a	8	8	10 ^a	49 (82)
D	8	7	6	6	5	5	37 (62)
E	8	8	7	7	8	8	46 (77)
F	7	6	7	7	5	9 ^a	41 (68)
G	6	5	2	5	4	7	29 (48)
H	4	5	4	7	7	8	35 (58)
I	5	8	8	9 ^a	7	10 ^a	47 (78)
J	7	4	6	7	6	8	38 (64)
Total	64	65	65	69	61	82	406 (68)

Blind 1: blindfold over eyes versus no blindfold; Blind 2: blindfold over eyes versus blindfold on forehead; Blind 3: blindfold over eyes versus blindfold on chin; Bucket: bucket on head versus bucket in hand; Hands: hands over eyes versus hands over ears; Book: book over eyes versus book in hand. Data from [Bishop and Young \(in press\)](#).

^a Preferences of 9 or 10 out of 10 are better than would be expected by chance from binomial distribution.

This finding suggests that, at least in this begging paradigm, prior experience may play a major role since the blindfold and bucket options were novel to the dogs, but they are likely to have had prior experience of people reading books and learned not to beg from people engaged in these activities.

3.2.2. Use of demonstrators

The second method used to investigate perspective taking is based on using human demonstrators as cues to locating hidden food ([Povinelli et al., 1990](#); [Heyes, 1993](#)). Chimps are first trained to use humans as indicators of the location of food, for example pointing at food that has been provisioned behind one of the number of screens. The chimps are then tested with two human indicators, one of whom knows the location of the food (saw where the food had been placed) and one who does not (e.g. was out of the experimental room when the food was placed or had a paper bag over his/her head). Again chimpanzees chose the locations indicated by Knowers in preference to locations indicated by Guessers. This study, therefore, suggests that the chimps were capable of taking the perspective of the demonstrators and acting sensibly on that information ([Povinelli et al., 1990](#)).

Whilst these experiments provide compelling evidence for perspective taking in non-human animals, the interpretation of the work has been criticised ([Heyes, 1993, 1994](#)). The specific criticism is that the chimps could have learnt to use the demonstrators as discriminatory cues without understanding the different states of knowledge of the demonstrators. The chimps could have made a simple association between the person in the room, their signal and the location of food, without actually appreciating that they are likely to be more knowledgeable about the test situation because they have actually seen what happened. Certainly, the chimps were tested often enough to have the opportunity to make these simple associations. Another problem is that there may also have been subtle

distinctions between the two demonstrators at the time of the discriminating task, e.g. the Knower pointed more confidently than the Guesser. The chimps may have used these subtle cues as the discriminator with no reflection on previous events.

A potential solution to this has been developed by Held et al. (2001a) using trained conspecifics as the demonstrators. Their chosen test species was the domestic pig (*Sus scrofa*). They first showed that pigs could use other pigs as information sources when locating food (Held et al., 2000). For example, a pig that had not seen the location of baiting would follow another pig that had seen the baiting to the correct location. Unfortunately, when they allowed pigs to choose between demonstrator pigs that had seen a food-baiting event and demonstrator pigs that had not, 12 out of 13 test pigs avoided both of the demonstrators' choices due to agonistic confrontations when two pigs went to the same food location (Held et al., 2001b). Only one pig consistently followed others and this pig did prefer to follow Knowers in 21 out of 24 trials, suggesting some appreciation of the difference in information held by the two informants.

Domestic dogs may provide an alternative model for investigating these perspective-taking paradigms: firstly, because they are relatively easy to train to locate rewards, and secondly, because they live so closely with people. Hidden food location protocols have been used to investigate a wide range of learning processes in dogs including spatial memory (Gagnon and Dore, 1992, 1994; Fiset et al., 2000) and the response to human (Hare et al., 1998; Miklosi et al., 1998; McKinley and Sambrook, 2000; Soproni et al., 2001; Pongracz et al., 2002) and conspecific social cues (Hare and Tomasello, 1999). Interestingly, in these experiments dogs appear to be better than chimpanzees at using social cues (such as pointing) to locate food (Povinelli et al., 1997, 1999; Tomasello et al., 1997). For example, Miklosi et al. (2000) found that dogs could use human signals such as pointing, orientation and even just glancing at a location to influence the target choice of dogs. They also took considerably less training than primates to learn these associations (Povinelli et al., 1999). Thus, social signals appear to be more powerful than non-social cues for domestic dogs.

