STIMULUS PROPERTIES, EXPERIENCE AND GENERALIZATION: A PROXIMATE ANALYSIS OF CANINE RESPONSIVENESS TO HUMAN GESTURES

By

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To Chet and my parents for their unconditional support and encouragement

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STIMULUS PROPERTIES, EXPERIENCE AND GENERALIZATION: A PROXIMATE ANALYSIS OF CANINE RESPONSIVENESS TO HUMAN GESTURES

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The origin of domestic dogs' success in human environments over the last 14,000 years has been a topic of interest to scientists for over a century. Modern claims of dog's special responsiveness to human gestures have led some to propose that dogs are biologically prepared to coexist with humans due to evolutionary changes that resulted in the inheritance of a human-like social cognition. The proponents of this hypothesis have predicted that domestic dogs should be responsive to the communicative meaning of human gestures independent of socialization or life experience with humans and that non-domesticated canids should not share the capacity to respond to human actions in the same way. Through a series of experiments I have demonstrated that neither of these predictions hold true. Instead both domestic dogs and undomesticated wolves are capable of responding appropriately to human gestures given early socialization and relevant life experiences with human stimuli. Some populations of domestic dog are not spontaneously successful on human-guided tasks unless they receive additional experience and all subjects, both dog and wolf, respond differentially to human stimuli with distinctive topographical properties. Canine response to human gestures appears to be learned and can be modified quickly to

match the environmental contingencies in place. This flexibility in responding is consistent with the predictions of the Two Stage Hypothesis, which emphasizes the importance of interactions between phylogenetic and ontogenetic factors the development of dogs' social behavior.

CHAPTER 1
GENERAL INTRODUCTION

Background

In the human developmental literature, point following behavior is often considered a measure of joint attention and has been identified as a predictor of healthy sociocognitive development, language formation and even theory of mind (Carpenter, Nagell, & Tomasello, 1998; Goldin-Meadow, 2007; Tomasello, Carpenter, & Liszkowski, 2007). Consequently, to some, following the point of another individual implies a deep understanding of communicative intent or even knowledge of the mental states of others (Gómez, 2007; Tomasello et al., 2007).

While the comparative study of joint attention, gesture following, and responsiveness to attentional state was at one time primarily restricted to humans and non-human primates, in recent years there has been a dramatic shift in interest to include a much broader range of species in research of this type. This has included the study of horses (McKinley & Sambrook, 2000), cats (Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005), parrots (Giret, Miklósi, Kreutzer, & Bovet, 2009), jackdaws (Von Bayern & Emery, 2009), ravens (Schloegl, Kotrschal, & Bugnyar, 2008), goats (Kaminski, Riedel, Call & Tomasello, 2005), dolphins (Pack & Herman, 2004), and seals (Scheumann & Call, 2004). However one subspecies has drawn substantially more focus than the rest: *Canis lupus familiaris*, the domestic dog. As a result comparisons between canid species and subspecies have become an important focal point in the debate about the origins and mechanisms underlying responsiveness to social gestures; especially responsiveness to human gestures (Udell, Dorey, & Wynne, 2010b for a review). Over the course of more than a decade of experimentation, pet domestic

dogs have demonstrated that they are capable of following many different forms of human gesture to locate hidden objects (Miklósi, Polgardi, Topál, & Csányi, 1998; Udell, Giglio, & Wynne, 2008; Soproni, Miklósi, Topál, & Csányi, 2002). While substantial amounts of variation in performance exists between individuals and groups of dog, at least some have proven capable of following gestures as subtle as an eye shift (Miklósi et al., 1998), as challenging as a momentary distal point (Udell, Dorey, & Wynne, 2008), and as unusual as a far elbow cross-point (where the experimenter stands behind an empty container sticking her contralateral elbow out while pointing towards the target with her finger extended in front of her body) (Soproni et al., 2002). These findings have led to several predictions about possible evolutionary origins of this behavior, including convergent evolution with humans (Hare & Tomasello, 2005) and the development of a more human-like social cognition through domestication (Hare, Brown, Williamson, & Tomasello, 2002). However, the underlying mechanisms for point following behavior in the domestic dog are still under debate (Reid, 2009; Udell et al., 2010b) and in recent years a shift towards a more balanced approach between ultimate and proximate explanations of canine social behavior has taken place.

Why Canids?

