What did domestication do to dogs? A new account of dogs' sensitivity to human actions

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ABSTRACT

Over the last two decades increasing evidence for an acute sensitivity to human gestures and attentional states in domestic dogs has led to a burgeoning of research into the social cognition of this highly familiar yet previously under-studied animal. Dogs (*Canis lupus familiaris*) have been shown to be more successful than their closest relative (and wild progenitor) the wolf, and than man's closest relative, the chimpanzee, on tests of sensitivity to human social cues, such as following points to a container holding hidden food. The "Domestication Hypothesis" asserts that during domestication dogs evolved an inherent sensitivity to human gestures that their non-domesticated counterparts do not share. According to this view, sensitivity to human cues is present in dogs at an early age and shows little evidence of acquisition during ontogeny. A closer look at the findings of research on canine domestication, socialization, and conditioning, brings the assumptions of this hypothesis into question. We propose the Two Stage Hypothesis, according to which the sensitivity of an individual animal to human actions depends on acceptance of humans as social companions, and conditioning to follow human limbs. This offers a more parsimonious explanation for the domestic dog's sensitivity to human gestures, without requiring the use of additional mechanisms. We outline how tests of this new hypothesis open directions for future study that offer promise of a deeper understanding of mankind's oldest companion.

Key words: dog, *Canis lupus familiaris*, wolf, *Canis lupus*, domestication, canine evolution, object choice paradigm, social cognition, Two Stage Hypothesis, socialization, conditioning.

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I. INTRODUCTION

". . . we know that at the present day there is
hardly a tribe so barbarous, as not to have
domesticated at least the dog. . ." (Darwin,
1859, p.13)

The ubiquity of domestic dogs (*Canis lupus familiaris*) in
modern human society can scarcely be overstated. Nearly
forty percent of American households include pet dogs, giving
a total of over 70 million dogs in human homes in the USA
alone (American Pet Products Manufactures Association,
2007; American Veterinary Medicine Association, 2007).
Seldom does a resident of the developed world pass a day
without seeing a dog. The tolerance of dogs by humans is
largely, perhaps entirely, due to their behaviour. Dogs are
very sensitive to human actions. Over the last decade, a
series of studies has investigated dog sensitivity to human
body language and attentional state (see Udell & Wynne,
2008, for a review). These reports have demonstrated that
dogs can use human gestures such as pointing, head turning,
gazing and nodding to locate hidden food items (e.g. Miklósi
et al., 1998; Udell, Giglio & Wynne, 2008*b*). Dogs generally
excel on human-guided tasks and respond to human gestures
and social cues much like a human child, while chimpanzees
(*Pan troglodytes)*, human's closest genetic relatives, are much
less sensitive to these kinds of cues (Brauer *et al.*, 2006; Hare
& Tomasello, 2005).

Aside from their current ubiquity in human societies,
domestic dogs are particularly interesting for the assessment
of the influence of domestication on cognition and behaviour
for at least two reasons. First, unlike many other domesticated
populations, the wild progenitor of the domestic dog, the
wolf (*Canis lupus lupus*), is available for study. Second, another
canid, the silver fox (*Vulpes vulpes*) has undergone experimental
domestication in recent years, providing detailed information
on the process and outcome of domestication in canids (Trut,
1999). These conditions have provided an opportunity to test
the effects of genetic inheritance, while controlling for life
experiences, between domesticated and non-domesticated
groups of canids.

Several authors have proposed that the behavioural adap-
tations that make dogs a good fit for the human environment
are a direct consequence of genetic changes that occur
during domestication, independent of environment or life
experience (e.g., Hare & Tomasello, 2005; Miklósi, Topál &
Csányi, 2007). We term this the "Domestication Hypothe-
sis." This hypothesis attributes the domestic dog's sensitivity
to human social cues, and the resulting social behaviour, to
an advanced human-like social cognition selected for during

domestication (Hare *et al.*, 2002; Hare & Tomasello, 2005;
Miklósi *et al.*, 2003). Domestication is a phylogenetic process
of natural and artificial selection, the outcome of which is a
species fitted to human needs (Zeder, 2006). These authors
argue that canine domestication has resulted in an animal
that displays a level of human-compatible social and cognitive
sophistication unknown in any other nonhuman animal.

We do not doubt that domestication influences behaviour,
and that dogs are highly successful in human environments.
We will argue, however, that phylogeny alone is not sufficient
to account for the human-compatible behaviours of domestic
dogs. We discuss the mounting empirical evidence that
(1) domestication alone is neither necessary nor sufficient
to predict an individual's performance on human-guided
tasks (2) that wolves possess the necessary biological and
cognitive prerequisites for responsiveness to human gestures,
(3) that previous comparisons between domesticated and
non-domesticated species have failed to account for crucial
differences in development stages, and (4) that an individual's
experiences and environment throughout development serve
as important predictors of future social responsiveness. This
has led us to propose the Two Stage Hypothesis, which
states that dogs' ability to follow human actions stems from a
willingness to accept humans as social companions, acquired
in early ontogeny, combined with conditioning to follow
the limbs and actions of humans to acquire reinforcement.
Our hypothesis takes both phylogeny and various aspects of
ontogeny into account. Furthermore, it proposes criteria for
successful interaction with humans which can be applied to
canids and noncanids alike and to domesticated and non-
domesticated species. Before outlining the details of this new
hypothesis, we define what is meant by the domestic dogs'
sensitivity to human cues and provide examples of common
tests for human-like social cognition. We then review what is
known about canine domestication in order to contextualize
the competing theories, and discuss the assumptions of the
Domestication Hypothesis and the evidence in favour of
an alternative hypothesis. We conclude with suggestions for
how terminology, methodology, and data collection might
be reformed and propose future directions for research on
social cognition.

II. SENSITIVITY TO HUMAN SOCIAL CUES

Domestic dogs possess a sensitivity to human cues that allows
them to succeed on a variety of tasks involving human-given
stimuli. To remain consistent with previous literature, the
term 'sensitivity' will continue to be used here to describe

an animal's responsiveness to a stimulus; however it will be defined strictly in terms of specified behaviours in the presence of available stimuli. While we recognize this is a limited definition of the term and that an animal might be more generally sensitive to a stimulus while failing to respond overtly in a specified way, it is the only definition that can be addressed fully by the empirical data to be discussed in this paper. Thus dogs are said to be sensitive to a human social stimulus when they reliably alter their behaviour in the presence of such stimuli to obtain reinforcement that depends on the instruction or mediation of a human companion – a behaviour that likely contributes to the domestic dog's success in human environments (see Udell & Wynne, 2008). Here we briefly describe four categories of human cue use by dogs: behaving with regard to attentional state; word learning; social learning and imitation; and point following (for a more complete review see Udell & Wynne, 2008). These four categories of research provide evidence for the domestic dog's sensitivity to human cues.

(1) Theory of mind: behaving with regard to attentional state

Although the term 'theory of mind' is itself controversial (Heyes, 1998) many of the studies investigating theory of mind in non-human primates have been replicated with dogs. theory of mind has been defined in different ways, but Heyes' (1998) definition seems most appropriate here: "...an animal with a theory of mind believes that mental states play a causal role in generating behaviour and infers the presence of mental states in others by observing their appearance and behaviour under various circumstances" (p. 102). Without entering into the controversies surrounding the use of the term at this point, several studies indicate that dogs modify their behaviour with regard to the attentional state of humans. Dogs selectively avoid food that they have been forbidden to eat when their owner is watching them, but if their owner is not looking, or has an obstructed view, most dogs readily eat the forbidden food (Brauer, Call & Tomasello, 2004; Call *et al.*, 2003). Dogs preferentially beg from an individual that can see them as opposed to an individual with an obstructed view. This has been shown when the dog is given a choice between a seeing person and someone with her back turned, her eyes covered by a blindfold, or holding a book in front of her eyes (Cooper *et al.*, 2003; Gácsi *et al.*, 2004).

(2) Word learning

In a study by Kaminski, Call & Fischer (2004) a border collie known as Rico was not only credited with the ability to retrieve over 200 different items by vocal command, but was able to retrieve a novel item from a group of familiar items in response to an unfamiliar item name in 70% of trials. It was suggested that this could be an example of "fast mapping" in dogs, implying that Rico might be learning the names of items *via* exclusion learning much like a human child would. Although the lack of evidence

of a net increase in Rico's vocabulary renders these claims inconclusive, Rico's performance nonetheless offers a strong example of the potential of dogs to learn and respond to human-given stimuli in the auditory realm.

(3) Social learning and imitation

Several studies have found indications that dogs can learn by observing humans. For example, dogs that were shown by a human demonstrator which way to walk around a V-shaped fence to obtain either a toy or food were more likely to take the same path than dogs that were shown the location of the desired object but did not watch a demonstrator (Pongracz *et al.*, 2001).

Rooney & Bradshaw (2006) conducted two experiments to examine what dogs learn from watching human-dog interactions. In the first experiment an observer dog watched a human and a conspecific play tug of war. Dogs experienced one of three conditions: control, human-win or dog-win. In both the competitive conditions, the observer dog saw the human display play signals (e.g. play bow, shuffling of the feet and lunging) in addition to watching the outcome of the interaction. In the control condition, the human sat in a chair and stroked the demonstrator dog. The authors found that the observers were more likely to approach the winner of the game and did so sooner than in the control condition.