Tests for the ability to use others as information sources, based on the methodologies developed by, e.g. Povinelli et al. (1990) and modified by Held et al. (2001a) have been attempted using dogs by our group (Ashton and Cooper, unpublished data; West, unpublished data). In the first of these studies, Ashton and Cooper trained nine dogs to locate food that had been placed behind one of the four screens. All dogs selected successfully learnt this task when they had seen the baiting of the target with a latency to reach food of approximately 7 s and a rate of 1 error or incorrect choice every 10 tests (0.1 errors per test). They were then "blinded" by placing a blanket over their start box (Fig. 2A). When "blinded", the dogs made more mistakes during food-locating tasks (1.5 errors per test) and took longer to locate food (an average latency of 15 s to reach baited target) than when they had seen the act of baiting. Next, "blind" dogs were allowed to use a dog that had seen the baiting as an information source. Under these circumstances "blind" dogs followed the "informed forager" to the baited target, such that they found the food faster (5 s) and with fewer mistakes (0.2 errors per test) than if they had been on their own. It was, however, not clear if they were using their conspecific as an information source or just following it, then responding to the food, when they came across it. This issue was not resolved in the Knower:Guesser paradigm, when blind test dogs were required to



Fig. 2. Knower:Guesser paradigm as used by Ashton and Cooper (unpublished data). (A) “Blind” dogs in covered start box were found to follow demonstrator dogs able to see the baiting of food targets behind screens. (B) Demonstrator dogs housed in either the covered or the uncovered side start boxes are trained to seek food in specific target locations behind screens and act as information sources to test dog in covered, central start box. Photo courtesy of Jonathan Cooper, University of Lincoln.

discriminate between a dog that had seen where food was provisioned and a dog that had not, even though both had been trained to fixed locations (Fig. 2B). In the test situation, dogs appeared to be more interested in positive social interaction than locating food as they always followed another dog, but did not discriminate between apparently informed and uninformed dogs. Species-specific limitations, such as avoidance in pigs and social interaction in dogs, may therefore limit the usefulness of this methodology when using groups of animals released into a test arena.

An alternative approach is to use human demonstrators as simple discriminative stimuli. We modified Povinelli et al.'s (1990) protocol using a larger sample of dogs for a small number of trials each, rather than repeatedly testing the same test individuals (West, unpublished data). The dogs had a choice of three baited target locations, and two human indicators. Each dog was present in the room when the targets were baited, but could not see the bait location itself. It could, however, see one human (the Knower) in a position where they would have been able to see where food had been placed. The second demonstrator (the Guesser) was outside the room when the location was baited but returned to the room in order to indicate a non-baited location prior to the dog being released. Fifteen dogs were tested six times, which represented one trial each of each demonstrator–target combination. No dog chose the target that was not indicated by either demonstrator. In the first trial of the six, they did discriminate between the two demonstrators with 14 dogs choosing the Knower's direction (Table 3; $P < 0.001$), but in subsequent trials there was no preference with dogs performing no better than what would be expected by chance ($P > 0.05$).