Much may be learned from comparing the performance of different species and populations of canids on human-guided tasks. The study of canines in this domain is valuable for a number of reasons including the fact that (1) both wild type and domesticated canids varying in degree and type of relationship with humans exist in nature and in captivity (2) both human-socialized and unsocialized members of many species including domestic dogs, coyotes, foxes, and wolves exist in known populations (3) detailed information about biological changes associated with canid domestication

(Trut, Plyusnina, & Oskina, 2004) and the domestic dog genome (Lindblad-Toh et al., 2005) exist and (4) domestic dogs share a unique obligatory symbiosis' with humans that varies by population and location, and is not yet fully understood (Coppinger & Coppinger, 2001).

The specific rationale for using domestic dogs as a model for understanding responsiveness to human gestures has also been influenced by the theoretical paradigms of investigators exploring the origins of dogs' human-guided behaviors. In recent years two competing hypotheses have resulted from this ongoing theoretical debate: The Domestication Hypothesis and the Two Stage Hypothesis.

Early Approach: The Domestication Hypothesis

When it was first determined that dogs would readily follow human points to a target, in some cases outperforming chimpanzees on human guided tasks (Hare et al., 2002), several researchers proposed that domestic dogs might share a universal, possibly innate or preprogrammed, sensitivity to human gestures (Hare et al., 2002; Miklósi et al., 2003). It was also argued that dogs did not require socialization or experience with humans to achieve these results (Hare et al., 2005; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008) and that this ability was not shared by dogs' closest undomesticated relatives, grey wolves (Hare et al., 2002, 2010; Miklósi et al., 2003). This view became known as the Domestication Hypothesis (Hare et al., 2010; Hare & Tomasello, 2005; Topál et al., 2005), which credits the process of genetic domestication for the development of a human-like social cognition in domestic dogs. It is this human-like social cognition that is said to enhance the domestic dogs' sensitivity to human actions (Miklósi et al., 2003) allowing them to extract communicative meaning from human gestures (Hare & Tomasello, 2005).

This early approach to understanding the origins of dogs' responsiveness to human gestures was based on an evolutionary framework supported by estimates that dog domestication had occurred over 135,000 years ago (Vila et al., 1997). Some scientists have contended that in addition to domestication, humans and dogs shared similar environmental and social pressures that could have led to convergent evolution (Hare & Tomasello, 2005; Kubinyi, Virányi, & Miklósi, 2007) resulting in parallel socio-cognitive abilities in dog and man. Despite the fact that the most widely accepted evidence now places canine domestication within the last 14,000 years (Nobis, 1979), attributing earlier dates to overestimates arising from misinterpretation of DNA and fossil evidence (Morey, 2006), the Domestication Hypothesis still provides an active framework for the design and interpretation of research for some within this field (Hare et al., 2010; Topál et al., 2009).

The claim that dogs may be more human-like than our closet primate relatives may sound like a new direction in comparative research; certainly it has been treated as such in the recent literature. However in many ways these conclusions serve as a recapitulation of all but forgotten thoughts prominent in the 19th century. While it is generally known that Darwin held both the intelligence and emotions of dogs in high esteem (Darwin, 1872), this was only one part of a broader paradigm that suggested that dogs might more closely resemble humans in some respects, especially in terms of psychology, than non-human primates including other apes (Ritvo, 2000). In fact Romanes dedicated an entire chapter of his book, *Animal intelligence,* to dogs, stating that "the intelligence of the dog is of special, and indeed of unique interest from an evolutionary point of view, in that from time out of record this animal has been

domesticated on account of the high level of its natural intelligence" (Romanes, 1906, p. 437). In one of the strongest statements in this chapter he directly compares the status of dogs and monkeys, echoing more recent interpretations of dogs' attentiveness to human behavior:

> The emotional life of the dog is highly developed— more highly, indeed, than that of any other animal. His gregarious instincts, united with his high intelligence and constant companionship with man, give to this animal a psychological basis for the construction of emotional character, having a more massive as well as more complex consistency than that which is presented even in the case of the monkey, which, as we shall afterwards see, attains to a remarkably high level in this respect. (Romanes, 1906)

Although it is true that humans and domestic dogs have shared a special evolutionary relationship, interpretations that attribute the social behavior of the dog or the unique qualities of the human-canine symbiosis to convergent evolution or domestication alone have often overlooked important lifetime variables that dogs encounter in human society. This has imposed artificial limitations on the ability of scientists to account for the full richness of canine social behavior including the exceptional propensity for learning and flexibility demonstrated by dogs in social situations, and the diverse range of social behaviors exhibited by different populations of domestic dogs around the world (Udell et al., 2010b; Udell & Wynne, 2010).