In a second experiment, in which the observer watched a combination of winning *versus* losing and signaling *versus* not signaling in a procedure similar to the first experiment, the authors found that observers approached the winners more rapidly when play signals had been given than if play signals had not been observed. The authors concluded that the observer dogs gained information from witnessing the outcome of the game and the context in which it was observed.

Topál *et al.* (2006) investigated whether a dog could show imitative behaviour by matching the actions of a human demonstrator. Two classes of actions were used: body-orientated actions (e.g. spinning in a circle) and manipulative actions (e.g. picking up a shoe and dropping it off at a given area). In this study the dog was first trained to perform a small set of actions on the verbal command "Do it." Once the subject was performing these trained behaviours at high levels, the dog was tested on its ability to imitate novel human-demonstrated actions. Topál *et al.* (2006) found that the dog reproduced both kinds of actions correctly on over 70% of trials.

(4) Following points

Perhaps the simplest example of human cue use is the ability to follow a human point to one of two locations. In an object-choice task one of two containers is chosen as a target. This target either serves as a hiding place for a piece of food or functions as a platform where a piece of food is placed upon the dog's approach. A trial begins when the dog observes a human experimenter pointing in the direction of the target container. When the dog is released

it can choose to approach either container, but only by approaching the container indicated by the human's point will the dog receive the hidden item. Although many forms of traditional pointing, using one's outstretched arm and hand, have been used as the stimuli in object-choice paradigms (Hare & Tomasello, 1999; Miklósi *et al.* 1998; Soproni *et al.*, 2001, 2002; Udell *et al.*, 2008*b*), many types of gestures can and have been used to assess the domestic dog's sensitivity to human cues, including head turning, nodding, bowing, and glancing in the direction of the target container (e.g. Miklósi *et al.*, 1998; Soproni *et al.*, 2001; Udell *et al.*, 2008*b*). These studies demonstrate that dogs can use a wide variety of human-given cues to identify a target container at above chance levels, challenging scientists to identify the factors that make such a wide range of human stimuli salient to dogs.

Point-following is often one of the first tests of sensitivity to human cues conducted with individuals in a species or population. As a result, the largest range of canid species and populations can be compared when looking at their performance on object-choice tasks requiring the use of a human point. Therefore the remainder of this paper will focus on research that uses human point-following as an indicator of sensitivity to human cues. We do not assume that point-following in the context of an object-choice task is a perfect indicator of an individual's success on other tasks requiring the use of human cues, nor do we suggest that an individual's success in following a specific topography of human point necessarily predicts its success in following other human gestures or alternative modes of communication, e.g. verbal cues. Nonetheless, comparing the performance of dogs, wolves, and foxes on a single task provides an opportunity to discuss the potential contributions of domestication, development, environment, and experience across species and populations in a structured way. We will specifically address the factors that we believe contribute to an individual's ability to respond to specific stimuli, clarifying the importance of distinctions between categories and specific stimulus topographies. Future directions for more complete comparisons among individuals, species, and populations will also be suggested.

III. THE DOMESTICATION OF DOGS

Domestication involves both natural and artificial selection. Natural selection may act to develop individuals that are more tolerant of humans so that they can exploit human domiciles as food sources. Artificial selection can lead to animals with traits explicitly desired by humans. Domestication must be distinguished from ontogenetic processes such as taming or training that also take place in individual members of species (not just domesticated ones) living with humans. Though the most common cases are tame domesticated animals and non-tame wild animals, individuals may also be genetically domesticated yet wild (such animals are often termed 'feral', indicating their lack of socialization to humans from an early age), or wild-type (not genetically domesticated) yet tame.

Feral or un-tamed individuals make up 75% of the domestic dog's world population (Stafford, 2007). Unlike pets these dogs exist on the fringes of human society as scavengers; they are typically unresponsive to humans and often react to human attention with fear or aggression (Coppinger & Coppinger, 2001). Tame wild animals are tolerant of human approach and may be responsive to human actions. Such individuals may be found in zoos and other wildlife establishments, especially if reared by human caretakers from close to birth. Although approximate categories of this type simplify discussion and thus will continue to be used here, it is important to note that these descriptors are not all or none qualities but instead exist on interacting continua. Individual animals may be better classified according to their location on the interacting dimensions of genetic domestication and developmental experiences. This will be discussed in more detail in the following section where a third dimension- time of initial socialization- will also come into play.

Genomic and morphological evidence suggests that the canids that became dogs may have started differentiating themselves from wolves as long as 100 thousand years before the present day (kyr bp: Vila *et al.*, 1997). However, dogs are absent from Franco-Cantabric cave art before 16 kyr bp (Delporte, 1990). The earliest archaeological evidence of dogs as human companions, in the form of a co-burial of humans with a dog, dates from 14 kyr bp (Nobis, 1979). Images of dogs begin to appear around the world on the order of 10 kyr bp (Brewer, Clark & Phillips, 2001). By Roman times, Pliny the Elder (AD 23–79) recognized several different breeds – or at least broad classes – of dogs. Modern breeds only became closed populations in the late nineteenth century (Ritvo, 1987), and genetic analysis indicates that most modern breeds of dogs remain closely related (Vila *et al.*, 1997; Wayne & Ostrander, 2007).

It seems likely that as humans entered a more sessile agricultural lifestyle, wolves began to scavenge for food from them, which led to changes in wolf morphology and behaviour (Coppinger & Coppinger, 2001; Morey, 1994). Traits such as reduced fear and aggression in the presence of humans led to higher fitness in these animals by enabling them to exploit an additional source of food. At some stage, dogs moved from just scavenging on the fringes of human settlements to become more integrated into human societies. Although human action may have played only a small role in the early stages, at some point humans began actively controlling dog mating in order to establish desirable traits (Dobney & Larson, 2006). In the United States today around half of all dog matings are arranged by humans (New *et al.*, 2004).

(1) The ontogeny of social behaviour in canids

Domestication in canids is accompanied by characteristic physical and behavioural changes. In fact, all domesticated mammals share traits such as dwarf and giant varieties, piebald coat colour, and changes in reproductive cycles (Dobney & Larson, 2006; Trut, 1999). Some domesticated species also display curly hair, shortened tails, and floppy ears

(Dobney & Larson, 2006; Trut, 1999). Many of these changes build on one another to alter the behavioural repertoire and the sensory experiences of the developing domesticated individual (Dobney & Larson, 2006). Still other behavioural changes may have broadly accompanied domestication across species, from plasticity in behavioural development to a reduced responsiveness to environmental change, including reduced reactivity in the presence of humans or dominant conspecifics (see Price, 1984 for a review). However the range of traits that domesticated animals share and the mechanism(s) that underlie such physical and behavioural characteristics are a continuing topic of study. We have chosen to limit our current focus to domestic dogs and to several relevant non-domesticated canids.

In dogs, domestication has led to breeds that exhibit an underdevelopment of traits important in the communication and social behaviour of the wolf. In some cases these changes are the result of paedomorphosis – the retention into adulthood of juvenile traits (Goodwin, Bradshaw & Wickens, 1997). Different breeds of domestic dog have been shown to display varying degrees of paedomorphosis, resulting in breeds that differ in the age at which developmental milestones are met (Scott & Fuller, 1965) and in the physical and behavioural traits present in adulthood (Goodwin *et al.*, 1997).

As might be expected, social behaviour, con- and inter-specific, can be greatly affected by many of these developmental factors. One of the most obvious consequences of selective breeding in dogs is the altered appearance, and in some cases complete absence, of many physical traits used in social signaling by adult wolves, especially traits relating to the muzzle, ears, coat, eyes, and tail. This in turn has altered the communicative behaviour available to domestic dogs in social situations. For example dogs with floppy ears, such as basset hounds, have a limited range of ear motion in comparison to breeds with naturally upright ears. Some breeds, such as poodles, have curly coats that stay rigidly in place independent of level of arousal. Both the flexible positioning of a dog's ears and the ability to raise its neck fur or hackles contribute to a system of signaling used to indicate fear and aggression (Coppinger & Coppinger, 2001).

Goodwin *et al.* (1997) found that individuals from breeds of dog that were more distant in physical appearance from adult wolves, for example cavaliers and bulldogs, had very different agonistic behaviour patterns, especially with regard to visual signaling, than individuals from breeds possessing many lupine, or wolf-like, traits, such as huskies. In fact, breeds most physically distinct from adult wolves display agonistic signals at a lower rate, resulting in a behavioural repertoire that is more similar to that of wolf pups (Goodwin *et al.*, 1997). This study also demonstrated another interesting effect of domestication. Some highly domesticated breeds that were physically capable of displaying wolf-type signals, such as golden retrievers, signaled extensively during play; however signals that would precede aggression in adult wolves did not appropriately signal escalated aggression in these golden retrievers. According to Goodwin *et al.* (1997),

this maintenance of juvenile play behaviour in adulthood demonstrates a reduced need for adult-type signaling. In other words, the full development of the domestic dog's signaling repertoire may have become less important when provisioning by humans reduced the risk or cost associated with injury and competition for resources with conspecifics. Thus, slowed or stunted development can influence social behaviour in several ways.