This experiment has two findings of particular note. First, the preference for the Knower in the first trial suggests that the dogs had transferred knowledge from previous situations

Table 3

Results of Knower:Guesser paradigm using humans as discriminative cues for 15 dogs (one of which only completed three trials)

ID	Test 1	Test 2	Test 3	Test 4	Test 5	Test 6	Total (K)
1	K	K	K	K	K	G	5
2	K	G	K	K	G	G	3
3	K	K	K	G	K	K	5
4	K	G	K	G	G	G	2
5	K	K	K	K	G	K	5
6	K	G	K	K	G	G	3
7	K	G	G	K	G	K	3
8	G	K	G	K	K	K	4
9	K	G	K	K	K	K	5
10	K	K	K	G	K	K	5
11	K	K	G	–	–	–	2
12	K	K	G	K	G	K	4
13	K	G	G	K	G	K	3
14	K	G	G	K	K	G	3
15	K	K	K	G	K	G	4
	14/15	8/15	9/15	10/14	7/14	8/14	56/90
Percent	93	53	60	71	50	57	64

Given a choice between a target indicated by the person who had remained in the room during baiting (K), a target indicated by a person who had not been in the room during baiting (G), or a target indicated by neither person (N), dogs always chose either K or G. In the first trial, dogs had a preference for the Knower's target ($P < 0.001$), but in subsequent trials no such preference was evident.

(e.g. the home) about the reliability of present and absent people as information sources. The high proportion of successful responses in the first trial also overcomes the criticism put forward by Heyes (1994) of Povinelli et al.'s (1990) work, that the animals may form a rapid association between the alternative cues and the rewards they indicate, such that the preferences may be explained as simple associative learning rather than explicit problem solving. The second interesting finding is that the dogs subsequently did not persist with using the perspective-taking rule. In fact, the population appeared to be following no consistent rule, although individuals may have used different rules. This points to the value of using novel tests when investigating cognitive functions in animals. Having successfully solved the food-locating task when the only discriminatory cue was the signal of the demonstrator, the dogs may fail subsequent tests as they are attempting to apply information they have learnt from previous trials. This may, for example, involve a return to a previously rewarded location, or the use of a previous demonstrator (in the experiment the demonstrator and location were controlled for in the experimental design). If dogs react to test situations in this way (i.e. "on first trial transfer information from other situations: in subsequent tests apply what you have learnt about the current test situation"), then this not only demonstrates the danger that repeated testing leads to simple conditioned responses (Heyes, 1994), but also suggests that higher cognitive abilities are most likely to be used in novel situations. If this is the case, then investigating these processes may be most practical in species with a large, readily accessible test population such as pet dogs.

4. Recommendations for studying social cognition in domestic dogs

In summary, the domestic dog appears to make a good model species for the investigation of cognitive processes, particularly those related to social function. Dogs may have inherited the capacity for certain social skills from their social living, co-operatively hunting ancestors. This may have been enhanced by artificial selection under domestication for co-operative skills or the tendency to form close social ties with humans. A number of methodologies may be adopted from studies of pre-verbal humans and apes to investigate the social skills in dogs. However, rather than simply taking methods off the shelf and substituting dogs, the species-specific behavioural repertoires need to be considered. There has been some success in investigating both dog's expectancies and their ability to transfer information between situations to solve new problems. Dogs give preference to social cues (other dogs and humans) over abstract non-social cues as information sources about reward location, and appear to have less difficulty than primates in using social cues for this purpose. Domestic dogs, however, only show the ability to distinguish between knowledgeable and unknowledgeable people (and not other dogs) when faced with a choice. Previous studies with dogs lead to the general recommendation that, where possible, single trial experiments should be used to investigate transfer of knowledge. This rules out the possibility of a conditioned response over successive trials, and animals may be more likely to use transfer of knowledge from another situation (i.e. thinking) when exposed to a new problem.

Acknowledgements

We would like to thank Melissa Albentosa for comments on this manuscript and Susanne Held, Mike Mendl and Adam Miklosi for discussions relating to this review and the development of methodologies for work with dogs. We also thank The Universities Federation for Animal Welfare for funding Clare Ashton's Vacation Scholarship, De Montfort University for supporting Rebecca West's graduate studies, Andrea Ferguson and Sue McKinley for help on experimental trials and Colin Riches and University of Lincoln Animal Care Unit staff for help with caring for dogs.

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