Integrative Approach: The Two Stage Hypothesis

The origin of the domestic dogs' social behavior in the presence of humans can be understood at two levels. First are the phylogenetic influences on behavior that arise as a result of the unique evolutionary past of domestic dogs. Second are the ontogenetic influences on behavior. These include the individual development of the dog and the history of individual life experiences it has within a specified environment. Although each level can serve, independently, as the focus of experimental study, in

actuality neither exists in isolation. Therefore the origins of a dog's behavior are always a product of interactions between the two.

Early studies on the domestic dogs' responsiveness to human gestures had claimed that socialization or lifetime experience with humans was unnecessary for dogs' to understand the communicative intent of human behavior (Hare et al., 2002; Riedel et al., 2008). However such findings were in contrast to decades of work dedicated to understanding the development of canine social behavior (Udell et al., 2010b). For example, Scott and Fuller (1965, p.176) demonstrated that domesticated dog puppies raised entirely apart from humans "later react toward them [humans] with extreme fear and hostility". Furthermore, 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, Soproni, Dóka, & Miklósi, 2009; Lempers, 1979) making it unusual if not unlikely that ontogenetic experience would not be essential for effective *inter*specific communication between humans and dogs. However, new research has once again confirmed that experience with humans during development, as well as other lifetime variables, are critical for the expression of dogs' human-oriented social behaviors including responsiveness to human gestures (Dorey, Udell, & Wynne, 2010; Udell et al., 2010a; Wynne, Udell, & Lord, 2008). Such findings have culminated into the Two Stage Hypothesis, which credits both phylogeny and ontogeny in the development of a dog's human guided behavior (Udell et al., 2010b). More specifically this hypothesis predicts that individuals that have (1) been socialized to human's during their species specific critical period for socialization and (2) that have had relevant life experiences

where specific human body parts have predicted reinforcement for behaving in a characteristic way (often following or orienting in the direction of the human body-part or arm) will be more likely to succeed on human guided tasks that require this behavioral response than individuals that have not been socialized or have not had sufficient experience with these stimuli, regardless of whether or not the subject is domesticated.

This approach places greater importance on the interactions between a dog's evolutionary history, environment, development, and life experience instead of attributing domestic dogs' sensitivity to human stimuli to genetic inheritance alone. More broadly the Two-stage hypothesis allows for the possibility of socialization and attention to the stimuli of non-humans (for example Livestock guarding dogs may be expected to respond to the gestures of sheep as pets respond to the gestures of humans) and could also be applied when predicting the behavior of non-canid species (Udell et al. 2010b). In fact, point following behavior is not present from birth even in humans. Several studies show that human infants begin to follow simple pointing gestures around nine months of age (Murphy & Messer, 1977; Lempers, 1979), and begin to follow distal points (further than 50 cm from target) around 12 months (Lempers, 1979). Thus it seems plausible that during development even human infants might learn to respond to points as discriminative stimuli in response to relevant life experiences. From this perspective dogs may still serve as a model for understanding some aspects of human social behavior, but acknowledgement of and attention to proximate factors is necessary.

Domestic dogs fill a diverse array of niches within human societies. The majority of the world's dogs do not exist as pets, but as scavengers engaging in an obligatory

symbiosis with humans from whom they acquire their nutrition, often in the form of trash or byproducts of human food preparation or consumption, and occasionally shelter and protection (Coppinger & Coppinger, 2001). In the majority of research on domestic dogs' responsiveness to humans, however, the term domestic dog most accurately refers to pets living in the human home or human-oriented working dogs (Udell et al., 2010 a, b). Dogs in such populations share a truly unique relationship with humans in terms of their life experiences (Udell & Wynne, 2008); consequently the place of pet dogs in modern society might predict a greater divergence in behavioral response- when compared to other animals- than their evolutionary history. For example in the United States there are over 74.8 million dogs living as pets, at a cost to their owners of over $100 billion a year (American Pet Products Manufacturers Association, 2007. http://www.appma.org/press_industrytrends.asp), an expense many Americans are willing to take on to support and pamper an animal that is often viewed as a member of the family or even a child. In a home environment a dog is completely dependent on human caretakers for all of its needs from the day it is weaned. The majority of reinforcers, including biological necessities, a dog will have access to throughout its life are controlled by humans. This is comparable to the situation of young human children, and may explain in part the similarities in sensitivity to human social stimuli shown by dogs and children (Udell & Wynne, 2008). However, unlike children, domestic dogs remain dependent on humans for primary reinforcers, such as food, water, and access to mates throughout their lives.