Frank & Frank (1982) studied the social development and problem-solving behaviour of wolf and dog pups. Malamutes served as the domesticated comparison to wolf pups because they are similar in size and morphology to wolves. Notwithstanding their similar adult body forms, Frank & Frank (1982) noted that Malamute puppies were extremely fetalized in comparison to wolf pups of the same age. The wolf pups were developmentally ahead of the dog pups at several milestones. Wolf pups could climb over their 45 cm pen at 19 days, while at 32 days Malamute pups were not yet able to climb over their 15 cm barrier. Furthermore, at six weeks of age wolf pups had much better motor performance than their Malamute counterparts who struggled to take three to four steps at a time. Although the wolves continued to be more active throughout the rearing process, Malamutes did catch up with wolves in their ability to navigate their surroundings by 10–12 weeks of age. However, even in adulthood, other differences remained. The Malamutes were much more likely to initiate social interaction with humans throughout development, despite the fact that the level and appearance of complex social interactions with conspecifics appeared fragmented or incomplete in Malamutes compared to wolves.

As Frank *et al.* (1989) pointed out, the conclusions that can be drawn from Frank & Frank (1982) are limited by the fact that both the Malamute and wolf pups were reared by a wolf foster mother. This is supported by Klinghammer & Goodmann's (1987) observation that, for effective socialization with humans, wolves must be removed from their mother between 10 and 14 days of age and raised with a 24 hour human caregiver until three to four months of age. Removal of a wolf pup from its mother after 21 days of age is significantly less likely to lead to a wolf adequately socialized to human presence (Klinghammer & Goodmann, 1987).

Notwithstanding this limitation of Frank & Frank (1982), it is clear that complex social behaviour was observed earlier in the wolf pups than in the Malamutes, and the sensitive period for socialization also ended earlier in wolves than in domestic dogs. In comparison to wolves, dogs only begin socialization once they can walk, which on average occurs around three weeks of age, and they continue to form primary social relationships until at least 12 weeks of age (Scott & Fuller, 1965), and potentially up to 16 weeks of age for some breeds (Coppinger & Coppinger, 2001). These relationships can be formed not only with conspecifics, but also with other species, including humans, if the appropriate level of exposure occurs. Scott & Fuller (1965) define this time window as the critical or sensitive period for socialization.

Even for domesticated animals socialization is indeed critical to the formation of social bonds. Scott & Fuller (1965) demonstrated that domesticated dog puppies raised entirely apart from humans "may later react toward them [humans] with extreme fear and hostility" (p. 176). In fact for dogs in some working domains, such as sheep-guarding dogs, a strong human-dog bond is undesirable and is minimized by socializing the dogs to sheep, instead of humans, from a young age. Dogs properly raised in this manner will choose to stay with the flock and interact with sheep instead of initiating contact with an approaching human or even another dog (Lorenz & Coppinger, 1986).

For wolves this critical period for socialization begins earlier and is shorter than in dogs, making it important to begin intense interspecies socialization before two to three weeks of age (Klinghammer & Goodman, 1987). In other words, the slower development of domestic dogs allows for an extension of the sensitive period for socialization, increasing the probability that domesticated individuals will form social bonds with humans in comparison to their non-domesticated counterparts. Furthermore, the slower development of motor skills, noted by Frank & Frank (1982), might force domesticated pups born in human homes to remain in close proximity to humans during the first few weeks of life when wolf pups are already leaving their pen and exploring other aspects of their environment. Indeed, when a more intensive hand-rearing socialization procedure was put into place with a new litter of wolf pups, Frank, Hasselbach & Littleton (1986) found that these wolves had a substantially improved level of responsiveness towards humans. Not only did they show reduced fear in the presence of humans, but social interaction with humans could be used as reinforcement. Instead of the elaborate luring and trapping procedures required to pen the wolves in their first litter, the new litter of highly socialized wolves simply had to be called by name. Frank *et al.* (1986) noted "Insofar as socialization to humans might involve sensitization to human behavioral cues, therefore, the incompletely socialized wolf pups may have been operating at a comparative disadvantage in the training situation, much like a nearsighted child trying to learn to read" (p. 35).

(2) Artificial domestication of foxes: the farm fox experiment

A research project initiated by Dimitri Belyaev in the late 1950s and extending over more than forty years, investigated the effects of artificial selection on silver foxes. In each new generation of foxes, individuals were rated on their behavioural response to humans during a series of tests. This included measuring a fox's reaction to a human approaching its cage, having a human hand in its cage, and its willingness to eat from a human hand. Foxes achieving high scores on the full battery of tests were placed into the Class I or "tame" group and were used to breed later generations of "tame" individuals. The selection pressure for this group was intense, with only 3% of males and 8–10% of females serving as parents for the next generation of pups. It is

important to note that the foxes were only briefly tested for their reaction to humans: they were *not* raised in continuous human contact as in a human household. This project raises three important points about the influence of domestication on morphological and behavioural neotenization in a canid (Trut, Plyusnina & Oskina, 2004).

The first interesting conclusion from this study is that the process of artificial selection can lead to surprisingly rapid effects on behaviour and morphology in a proportion of individuals. By the sixth generation of selection, four out of 213 individuals in the Class I group were classified as the first of the "domestication elite,"–a group of foxes that did not form aggressive-fearful reactions to humans after repeated physical contact (Trut *et al.*, 2004). By the eighth generation, morphological changes were first observed. While this shows that changes attributed to domestication can sometimes be seen in the phenotype of some individuals quite early in the selection process, it was not until the 30th generation that almost half of the pups could be classified as "domestication elite." Even after 42 generations, 30% of the offspring still did not meet the criteria for the "domestication elite" distinction. Therefore even under extreme selection pressures variability exists among individuals and in the number of generations it takes to reach the specific behavioural criteria for domestication.

The second important point is that physical traits that were not selected for, such as floppy ears, rolled tails and splotchy coats, began to appear in the population by the eighth generation. By the 15th generation some individuals had shorter tails and legs (Trut, 1999). Thus selecting for one aspect of behaviour, "tameness," led to the appearance of a whole package of related physical traits and behaviours typically attributed to domestication.

Finally, this study is most important for the light it sheds on the mechanism responsible for the expression of the "tame" behavioural qualities and unintended physical byproducts seen in the selected group. According to Trut (1999), selection for the phenotype "tameness" resulted in changes in several important ontogenetic processes, which, among other things, influenced neurohormonal and neurochemical mechanisms. In turn, these experimentally domesticated foxes retained physical traits characteristic of fox pups into adulthood and were slower to develop adult behavioural repertoires. For example, researchers observed a substantial delay in the age at which domesticated foxes experienced the initial surge of plasma corticosteroids levels that mark the onset of fear responses in a maturing fox. This in turn shifted and extended the sensitive period of social development in domesticated foxes, relative to that of undomesticated foxes (Trut, 1999).

As in wolves, the sensitive period for social development of non-domesticated foxes is short, ending before 45 days (Trut *et al.*, 2004). At this time the onset of fear and avoidance responses reduces exploratory behaviour and the acceptance of novel stimuli becomes more difficult (Trut *et al.*, 2004). By generations 28–30 the socialization window of the experimentally domesticated foxes had increased to 12 weeks of age and often longer for individual pups, making

their timeline of social development more similar to that of domestic dogs (Trut *et al.*, 2004). As a result, domesticated fox pups were more likely to score high on initial tests requiring a reduced fear of humans because they were open to social exploration for several weeks longer than their non-domesticated counterparts. This would also have allowed them more time to bond with humans during their sensitive period for social development, thus extending their tame behaviour into adulthood.

IV. THE DOMESTICATION HYPOTHESIS

Several researchers have proposed that domestication is the sufficient cause of a canid's sensitivity to human social behaviour. Hare & Tomasello (2005) suggested that during domestication, humans and domestic dogs experienced convergent evolution of advanced social cognition in response to similar social selection pressures. This view, the Domestication Hypothesis, predicts "both that dogs should be more skillful than wolves [on human guided tasks] and that variations in experience with humans should not affect the performance of either species [in using human social cues]" (Hare *et al.*, 2002, p. 1634). Thus a dog's sensitivity to human cues, for example the ability to follow a human point to a target location, is solely due to heredity (genetic domestication), with a greatly restricted role for ontogeny in these behaviours.

To test these predictions, Hare *et al.* (2002) compared the performance of seven adult wolves and seven adult dogs on an object-choice task in which the subject had to find a hidden piece of food in one of two containers. The dogs and wolves were exposed to four forms of human pointing. The conditions were: nothing (control condition); a human tapping and looking at the correct container; a human pointing and gazing at the correct container; a human pointing at the correct container but looking forward. Hare *et al.* (2002) found that dogs as a group succeeded in all experimental conditions, whereas the wolves as a group only succeeded in the point and gaze condition. Individually all dogs were successful in finding the food at above chance levels using at least one cue, whereas no individual wolf was above chance on any cue.

Other researchers have also found differences in performance between wolves and dogs on tasks requiring the use of human cues (Miklósi *et al.*, 2003; Kubinyi, Virányi & Miklósi, 2007; Virányi *et al.*, 2008). These studies have also used forms of human pointing and found that dogs outperform wolves on these tasks, though they also reported that socialized wolves can succeed on simpler human-guided object-choice tasks. They demonstrated that wolves raised with humans are capable of following a simple form of human point in which the hand comes into contact with the pointed-to object (Miklósi *et al.*, 2003; Virányi *et al.*, 2008). Nevertheless, consistent with Hare *et al.* (2002) and Hare & Tomasello (2005), they found that human-socialized wolves failed on a more difficult form of pointing, the momentary

distal point, in which the human's hand stays at least 50 cm back from the object pointed to, and returns to the human's midline before the wolf is released to make its choice.