Therefore the study of lifetime variables, which interact with an individual's inherited predispositions to produce a unique repertoire of behavior, represents an

important area of study that is required to fully understand the social behavior of domestic dogs. Nonetheless the study of proximate mechanisms contributing to the social behavior of dogs is just beginning to draw the attention of scientists interested in the dogs' response to human action.

Domestication and Development

Wolves and dogs are different. This is an unarguable fact. The question is how are they different, and do these differences have any influence on their ability to respond to the gestures of their social companions, be it a conspecific or human being? Although the most recent literature suggests that wolves do not differ in their *capacity* for responsiveness to human gestures, it has been proposed that an individual wolf's ability to follow such gestures may be strongly influenced by its acceptance of humans as social companions (Udell et al., 2010b). Acceptance depends on regular interactions with humans during the critical period for socialization, and this window marks an empirically known place of divergence between domesticated and undomesticated canids.

An ongoing research project initiated by Dimitri Belyaev in the late 1950s, has investigated the effects of selection for tameness in canids using silver foxes as a model. In each new generation of foxes, individuals were rated on their behavioral 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. This became known as the experimentally domesticated population, and the tamest among them, the Domesticated Elite. The selection pressure for this

group was intense, with only 3% of males and 8 to 10% of females serving as parents for the next generation of pups (Trut et al., 2004). While this project raises many important points about the influence of domestication on morphological and behavioral neotenization in canids, it is possibly most important for the light it sheds on the mechanism responsible for the expression of the “tame” behavioral qualities in the experimentally domesticated population. According to Trut (1999), the 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 behavioral 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 critical period of social development in domesticated foxes (Trut, 1999).

As in other non-domesticated canids, the sensitive period for social development in 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 behavior and the acceptance of novel stimuli becomes more difficult (Trut et al., 2004). In contrast, by generations 28-30 the window of socialization in the experimentally domesticated foxes had increased to 12 weeks of age and often longer for individual pups (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 behavior into adulthood.

Wolves, having the unaltered canid developmental trajectory, follow the same trend as the undomesticated foxes. They must be intensely socialized by humans from the second week of life if a lasting positive relationship is to be formed; by six weeks of age they are outside the window for primary social development (Klinghammer & Goodman, 1987). On the other hand domestic dogs, like the experimental foxes, have an extended critical period for socialization lasting up to 14 weeks in some breeds of dog (Coppinger & Coppinger, 2001; Scott & Fuller, 1965). This makes them much easier to socialize and places a more lenient time restriction on the beginning of this process (Udell et al., 2010b).

While it is possible to socialize both dogs and wolves to humans, differences in developmental timing may play an important role in the prevalence of truly human-socialized members of each group available for test. These differences also have implications for designing equivalent comparisons in longitudinal studies aimed at understanding human-canine interactions at different stages of development. For example, if wolves and dogs are to be treated equivalently by humans at different stages in their social development, experiences and interventions might have to begin at an earlier chronological age in wolves since domestic dogs develop more slowly, both physically and socially, in comparison to their undomesticated counterparts. Furthermore behavioral measurements taken at the same age in young dogs and wolves would likely represent animals in different developmental stages, which could result in perceived absolute differences between the two sub-species that might more

accurately be tied back to the already known divergence in developmental progression. Therefore, especially in young individuals, a thorough understanding of the biological and developmental differences between domesticated and undomesticated canids is important to both the design and interpretation of research on responsiveness to human gestures.

Environment and Experience

While there is ample work to be done in both domains, careful analyses of proximate mechanisms contributing to the social behavior of canids are long overdue. Therefore the main purpose of the experiments presented here is to address several unanswered questions about the range of wolf and dog responsiveness to human gestures and to carefully evaluate proximate variables that may influence an individual's performance on human-guided tasks. In addition to the role of experience, learning and generalization across gesture types, I will investigate the importance of gesture topography and a shelter environment on dogs' response to human stimuli. I will also attempt to functionally define a human point in terms of the behavioral response of dogs in the presence of different stimuli traditionally treated as members of this stimulus class, and will assess whether or not the idea that gestures contain universal communicative meaning for dogs is necessary to explain performance on human-guided tasks.

CHAPTER 2
ASSESSING THE RANGE OF HUMAN GESTURES UTILIZED BY WOLVES IN COMPARISON TO PET DOMESTIC DOGS

It is well accepted that pet domestic dogs are not only capable of utilizing a human point to solve object choice tasks, but that they are proficient in using a wide range of diverse human gestures made with different parts of the human body as well (Udell et al. 2010b). While it has been demonstrated that wolves possess the capacity to follow a human point to a target (Udell, Dorey, et al., 2008; Gácsi, Gyori et al., 2009), it is still possible that domestic dogs are unique in their ability to spontaneously utilize a large range of novel human gestures. This could have implications for the interpretation of the mechanisms underlying the use of human stimuli in dogs and wolves. For example, if wolves are incapable of utilizing a range of human gestures, it might be suggested that the successful use of a specific point type is an isolated product of experimental design as opposed to evidence of a shared social capacity to respond to human action. However if dog and wolf performance is comparable under similar environmental conditions over a range of gesture types, then the most parsimonious explanation is that the same mechanisms underlie the behavior of both canid sub-species.

Although it is often claimed that dogs have an inherently unique response to human gestures (Hare et al., 2002; Hare & Tomasello, 2005; Miklósi et al., 2003), many of the current distinctions made between the performance of domestic dogs and other species and subspecies, especially wolves, may be artifacts of a literature that contains much more data on domestic dogs than most other comparison species. This is demonstrated in part by the changing perceptions of wolf performance on the most basic forms of human-guided tasks over the last decade.

Evolving Perceptions of Wolves

Early studies comparing the performance of domestic dogs and wolves on human-guided tasks found that unlike dogs, wolves did not follow human gestures to a target location concealing food (Agnetta, Hare, & Tomasello, 2000; Hare et al., 2002). For example an early study by Agnetta et al. (2000) found that two captive wolves did not follow a human point with gaze or gaze alone to a target object. Likewise Hare et al. (2002) found that none of the seven wolves tested reliably followed a cross-body tap and gaze (where the experimenter used his cross-lateral hand to tap the target while looking towards it), point and gaze (where the experimenter used his cross-lateral hand to point towards the target while looking at it), or point (where the experimenter used his cross-lateral hand to point towards the target while looking straight ahead) at the individual level; however the wolves did perform above chance on the cross-body point and gaze condition as a group. However, both of these early experiments contained significant methodological confounds including the use of wolves that may not have been properly socialized to humans and the testing of wolf subjects from behind a fence while dogs were tested with no such barrier (Udell, Dorey et al., 2008; Udell et al., 2010b; Virányi et al., 2008). Additionally, the two wolves tested by Agnetta et al. (2000) were tested together at the same time within the same enclosure.

Another wave of research on wolves' ability to utilize human gestures began in 2001 when researchers in Hungary hand-reared their first litter of wolf pups (Virányi et al., 2008). During a series of experiments taking place over several years, individuals selected from a total of nine socialized wolves were exposed to the following gestures: Dynamic touch & gaze (the experimenter used her ipsilateral-hand to touch the target while looking at it), touch (the experimenter used her ipsilateral-hand to touch the target

for about 1 s, before returning to a neutral position), momentary proximal point (the experimenter used her ipsilateral-hand to point towards the target for about 1 s coming within 10 cm it, before returning to a neutral position), momentary distal point (the experimenter used her ipsilateral-hand to point towards the target for about 1 s coming within 50 cm it, before returning to a neutral position), dynamic distal point (the experimenter used her ipsilateral-hand to point towards the target coming within 50 cm it, remaining in place until a choice was made), and standing behind the correct container (also commonly referred to as local enhancement). The success of individual wolves across different point types, and even the average performance of the wolves varied substantially. The most point type that wolves were the least likely to follow reliably in these studies, however, was undoubtedly the momentary distal point. The authors of these studies suggested that while domestication or evolutionary explanations may not rule out the possibility of wolves successfully following simpler forms of human pointing, such as touching a target, proximal pointing, and local enhancement, lack of a predisposition to look at human faces may have inhibited them from spontaneously following a wide range of gestures including more challenging forms of human point, such as the momentary distal point (Miklósi et al., 2003; Virányi et al., 2008). In other words domestic dogs may be unique not because they can follow a human point, but because of the wide range of human gestures that they appear to spontaneously utilize in object choice tasks (Agnetta et al., 2000; Miklósi et al., 2003; Virányi et al., 2008).