Hare *et al.* (2005) compared the behaviour of experimentally domesticated foxes from the farm fox experiment described above with that of wild-type foxes and with domestic dogs on an object-choice task using a simpler form of human point accompanied by gazing. All subjects were between two and four months of age at the time of testing. It was not reported that any of the foxes had been intensely socialized, although all foxes likely had some previous experience with researchers and caretakers at the facility (see Trut *et al.*, 2004). As Hare *et al.* (2005) predicted, experimentally domesticated foxes were as successful as domesticated dogs on this task, implying a dog-like sensitivity to human gestures. Non-domesticated foxes did perform above chance on the point and gaze task, but their levels of success were significantly lower than those of dog pups and domesticated fox kits of the same age, even after additional social experience with the experimenter that was intended to reduce the foxes' fear of a novel person (Hare *et al.*, 2005).

A recent paper further argued that ontogeny plays no role whatever in the development of a domestic dog's sensitivity to human social cues (Riedel *et al.*, 2008). They compared the performance of puppies in four age groups from six to 24 weeks on object-choice tasks in which a human pointed at a food-bearing container in one of three ways. The experimenter either pointed across her body at the correct container, gave the same cue but repeated it four times before the dog's release, placed a marker on top of the correct container, or did nothing at all. Riedel *et al.* (2008) reported that the six-week-old puppies were successful on all human-guided choice tasks, and that the puppies did not improve in their performance over testing trials or with age. They concluded that, ". . .dogs' ability to follow human communicative cues is a skill present in dogs before exposure to humans can have ontogenetically major influences on dogs' behaviour. . .this is strong evidence that human exposure has no major effect on dogs' ability to use human-given communicative cues and that this skill therefore represents a special adaptation in dogs which is present from early [sic] age" (Riedel *et al.*, 2008, p.10). This claim that domestication resulted in the selection of genes directly responsible for human-like social behaviours and sensitivity in the dog, without regard to ontogeny or experience, can been seen as the most extreme form of the Domestication Hypothesis.

Other proponents of the Domestication Hypothesis have suggested that the primary difference between domestic dogs and wolves lies in the ability of each species to accept humans as social companions. Gácsi *et al.* (2005) compared the social behaviour of hand-reared dog and wolf pups from three to five weeks of age on a series of tasks requiring the subjects to choose between their human caregiver and either: (*a*) a nursing bottle, (*b*) an unfamiliar adult dog, (*c*) an unfamiliar experimenter, or (*d*) a familiar conspecific pup. Dogs and wolves did not differ in their preference for a

human caregiver in any test occurring between three and four weeks of age, nor in their overall preference for the caregiver across all three age groups. Five-week-old dog and wolf pups were said to differ, however, in their preference for the alternative individual in conditions with an unfamiliar adult dog (*b*) and an unfamiliar experimenter (*c*). Dog pups at this age spent more time with the unfamiliar experimenter in condition (*c*) than with the adult dog in condition (*b*). Wolf pups showed the opposite trend.

Topál *et al.* (2005) tested these same hand-reared wolf and dog pups again at four months on a canine version of the Strange Situation Test (for original methods see Ainsworth *et al.*, 1978), to determine their level of attachment to their human caregivers. Wolves spent significantly more time in contact with a human partner than the comparison group of hand-reared dog pups. Furthermore, both hand-reared wolf pups and hand-reared dog pups preferred physical contact with a stranger than with their owner, whereas mother-reared pet dog pups did not differentiate between the two individuals.

Topál *et al.* (2005) place considerable weight on their finding that pet and hand-reared dogs were more likely to greet their owner or caregiver in departure and arrival situations, while wolves did not discriminate between familiar and unfamiliar humans in these contexts. Based on this difference, they concluded that ''the comparative analysis of the subjects' behavior towards human participants in the experimental situation shows that, even after extensive socialization, wolves do not show patterns of attachment to humans comparable to those observed in pet dogs of different rearing conditions.'' We will take a closer look at the support for these conclusions in Section V.2.

V. THE ROOT OF SOCIAL DIFFERENCES: RETHINKING THE ROLE OF DOMESTICATION

(1) Developmental windows

In understanding cognitive and behavioural development, an important distinction must be made between chronological age and developmental stage. This is particularly relevant when looking at adult behaviours that are affected by social development. Much of the research on social interactions between humans and domesticated *versus* non-domesticated canids has stressed age consistency without regard for stage of cognitive development (Hare *et al.*, 2002; Miklósi *et al.*, 2003; Hare *et al.*, 2005; Kubinyi *et al.*, 2007; Virányi *et al.*, 2008). This emphasis on chronological age introduces a confound due to differences in the timing of developmental stages in each species.

The farm fox experiment elucidates the need for this concern. Because of changes in the rates of behavioural development in experimentally domesticated foxes, Trut *et al.* (2004) found that the sensitive period for effective social adaptation of domesticated individuals increased in comparison to individuals in the non-domesticated control group. Thus even if tested on the same social task at the same age, a domesticated fox would have a very different behavioural response to novel social stimuli than a non-domesticated individual, because each would be in a different stage of social development at the time of testing. As previously noted, Hare *et al.*'s (2005a) subjects, both dog and fox pups, were tested between two and four months of age. Trut *et al.* (2004) identified the sensitive period of social development for non-domesticated foxes as ending on average at around 45 days (i.e.1.5 months), and the sensitive period for domesticated foxes as extending past three months of age. Thus Hare *et al.* (2005) tested one group of foxes (the experimentally domesticated group) while they were still within their social developmental period, and the other group (undomesticated) when they were already well beyond their sensitive period of social development – even though the two groups of foxes were tested at the same chronological age. As a result, the behavioural differences Hare *et al.* (2005) noted may have been a byproduct of their choice of testing age for the two groups, which fortuitously led to the testing of the domesticated and undomesticated groups at critically different stages in their social development.

This could explain why the domesticated foxes were more likely to use a human stimulus to find hidden food than were the non-domesticated foxes. No assumption of differences in advanced social cognition due to breeding for domestication would be necessary. Furthermore, this alternative explanation would also account for the better performance of the domestic dog pups on the same task. They were also still within their sensitive period of socialization during testing. Because individuals still in their sensitive period of socialization require less experience to produce a greater effect on their behaviour (Scott & Fuller, 1965), any interaction with humans during this time would rapidly increase their receptiveness to human stimuli. However, for individuals past their sensitive period, even intense socialization and experience with unfamiliar stimuli and people may not lead to equivalent levels of success (Klinghammer & Goodman, 1987). Because the sensitive period for domesticated individuals is longer, even if both groups had experienced the same amount of exposure to humans in the months prior to testing, the domesticated individuals would always have had more experience with humans during their sensitive period than would non-domesticated individuals during this same chronological time frame.

(2) Proximity to humans

Tests of the Domestication Hypothesis have often failed to recognize that domestication correlates with proximity to humans. In fact the very definition of domestication requires a special relationship between humans and the target plant or animal population (Zeder, 2006). Thus studies demonstrating that domesticated animals are sensitive to human cues cannot be used as evidence that this sensitivity is a direct genetic byproduct of domestication unless they also demonstrate

that each species' wild counterpart does not show this same sensitivity under equivalent environmental conditions.

Unfortunately, much of the literature testing the Domestication Hypothesis demonstrates that a variety of domesticated species can use human cues to solve object-choice tasks (see Miklósi & Soproni, 2006, for a review), with no attempt to test their non-domesticated counterparts. For example, pet domestic cats (Miklósi *et al.*, 2005), domesticated goats (Kaminski *et al.*, 2005) and domesticated horses (Maros, Gácsi & Miklósi, 2008; McKinley & Sambrook, 2000) have all displayed varying levels of success on object-choice tasks requiring the use of a human point. If, as we propose, experiences during ontogeny are indeed critical, domesticated animals, because they typically live in closer proximity to humans, also have more opportunities to learn the reinforcement implications of stimuli offered by humans, a point which will be discussed further in Section V.3. This need not have any direct relationship to the genetic byproducts of domestication. In fact the current evidence shows little consistency in the levels of performance of the domesticated species tested. Instead pet populations of cats and dogs appear to share a higher level of success on human-guided tasks than domesticated animals living in shelters (Udell, Doery & Wynne, 2008*a*), zoos (Kaminski *et al.*, 2005), or boarding stables (McKinley & Sambrook, 2000) – living conditions that typically result in less frequent human contact.

For most domesticated species, the appropriate comparison species are not available, making the contribution from the canid literature especially valuable. It cannot be assumed, however, that the same phylogenetic and ontogenetic changes that led to human-responsive canids will be identical to those that have led to sensitivity to human cues in animals with different social structures such as cats, or in animals that are not predators, such as horses. Thus for proper comparison such questions must be put to empirical test.

Even when the proper comparison group exists, as in the case of dogs and wolves, differential familiarity with humans may still lead to differences in testing methods and outcomes. Such differences may be seen as necessary in cases where the wild or non-domesticated individuals may pose a threat to the experimenter or when accessibility to the animal is limited by the facility in which they are housed. For example, Hare *et al.* (2002) compared the performance of dogs and wolves on an object-choice paradigm using a human point, human tap, and human gaze as the stimuli. Pet dogs were tested indoors, in an isolated room, with no barriers between the experimenter and the dog. The wolves, on the other hand, were tested outdoors, with a fence barrier between them and the experimenter. The observed higher levels of success of dogs than wolves reported in this study may be simply due to the barrier presented to the wolves but not the dogs. This conclusion gains strength from Udell *et al.*'s (2008*a*) observation that a similar magnitude of decrement could be observed between two groups of pet dogs tested outdoors, when one group was tested from outside a fenced enclosure and the other with no such barrier between them and the experimenter. The proximity of an animal to human

environments may often determine what methods and testing environments are realistic. However, it is generally possible to alter the test environment of the domesticated species to closely match that of the non-domesticated one, and where that is not possible, the differences in testing methods should be acknowledged as a possible confound.