In 2008 it was demonstrated for the first time that a group of human-socialized wolves were capable of spontaneously utilizing a momentary distal point in an object

choice task (Udell, Dorey et. al., 2008). Not only were these wolves successful as a group, matching the performance of pet dogs tested under ideal conditions, but six of the eight wolves were successful at the individual level outperforming the four groups of domestic dogs tested. These findings were quickly followed by another study conducted by a different group of researchers showing again that adult wolves were capable of spontaneously succeeding on tasks requiring the use of a human momentary distal point (Gácsi, Gyori et al., 2009). While it is difficult to determine exactly why previous experiments failed to obtain these results, predictions regarding testing methods, socialization, and a reduction in human interaction prior to the time of testing have been made (Udell et al., 2010b). It is also important to note that Virányi et al. (2008) found that wolves that had previously failed to follow a momentary distal point could learn to do so given additional experience. Regardless of the reasons for previous failures, the successes reported by Udell, Dorey et al. (2008) and Gácsi, Gyori et al. (2009) provided the first solid evidence that non-domesticated wolves possessed the capacity to utilize more complex human gestures without explicit training to do so. Whether a specific individual or group of wolves will be successful likely depends on a multitude of variables including early and recent life experiences.

These progressive changes, from the view that wolves should be considered incapable of following human gestures, to the view that wolves are only successful in following simple proximal gestures, to the most recent findings that wolves are capable of spontaneously following even the more difficult momentary distal point, illustrates the importance of interpreting negative results, or even the absence of results, with caution. This is especially true when only small numbers of a species have been tested and

some under considerable methodological constraints. The changes in knowledge about wolves' ability to utilize human gestures over the past eight years represents the evolution, not of the canid subspecies under test, but of the science behind those findings. Improved methods have allowed for more careful and analogous comparisons between individuals and subspecies, quality and timing of socialization have been considered, and importantly, a larger number of subjects have been tested.

Assessing the Range of Salient Human Stimuli

Despite this progress, data from only 35 wolf subjects have been published across the last decade: Two in Agnetta et al. (2000), seven in Hare et al. (2002), nine in Miklósi et al. (2003) and Virányi et al. (2008), eight in Udell, Dorey et al. (2008), and nine in Gácsi, Gyori et al. (2009). In total these experiments included only nine different gesture types as stimuli in object choice tasks. With the exception of gaze and local enhancement, all stimuli have been small variations on points made with the human arm and hand and each group of wolves was only tested on a small subset of these nine gestures. While the limited number of wolves tested is likely due to the restricted availability of socialized wolves in comparison to domestic dogs, it is still an important factor to take into account when interpreting scientific results. In contrast more than 35 pet domestic dogs are often found in a single study investigating responsiveness to human gestures. For example, 180 dogs were studied in Gácsi, Kara, Belényi, Topál, & Miklósi (2009) and 38 dogs were included in Udell, Dorey et al. (2008). Dogs have also been presented with a much wider range of gesture types. In fact, more novel stimuli can often be found in one domestic dog study, for example 16 stimuli in Udell, Giglio et al. (2008) and 9 stimuli in Soproni et al. (2002), than the total number of gestures utilized across all six studies conducted with wolves. Therefore, it is difficult to assess

the range of gestures wolves would be capable of using if presented with the opportunity.

Interestingly, wolves have demonstrated success, either at the individual or group level, in spontaneously following six of the nine previously mentioned human stimuli to locate a target. This speaks well for breadth of performance possible given the constraints of the current literature. Therefore claims that dogs are more responsive to a diverse array of human gestures may have nothing to do with differences in subspecies ability or capacity but could simply be a construct of the comparably large body of available literature on pet dogs in comparison to that exploring the abilities of other species and groups.

Experiment 1

In the following experiment this issue is addressed, assessing the capacity for human-socialized wolves to utilize a wide range of human gestures in an object choice task. Seven human-socialized wolves were given the opportunity to utilize nine novel gesture types to locate a target in an object choice task. None of these gestures had ever previously been utilized in a study with wolf subjects to my knowledge. Seven pet domestic dogs were also tested as a comparison group to the wolf subjects using the same methods and same nine gesture types.