In 2001 a project began with the aim of providing a well-controlled comparison of the attachment hand-reared domestic dogs and hand-reared wolves formed to humans and the quality of their subsequent social interactions. Kubinyi *et al.* (2007) stated they had "reveal[ed] some dog-specific behaviors, especially with regard to their interactions with humans, by comparing dogs and wolves hand-reared identically" (p. 26). The researchers on this project took care to begin socialization early, ensuring that experience with humans occurred during the wolves' sensitive period of social development. However, given that the sensitive period for socialization of non-domesticated species must not only begin earlier but is comparatively shorter as well, identical treatment is not necessarily functionally equivalent treatment. Given the timeframe, equivalent treatment for comparison between dogs and wolves might require a caregiver to condense 16 weeks of socialization (the duration of the dog's sensitive period) into the three weeks available to wolves. Furthermore, the wolves in this project only lived with humans for four months after which time they were relocated to an enclosure to be integrated into a wolf pack; after this time their caregivers only visited once or twice a week. Domestic dogs used for comparison, however, continued to live in human homes and had daily contact with humans (Kubinyi *et al.*, 2007).

Although differences between dogs and wolves in this project were attributed primarily to the domestic dogs' superior ability to form attachments with humans, coupled with a predisposition for looking at humans (Kubinyi *et al.*, 2007), it is not clear that the source of these differences must lie in fixed capacities. Kubinyi *et al.* (2007) suggest that "in order to obtain comparative experimental results, the physical and social experiences of the two species have to be at a comparable level" (p. 28). However given different rates of development, young dogs and wolves perceive, interact, and are themselves altered by physical and social stimuli in different ways at the same chronological age. For example, once both sets of pups had reached 21 days of age, dogs would go on to experience up to thirteen more weeks of heightened stimulation in response to social interactions with humans, and these experiences continue to adjust the developmental trajectory of the animal including changes in brain structure (Coppinger & Coppinger, 2001). On the other hand, wolves at this age have moved past their sensitive period and begun to perceive social interactions in a new light, tinting all future experiences accordingly. The effect that further social interactions can have on wolves beyond this age is more limited than it was just one week earlier. That is not to say that continuous interaction with humans beyond the sensitive period of socialization is unimportant to wolves, especially for maintaining an established social bond (Klinghammer

& Goodman, 1987), but these interactions affect the animal differently than the same interactions would have during the sensitive period.

As noted above, Gácsi *et al.* (2005) and Topál *et al.* (2005) reported the results of a study comparing the capacity of dog and wolf pups to demonstrate attachment to a human caregiver. Gácsi *et al.* (2005) found no overall species differences in the preferences of dog and wolf pups for a human caregiver. Yet the authors still suggested that the dog pups may have been more prepared to form attachments with humans while wolf pups more easily bonded with dogs, despite the fact that no direct comparison of the dog or wolf pups' preferences between a dog and an unfamiliar human was carried out. Instead the proportion of time spent with either alternative was more likely a byproduct of each group's preference for the human caregiver on any given condition, a preference that did not remain consistent across presentations for either dogs or wolves. In fact, the second study on the same subjects (Topál *et al.*, 2005), demonstrated that at four months of age wolf pups sought out *more* overall contact with humans, both familiar and unfamiliar, than did any group of dogs.

Despite this fact, Topál *et al.* (2005) primarily emphasized the "small influence of intensive socialization in dogs on attachment to the human caregiver" (p. 1373), a finding that has been used to suggest that domestic dogs have a special capacity for attachment to humans that wolves, which require intensive socialization, do not share. This overlooks however the importance of socialization for domestic dogs to form attachments with humans (Scott & Fuller, 1965). The socialization of dogs to humans may not need to be as intense as that of wolves, but this is likely due to the lengthy period during which primary socialization is possible for dogs. There is no reason to assume that attachment to humans should increase proportionally with increasing intensity of socialization; it is just as reasonable to predict that beyond a certain optimal level of socialization, further increases in the intensity of socialization have a proportionally smaller effect on the animal's behaviour, or could even taper off entirely in effectiveness. Indeed the optimal intensity of socialization required for a species to accept another as social companions may correlate negatively with the length of the socialization window: dogs with their long sensitive period for socialization may require a lower intensity of interaction than wolves with their shorter sensitive period. Ultimately, we should not be asking whether socialization or development is more important, we should be asking what kind of socialization is necessary given a species-specific developmental trajectory and timeframe. From that point we can then ask what socialization has done to the trajectory of that animal's development.

(3) Conditioning

Given the history of dogs as the first species on which behavioural conditioning was ever demonstrated (Pavlov, 1927), it seems surprising that a possible role for conditioning in the responsiveness of dogs to human cues has been largely overlooked in the recent literature. The serendipitousness of Pavlov's (1927) discovery of what we now call classical conditioning also draws attention to the fact that conditioning does not require explicit training, or any intentionality in the pairings of stimulus and reinforcer, or behaviour with reinforcement. Pavlov was a distinguished physiological scientist interested in the basic workings of the digestive system, when he noted that dogs would often salivate before food had even been placed into their mouths (Nobel Lectures, 1967). Although Pavlov reported that dogs salivate when food comes into contact with their mouth or tongue from birth, he also noted that puppies that had only been exposed to milk did not reflexively salivate to the sight or smell of bread or meat (Pavlov, 1927). It was not until the puppies had eaten bread or meat on several occasions that the sight or smell of these items evoked secretions of saliva (Pavlov, 1927). Pavlov went on to demonstrate that a wide variety of stimuli, when repeatedly paired with the presentation or consumption of food, could elicit salivation, even when the pairings were undesired or unintentional. In fact, Pavlov recognized that unintentional conditioning was difficult to avoid and could occur even in very controlled experimental settings: "It was thought at the beginning of our research that it would be sufficient simply to isolate the experimenter in the research chamber with the dog on its stand, and to refuse admission to anyone else during the course of an experiment. But this precaution was found to be wholly inadequate, since the experimenter, however still he might try to be, was himself a constant source of a large number of stimuli. His slightest movements – blinking of the eyelids or movement of the eyes, posture, respiration and so on – all acted as stimuli which, when falling upon the dog, were sufficient to vitiate the experiments by making exact interpretation of the results extremely difficult" (Pavlov, 1927, p.20).

In recent years, a better understanding of the processes Pavlov described has led to an increase in their use in dog-training contexts. Clicker training is a method that uses a small handheld device that makes a consistent "click," which, when paired with food, can act as a secondary reinforcer. Most trainers know that dogs begin to associate the sound of the click with the presentation of food rapidly. In fact, Smith & Davis (2007) demonstrated that 16 out of 18 pet dogs could make this association in fewer than 20 trials. Scott & Fuller (1965) reported that if "One is to take the number of times that the neutral and primary stimuli have to be presented together before a response is obtained to the secondary stimulus alone. Adult dogs will frequently make such an association with one experience" (p.97). Puppies reach adult levels of responsiveness to this kind of conditioning by three weeks of age (Scott & Fuller, 1965).

Operant conditioning – the establishment, extinction and changes in rate of behaviour due to positive and negative consequences (Skinner, 1938) – is also well established in dogs. This process is not limited to isolated training classes or experimental sessions, but constantly influences the behaviour of the dog throughout its life. For example, a human carrying a plate of food to the dinner table is as much a stimulus as

a trainer with a treat in her hand. A dog that follows and attends to either may be more likely to obtain the food. A dog that consistently begs from the dinner table is a reliable indicator that somebody has provided food to the dog when it has approached the table in the past – quite independent of whether that person intended to train their dog to harass them at the dining table or not. In this way a pet dog which spends the majority of its time around humans is constantly behaving in the presence of human stimuli, with some responses in the presence of certain stimuli increasing because they have led to a high probability of reinforcement in the past – independent of any considerations of intentionality or motive. According to expert dog trainer Karen Pryor, even when a person is in control of the reinforcement, "The animal may be responding to criteria you had no intention of establishing but which were accidentally reinforced enough to become conditioned" (Pryor, 1985, p.43). Klinghammer & Goodman (1987) also noted the same considerations during the socialization of wolf pups "Trainers must also be aware that any interaction with an animal may result in behavioral shaping, intended or not. Therefore they must train themselves to be aware of behavioral sequences the animals show in their presence and practice searching for any behaviors of their own which may inadvertently shape the animals'" (p. 57).

It cannot be ruled out *a priori* that any proficiency a pet dog demonstrates in using a human gesture to locate food may not have been conditioned in the home prior to testing, even if no intentional training is reported. For example, it would not be hard to imagine how an outstretched hand, similar in topography to a point, could become a very salient stimulus in the life of a dog dependent on humans for survival. The outstretched hand might be used to move a food bowl into a position accessible to the dog, to fill the bowl with dog food, to offer a treat from the hand, or to throw a toy in a particular direction during play. All these contexts would require the dog to approach the end of the outstretched hand – or some point extrapolated from the end of the hand – to receive a reinforcing consequence.

In some cases, even exposure to the actions of the experimenter may be adequate for individuals without prior experience to become responsive to the gesture under test. Most studies that have assessed dogs' sensitivity to human cues have reinforced correct responses and refrained from rewarding incorrect responses. These are the necessary conditions for operant learning. This is not necessarily a problem if the goal is simply to identify individuals or species that are capable of using human gestures to find food or solve a designated task. However, it does become a problem when the effects of conditioning and exposure are not acknowledged as potential contributors to the development of the behaviour. Tests of the Domestication Hypothesis often expose subjects to many reinforced trials using the same or similar gestures repeatedly. In some studies the subjects have been presented with a single gesture for over 100 reinforced trials (Miklósi *et al.*, 1998; Virányi *et al.*, 2008). With such a large number of trials, even if the subject's performance in the first and second half of testing are compared to test for

learning effects, there is no guarantee that the conditioning necessary for above-chance performance did not take place within the first half or some smaller subset of testing trials.

Evidence is accruing that dogs can be very rapidly conditioned to human limbs and actions. Thorn *et al.* (2006) demonstrated that dogs residing in a shelter could learn to sit upon the approach of a stranger in fewer than 10 trials by simply reinforcing the target behaviour; no command, lure, or force was utilized, and the training session was conducted in less than 10 min. Bentosela *et al.* (2008) showed that pet dogs can learn in as few as three reinforced trials to gaze at their owner's face in order to obtain food reinforcement. The response was also extinguished by nonreinforcement just as quickly. Elgier *et al.* (2009) demonstrated that pet dogs that spontaneously followed their owners' points to find hidden food in one of two containers, could be trained in fewer than 30 reinforced trials to reliably seek food in the container to which their owner did *not* point. This shows the rapidity with which dogs can be conditioned to use human limbs as predictors of food location – even in situations which are highly unlikely to have arisen in the animal's life prior to the experiment. This is consistent with Udell *et al.* (2008*b*) which found that individual dogs that could not spontaneously find hidden food by following a human glancing with her eyes, elbow pointing, or head tilting, nonetheless learnt to do so within ten trials of testing.

VI. AN ALTERNATIVE HYPOTHESIS

There are many reasons to question the hypothesis that dogs, through selection during domestication, developed more complex and human-like social cognition than wolves.

First, domestic dogs have much smaller brains than wolves, which has been attributed to developmental neoteny in dogs (Coppinger & Coppinger, 2001). It seems *a priori* unlikely that a reduction in brain size would be accompanied by an increase in social complexity.

Second, while several studies (Hare *et al.*, 2002; Hare & Tomasello, 2005; Miklósi *et al.*, 2003; Kubinyi *et al.*, 2007; Virányi *et al.*, 2008) claim that wolves are not capable of spontaneous high levels of performance on tasks requiring the use of difficult human cues, such as momentary distal pointing, a more recent study indicates that, given intensive socialization with humans during a sensitive developmental window and continuing daily interaction with humans, wolves without previous exposure to the task are capable of outperforming domestic dogs tested under the same conditions (Udell *et al.*, 2008a, see also Gácsi *et al.*, 2009). Udell *et al.* (2008a) found not only that socialized wolves could use this difficult human cue without explicit training, but at an individual level more wolves than dogs were successful under closely comparable conditions. Furthermore, as a group, wolves and pet dogs both outperformed domestic dogs living in an animal shelter. This demonstrates that with proper socialization and daily human interaction, non-domesticated canids can be more successful at using

human cues than domestic dogs, and that domestic dogs in some environments, such as a dog shelter, lack the necessary ontogenetic experiences to excel on human-guided tasks (Udell *et al.*, 2008*a*).

Third, given that humans and dogs are not conspecifics it is improbable that dogs could have an innate ability to exploit the behaviour of humans to their benefit in the absence of individual experience. Humans and dogs do not visually signal with many of the same body parts. Humans do not possess tails or substantial amounts of hair on the back of their necks, nor do they signal with the position of their ears. Dogs do not signal with their forepaws or by use of an elaborate semantic vocal language. Both domestic dogs and wolves *do* communicate with conspecifics through body movements and thus may be prepared to respond to visual stimuli of individuals in another species with whom they have bonded. This, however, would not lessen the importance of individual experience, both to establish humans as companions, and to learn about topographically distinct human signals.

Fourth, experiences during ontogeny have been shown to play a critical role in the development of effective *con*specific social interactions in canids (Scott & Fuller, 1965) and *con*specific social interactions in humans (Behne, Carpenter, & Tomasello, 2005; Lakatos *et al.*, 2009; Lempers, 1979; Murphy & Messer, 1977). In fact the task of following a human point to a target location has been shown to improve with age and amount of experience even in human children. Research has found that infants begin to follow an adult's point after about nine months of age (Murphy & Messer, 1977; Lempers, 1979), and they do not show the ability to follow a distal point (further than 50 cm) until 12 months of age (Lempers, 1979). Two additional studies have used the same procedure used to test dogs, the object-choice task, with human children (Behne *et al.*, 2005; Lakatos *et al.*, 2009). In both studies the human subjects improved with age across a variety of point types. This makes it improbable that ontogenetic experience would not be essential for effective *inter*specific communication between humans and dogs.

Furthermore, Wynne, Udell & Lord (2008) reanalyzed Riedel *et al.*'s (2008) data on the impact of ontogeny on the ability of domestic dogs to follow human points. This reanalysis showed that the failure to identify learning in the performance of the domesticated puppies was due to insufficient statistical power. In fact, when the ability to use human cues was compared across ages and across trials, the six-week-old puppies improved their performance from the first to the second half of testing, and older individuals performed significantly more accurately on human-guided choice tasks than did the six-week-old pups. Since this reanalysis additional data has been collected directly demonstrating the importance of ontogeny in the development of these skills (Dorey, Udell, & Wynne, in press).

The Two Stage Hypothesis states that the sensitivity of a canid to human social cues depends on two types of ontogenic experience. First, interaction with humans during a sensitive developmental period leading to the acceptance of humans as social companions (Klinghammer & Hess, 1964; Lorenz, 1971). Second, learning that is not restricted to a particular phase of development to utilize the location and movement of parts of the human body to locate sought-after objects (classical conditioning, Pavlov, 1927; operant conditioning, Skinner, 1938). Unlike the Domestication Hypothesis of Hare & Tomasello (2005) and Miklósi *et al.* (2003), this alternative does not require the addition of a new mechanism, such as the evolution of human-like social cognition, during domestication. However this hypothesis still acknowledges the role of domestication in the social behaviour of domesticated species. We agree with Price (1984) that "there is reasonably good evidence that the qualitative nature of the behaviour patterns of domesticated animals has changed very little during the course of domestication. Quantitative changes, however, are more obvious" (p.23). Quantitative changes include changes in the timing of crucial developmental events, in the frequency and duration of behaviours, and in the level of stimulus thresholds. For example, domestication has lengthened the window of time during which social interactions with humans must begin in order to form successful social relationships, but has not necessarily changed an animal's capacity to form such relationships.

The Two Stage Hypothesis predicts that both domesticated and non-domesticated canids are equipped with the phylogenetic prerequisites to respond to human stimuli and to have mutually beneficial interactions with humans. It is possible that canids, may be "prepared" (in the sense of Seligman, 1970) to respond to stimuli displayed by social companions more readily than to other stimuli in the environment. We doubt, however, that this preparedness would be independent of environmental input. Rather, the Two Stage Hypothesis predicts that any preparedness to respond to social stimuli requires experience with members of the companion species during the sensitive period of social development. This experience may lead to both behavioural and physical changes in the animal, as environmental experience during development participates in shaping the adult behaviour. This provides an important place to look for interactions between the environment and biological changes that promote or restrict the formation of social bonds and subsequent social behaviour of an individual. Importantly, such processes would not require that the social companion be human. If our prediction is correct, dogs socialized to other dogs, cats, sheep, and so on, should be more sensitive to the social stimuli of those species than to the social stimuli of other species. Humans could fall at either end of that contingency. In fact the behaviour of sheep-guarding dogs mentioned above provides evidence that this is the case.

Postulating a special preparedness for dogs to respond to human social cues would demand the assumption of a similar preparedness to respond to the social behaviours of sheep and other livestock in livestock-guarding breeds of dogs. Far simpler, we suggest, to propose that domestication, and an extended period of socialization, gives dogs the opportunity to become anyone's best friend, not just man's. If proper

socialization with humans does not occur at the right time in development, a dog may still be capable of responding to and learning about stimuli given by humans, but this would be predicted to occur in the same way and at the same rate as a dog might learn about other environmental stimuli. No special sensitivity to human cues would be expected. Indeed, any attempt at conditioning a dog not socialized to human beings would have to overcome the substantial fear responses that such animals show (Scott & Fuller, 1965).

We suggest, therefore, that if a canid is adequately socialized to humans during its sensitive period of socialization and has experience with human behaviours that predict reinforcement – for example, the canid repeatedly receives food and toys from human hands, making certain movements of the hands discriminative stimuli predicting reinforcement – then the individual should perform above chance on a related task whether or not it is genetically domesticated. However, if an individual has not been properly socialized to humans, or has not had previous experience with relevant human behaviours, it should not spontaneously perform above chance even if the individual is domesticated. So while domestication is still important to the Two Stage Hypothesis, its significance is tied to the ontogeny of the individual and cannot be used as an all or nothing predictor of social capabilities.

VII. FUTURE DIRECTIONS

The Two Stage Hypothesis predicts that if a dog or wolf accepts humans as social companions through exposure during its sensitive period of development, and has had a chance to make associations between certain human stimuli and behavioural outcomes in its home environment, then it will be more likely to perform above chance on choice tasks requiring the utilization of similar human stimuli than individuals lacking either or both of these experiences.

While it is predicted that the conditions of the Two Stage Hypothesis are necessary for superior performance on tasks requiring the use of human communicative stimuli, this is not to claim these two conditions alone are sufficient to predict the performance of any animal. It is possible that many species, canid and non-canid alike, may be capable of succeeding on object-choice tasks using human cues if these conditions are met, however insufficient species have been tested using a consistent methodology to claim that these conditions alone are sufficient. For any species, however, performance on human-guided tasks should take both phylogeny and ontogeny into account. An animal may have the capacity for a certain behaviour, or the necessary phylogenetic prerequisites for a behaviour, but whether that behaviour is ever demonstrated depends on environmental events during development and throughout an animal's life. Conversely, an animal may lack the phylogenetic capacity to develop a certain behaviour, no matter how much environmental experience it undergoes (no dog will learn to fly, even if raised in a bird's nest).

Thus it is possible that species with social systems similar to those of canids have phylogenetic prerequisites that result in higher levels of responsiveness to the visual stimuli of their companions. This could include sensitivity to human stimuli given adequate early socialization and bond formation between the individual and humans. It is also possible that some under-tested breeds of domestic dog lack aspects of the behavioural repertoire necessary for the species' typical performance on object-choice tasks of this type. For example, not all dog breeds fully develop motor patterns such as eye, stalk, and chase that could contribute to the behaviour of following a moving target, like a human arm, to a specified location (Coppinger & Coppinger, 2001). Furthermore, certain breeds and individuals may lack the necessary visual acuity to make out the cues presented in these tests. Thus failure to perform a specific task does not necessarily imply insensitivity to human stimuli in a broader sense. One useful control test would be the demonstration that certain breeds were capable of using human cues in alternative tasks but underperformed in the traditional object-choice task.

For effective comparisons both within and across species, the first requirement is a standardization of terminology and methodology. In the absence of such standardization it is difficult to compare studies across research groups – or in cases even from within the same group. Here we present several suggestions for how this could be accomplished along with our concerns about some of the methods and practices presently found in this field. The hope is to highlight the areas where critical inconsistencies exist, so that we may begin working towards a shared model for future research that can be understood and replicated accurately notwithstanding its origin.

(1) Standardization of types of points

The need for a standardization of the types of human points presented in the object-choice paradigm is well exemplified by a review of studies on twelve species by Miklósi & Soproni (2006). To encapsulate accurately the different procedures, Miklósi & Soproni (2006) identified three temporal categories of point (static, dynamic, or momentary), each of which was further broken down into one of five spatial designations (at target/touching, proximal, distal, cross body, or asymmetric). Each combination of temporal and spatial designation had to be further divided into three categories depending on the presence of an accompanying attentional cue (no gazing, gazing at target, gazing at subject, gaze alternation). The end result was 60 possible categories of human point, with at least one species represented in each of 28 categories. In addition, 11 of these utilized categories *only* contained data from one species collected in one study, and no one category of point was shared by more than half of the 12 species, further limiting the ability to compare results.

Although the breakdown of categories of pointing in Miklósi & Soproni (2006) was a valiant effort to make the most of a difficult situation, our understanding of the data is limited still further when one acknowledges that even these category distinctions rely on consistent use of the underlying

terminology, which is often not the case in the literature, and that categories often overlap in troubling ways. For example, a momentary cross-body point with no gaze may also be proximal (by many definitions the tip of the point reaching anything less than 40 cm from the target) or distal (greater than 50 cm from the target) and could be asymmetric (with the experimenter standing closer to one of the containers) or symmetric (with the experimenter standing equidistant from the two containers). This adds further possible combinations not accounted for in the already large 60-category estimate. Note also that this number is just for one basic gesture – human pointing – and does not include the many other cues used in object-choice paradigms on a regular basis.

Another problem lies in the definitions of each category. For example, according to Miklósi & Soproni (2006) a proximal point is defined as the experimenter's finger coming within 10–40 cm of the target container, and a distal point is one where the experimenter's finger is more than 50 cm from the target container with no upper limit. However, Miklósi & Soproni (2006) also point out that previous studies have shown that a distance of 20 cm between the target container and the stimulus can make the task more difficult than if the distance is less than 20 cm. Why then should the range of proximal pointing extend from 10–40 cm with this critical distance in the middle? The best explanation is the lack of research into the specifics of the stimulus properties governing the behavioural response. In fact, many of the descriptions used to define the stimuli in pointing tasks are not intuitive nor are they stringently defined, and thus they are often misused or misunderstood. For example, the third dimension used to divide categories in the Miklósi & Soproni (2006) review was the presence or absence of gazing directed at the target, at the animal, or alternating between the two. However, in some studies gazing involves movement of the eyes alone (e.g. Soproni et al., 2001), whereas in others it can mean turning the whole head or body orientation in the direction of the target container (e.g. Hare & Tomasello, 1999). Even something so apparently clear-cut as the absence of gazing can indicate anything from a visual occluder over the subject's eyes (Pack & Herman, 2004), to a downward head orientation of the experimenter (Shapiro, Janik & Slater, 2003).

If all forms of gazing or pointing were equal predictors of a subject's behavioural response, this terminological confusion would not be a problem. However, there is ample evidence that an individual's success on one task requiring the use of a human cue is not a good predictor of its success in using the whole range of human cues available (Udell et al., 2008b). In fact, data show that an individual dog capable of using a human head turn to locate a target container (one definition of gaze) often cannot use eye gaze alone (with no head movement) on the same task, making the two stimuli distinct both in topography and in their ability to predict the behavioural response (Udell et al., 2008b). Thus it is important to accurately identify the stimulus so that groups are not compared that have been exposed to different functional stimuli resulting in different levels of performance.

The best way to move forward would be for researchers to decide which of two endeavors they wish to pursue in a given study: either to map the stimulus properties that predict an individual's success on a specified task, or to compare the ability of different groups or species to succeed in using a standardized stimulus to solve a standard task with set methods. Determining the role of various stimulus properties is very important task. However, this should not be done at the expense of having a solid set of comparable data across laboratories, subject groups, and species. A limited number of standard tests could be agreed upon for comparison purposes, especially until more is understood about the influence of diverse stimulus topographies and presentation methods on object-choice task performance. Because basic human pointing, using the full extension of the arm and one finger, is already commonly used, easy to perform, and large enough to reduce the need for concern about a species' visual acuity, we propose that this is the best place to start. Furthermore, studies focusing on interspecies or inter-group comparisons could reduce confounding variables by making the point the sole relevant human gesture presented in the trial (directing gaze and body orientation straight ahead, and standing equidistant from both containers). Of the remaining categories of point, momentary distal pointing, momentary proximal pointing, dynamic distal pointing, and dynamic proximal pointing are the most widely represented in studies involving different species and have been tested with a large number of subjects (Miklósi et al., 2006). Furthermore, these categories of point have been used in the majority of studies described herein because they have allowed for the most complete comparison of canid species and groups, and therefore contribute most strongly to the present theoretical debate. These four categories of human point would thus be the best stimuli for extended comparisons of performance on object-choice tasks at this time. To ensure that reports of success or failure using these four categories of point can be taken at face value, we suggest that future studies use the most compatible basic definitions for each point, as presented in Table 1, or explicitly define the point used by giving a measurement of the distance between the tip of the experimenter's finger and the closest edge of the target container at full extension, the exact movements and resting place of the experimenter's hand before and during the dog's approach toward the containers, and the presence of any additional stimuli relevant to the task.

(2) Standardization of pointing methods

The standardization of stimuli used in testing is of little value unless comparable testing methods are also used when direct comparisons are to be made. In Section V, we addressed some of the more obvious discontinuities in studies of canine social behaviour, including the presence of a fence barrier in wolf tests but not in those with dogs, testing different species groups indoors *versus* outdoors, and regarding age as a measure of equivalence despite critical differences in developmental progress.

Table 1. Basic definitions for human points (traditional topography with a human arm)

Distal point	The tip of the experimenter's finger is 50–80 cm from the closest edge of the target container at full extension.
Proximal point	The tip of the experimenter's finger is 5–15 cm from the closest edge of the target container at full extension.
Dynamic point	The experimenter's arm and hand are extended into a traditional point in the direction of the target container while the subject watches. The experimenter's arm remains in place and motionless until the trial ends.
Momentary point	The experimenter's arm and hand are extended into a traditional point in the direction of the target container while the subject watches. The experimenter's arm is then retracted back to a neutral position before the subject is allowed to make a choice (duration of point should be specified).
Static point	The experimenter's arm and hand are extended into a traditional point before the subject is present for the trial. The experimenter's arm remains in place and motionless until the trial ends. The subject should not see any arm movement until the end of the trial.

Other important differences should also be considered. For example, should the response containers in an object-choice paradigm both contain a small amount of food in a false bottom, contain no food but give off food scent, or have no food-related cues at all? Should the target container have the accessible food placed in it, or should it be presented after the animal's choice? The best way to determine the appropriate methods is to look at performance on control trials in which no human cue is given. Since dogs typically do not perform above chance on control trials when both containers have the scent of food (either a smear or a piece of food in a false bottom), even when a small amount of accessible food is present in the target container (e.g. Miklósi *et al.*, 1998; Udell *et al.*, 2008*b*), these procedures may be considered functionally equivalent. However, Udell *et al.* (2008*a*) noted that wolves could discriminate between a container holding accessible food and one with a piece of food in a false bottom in control tests in which no human cue was given. When the containers were not pre-baited, performance on control trials dropped to chance levels for all subjects. The fact that some canids may be able to smell the difference in food availability between two containers should be taken into consideration for future studies involving subjects from any species that might be compared with wolves.

An evaluation of performance during control trials is important for another reason. Even if the experimenter is sure that olfactory cues cannot be used to indicate the correct response (for example in cases where no pre-baiting occurs) other cues may be present in the environment that predict a specific response regardless of the intended stimulus under test. Unintentional cueing is not foreign to canine behavioural research. Collier-Baker, Davis, and Suddendorf

(2004) reported that the position of the displacement device used in invisible displacement studies could better predict a dog's performance on the task than an attribution of mental representation of the hidden object. The dogs in their study were using this additional physical cue in the environment as a stimulus, changing a displacement task to an associative learning task, a possibility that previous studies had overlooked.

Perhaps the single most important aspect of consistent methodology lies in defining what constitutes a trial and how each one of these trials is scored. In object-choice paradigms we propose that a trial should start once the stimuli have been presented and the subject is released to make a choice. The trial should be considered over once a predetermined choice response to either container has been made or when the trial times out. If the subject views the stimulus, is released to make a choice, and is then called back to the starting position to re-view the same stimulus before being released to make a choice, the subject has now participated in two trials and each should have an outcome that appears in the reported data. If the subject approached the target container, this should be recorded as a correct response, if it did anything else or timed out this should be coded as an incorrect response. Ideally incorrect responses should be further broken into incorrect choice and no-choice responses depending on whether the incorrect container was approached during the trial (see Table 2). This is crucial because, as we have discussed, dogs and many other species can learn a correct response very rapidly. If only trials during which a subject makes a response to one of the two containers are counted, with no-choice trials repeated and excluded from the data record, then the total

Table 2. Proposed definition of an object-choice trial and the four possible outcomes

Object-choice trial	Begins once the subject has been exposed to the stimuli and is released to make a response. Ends as soon as a choice response to either container is made or the trial times out.
Incorrect response	The outcome of a trial where the subject makes any response other than the correct response; this includes timing out, or no choice.
No choice	The outcome of a trial where the subject fails to come into contact with the response objects before the trial times out. Any behaviour not qualifying as a correct or incorrect choice.
Incorrect choice	The outcome of a trial where the subject first touches or comes within 10 cm of any response object (container) not designated as the target container.
Correct choice	The outcome of a trial where the subject first touches or comes within 10 cm of the target container.

number of times a subject is exposed to a particular stimulus configuration is not known.

(3) Future research

Effective tests of the Domestication and Two Stage Hypotheses must compare the responsiveness to human cues at different developmental stages of four groups of animals. Most studies have tested only socialized domesticated individuals, but comparisons with socialized undomesticated individuals, unsocialized domesticated individuals, and unsocialized undomesticated individuals are critical if the contributions of socialization and domestication are to be separated. Of course, unsocialized animals are very difficult to study, as they typically avoid humans, but less socialized individuals, such as dogs held at county pounds, or animals in zoos which are not routinely handled or socialized to humans but have habituated to human presence, could and should be tested. Understanding how socialization changes the developmental trajectory of an animal, and its ultimate consequences on behaviour, could act as a starting place for questions concerning the responsiveness of a species towards the behaviour of another unrelated species, and whether this aspect of development is actually responsible for the enhanced or expedited learning some canids demonstrate with regard to human stimuli.

Furthermore, for effective comparison of different animal groups it is essential that the tested animals' age be considered relative to their sensitive period for social development (assessed individually for each species and group). Simple matching of chronological age is not adequate because of the different developmental trajectories of domesticated and undomesticated animals.

More attention should also be given to what constitutes a typical dog. In the majority of studies discussed here 'dog' or 'domestic dog' is used to refer to a specific subset of the domestic dog population – pet dogs – and differences in socialization, upbringing, or training are not considered. Research has shown that there are marked differences in the initial performance of shelter dogs and pet dogs on object-choice tasks, and even within those sub-groups there are individual differences in performance (Udell *et al.*, 2008*a*). Further research into the similarities and differences found among groups and breeds of dogs will become increasingly important in understanding the gene-environment interactions that allow some canine subjects to perform significantly better than others on human-guided object-choice tasks.

In addition to wolves, populations of socialized undomesticated coyotes and foxes provide an additional resource for testing the prediction that socialization to humans during an individual's sensitive period and conditioning during an individual's lifetime will lead to success in using human gestures even in undomesticated canids. Another important population which should be tested includes dogs with known histories that have little socialization to humans or are not living in human homes. Such populations can be found in certain groups of working dogs, such as livestock-guarding dogs. Within each of these groups, individuals differing in

socialization, experience, and training can be investigated. This will provide a more complete comparison set for other domesticated and non-domesticated species that also exist in many diverse niches.

More studies are also needed on the ability of individuals from these different subject groups to become conditioned to different types of stimuli. Comparisons are needed of the effectiveness as conditioned stimuli of human limbs and non-human stimuli of comparable size and shape. These comparisons should be made in individuals with and without extensive exposure to humans. One novel approach would involve taking individuals that initially fail to use specific human gestures or non-human stimuli to locate hidden objects and explicitly training them to do so. Research of this kind would identify the type and length of exposure or conditioning necessary to develop the ability to use specific stimuli to identify a target location. This may also identify the limitations of different species' abilities to follow human gestures varying in size, position and topography. Importantly, non-domesticated species have primarily been tested for responsiveness to visual stimuli such as human gestures. Investigations into other modes of communication, e.g. human auditory cues and word learning in non-domesticated canids, could provide grounds for a more complete comparison between canid types.

More attention also needs to be given to changes in the social responsiveness to humans and human stimuli demonstrated by dog puppies and other young canids throughout development. It is important to determine the age or developmental milestones at which canids of each species begin responding to human gestures, both with and without explicit training. The time at which canids begin responding to human gestures or other human social stimuli might shed light on the processes and mechanisms that contribute to the sensitivity to human cues many dogs demonstrate as adults.

In general, it will be increasingly important to better understand the mechanisms that regulate the social behaviour of domesticated and undomesticated individuals. This will need to include both research on the genetic and morphological changes that occur during domestication, and the degree to which changes in behaviour are influenced by genetic inheritance, environment, and the interactions between phylogeny and ontogeny.

To suggest, as we propose, that domestication alone is neither necessary or sufficient to predict a canid's success in using human cues in object-choice tasks is not to say that domestication did not lead to changes in dog social behaviour that are relevant to the species' interactions with humans. As previously mentioned, one important consequence of domestication is that it causes delays in ontogeny, resulting in changes in the sensitive period of social development. This in turn extends the window of time humans have to effectively socialize domesticated canids and could explain why many more domestic dogs than wolves develop sensitivity to human behaviour: they simply have longer to accept humans as social companions and their proximity to humans provides the required exposure with minimal effort.

The genetic effects of domestication not only provide a starting point for dogs, shaping many of the physical traits and developmental windows the dog inherits, but the cultural aspects of domestication also increase the probability that an individual will end up in a human environment. This ultimately sets the stage for the many life experiences a dog will encounter as a pet, a human aid, an entertainer, or – on the other side of the ledger – as a scavenger on the fringes of human society, or a rejected pet serving out 14 days at a county pound prior to euthanization. For this reason it is futile to attribute a particular behaviour of the domestic dog to ontogeny or phylogeny alone. Yet for the same reason, domestic dogs make an interesting locus of study of the interaction of forces that ultimately shape and define the social behaviour of man's most familiar companion, *Canis lupus familiaris*.

VIII. CONCLUSIONS

(1) The domestic dog's proficiency on tasks that require the use of human stimuli is well documented. Furthermore, the availability of large populations of dogs from a variety of backgrounds and environments, as well as access to genetically wild canids which have experienced various degrees of socialization to humans, makes this species an ideal candidate for understanding the role of ontogeny and phylogeny in the development of sensitivity to human cues.

(2) Attributing the domestic dogs' sensitivity to human cues to the development of a human-like social cognition based on heredity (genetic domestication) alone, denying or greatly restricting the role for ontogeny in these behaviours, would be inconsistent with years of research that has demonstrated the importance of environment, development, experience, and socialization in the ontogeny of social behaviour in the domestic dog.

(3) Researchers who have stressed age consistency when testing canids on object-choice paradigms have overlooked developmental differences in canids, especially with regard to the sensitive period of socialization. Thus differences in developmental stage may account for behavioural differences in these tests.

(4) More parsimonious explanations for the domestic dog's sensitivity to human stimuli, considering the ecology and life experiences of the animals under test, deserve attention. The Two Stage Hypothesis has been proposed, suggesting (*a*) that social imprinting to humans during the sensitive period of social development, and (*b*) experiences with relevant human stimuli so that associations between specific stimuli and available reinforcement can be formed, are both important to the development of sensitivity to human action.

(5) The methods and terminology of the field need to be reformed and standardized, or at least more clearly defined, if meaningful comparisons are to be made between species, breeds, groups held under different conditions, or even the findings of different research institutions. Many important questions for further study exist, and working together we soon may be able to understand the origins and maintenance of the behaviours that make the human-dog symbiosis so fruitful.

IX. ACKNOWLEDGEMENTS

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