Methods

Subjects

Seven pet domestic dogs (*Canis lupus familiaris*) and seven hand-reared human-socialized gray wolves (*Canis lupus*) participated in this study (Table 2-1). All pet domestic dogs were living in human homes as pets at the time of testing and were volunteered by their owners for participation in the study. Every dog in this study was

also enrolled in Camp Marlin Doggie Daycare, a facility where dogs are dropped off by their owners several days a week during daytime hours and engage in daily activities with other dogs and human caretakers.

All wolves in the study were from Wolf Park, located in Battle Ground, Indiana, and had been hand raised by staff from 10 to 14 days of age. All the wolves in this study were thoroughly socialized to humans using a process similar to that described in Klinghammer and Goodmann (1987). Wolf subjects were housed in large outdoor enclosures, with Ruedi, Wolfgang, Woton, Kalani living together in the main pack, and Marion, Ayla, and Tristan living in different enclosures located on the premises. All wolves interacted with humans daily and received food treats directly from humans on a regular basis. As such they were thoroughly habituated to the presence of humans and would readily eat from human hands.

All subjects had previously participated in a study utilizing the object choice task paradigm, where food could be earned by approaching one of two preselected containers in the presence of a human point. However none of the subjects, dog or wolf, had experienced any of the gesture types utilized in this study. This was done because it was not possible to test sufficient numbers of object-choice task naive wolves; therefore dogs and wolves with equivalent experience in the testing paradigm itself were selected to avoid unintended initial differences between the groups.

Testing Layout & Materials

Dogs were tested in a large indoor room within Camp Marlin's Doggie Daycare on days that they were already scheduled to be at the facility, incorporating behavioral testing into their normal daily routine. Additional dogs enrolled in daycare were located in an adjacent room or in an outdoor yard separated by a door. Therefore subjects had

little visual access to other dogs during testing but maintained some auditory and olfactory contact. Each dog was tested by a familiar experimenter; a caretaker at the facility who had previously been trained to conduct object choice tasks of this type.

Wolves were tested in an outdoor holding pen where fences and vegetation separated the animal under test from conspecifics. Similarly to the pet dogs, auditory, olfactory and some visual contact with the other wolves was possible. Each wolf was tested by a familiar experimenter; a caretaker at the facility who had previously been trained to conduct object choice tasks of this type. The experimenter was located inside the pen during testing; no barrier was present between any of the subjects and experimenter.

The testing layout is illustrated in Figure 2-1. The subject was led into the testing area by an assistant, E2, who travelled to a marked spot 2.5 m back from the experimenter, E1. The experimenter stood between the two response objects, which were located on the ground 0.5 m to either side of her. Two cylindrical metal empty unmarked paint cans (15 cm diameter, 22 cm tall), filled with gravel and with lids tightly fastened, served as the response choice objects. No food was present in or on either container until and unless the subject indicated a choice of the correct can by touching or coming within 10 cm of it with its snout. This eliminated the potential for olfactory cueing based on the location of hidden food, something that has been identified as a potential confound in prior studies (Udell, Dorey et al., 2008; Udell et al., 2010b).

The correct container was determined pseudorandomly before sessions, subject to the constraints that no one location was designated correct more than twice in a row and each location was correct for 50% of the trials.

Food rewards included 2-cm cubes of cheese, pepperoni, Bil-Jac® Liver Treats, and Pet Botanics® dog food rolls.

Pretraining Trials

Once the subject was at the designated starting place in the testing area, next to the assistant E2, the experimenter called it by name until it oriented towards her. The experimenter then held up a piece of food in the subject's view and placed it on top one of the testing cans. The subject was released, allowed to approach, and eat the food. This was repeated three more times, totaling two food presentations on each can.

Experimental Testing

During experimental trials the subject was called back to the starting position by the assistant and was distracted with food or attention until the experimenter began the trial by calling the subject's name. Once the subject oriented towards the experimenter the condition-specific gesture was directed towards the target can and the subject was released to make a choice. If the subject approached the correct container the experimenter placed a piece of food on top for consumption while giving verbal praise. Incorrect choices, approaching the alternative can or neither can within a minute, had no direct consequences and the subject was called back to the starting position to begin the next trial.

If any individual made three incorrect responses in a row, two pretraining trials were given (one to each side) to ensure that the canid was still motivated to obtain the food if it saw the placement of the food directly. No individual ever failed a test of motivation within an experimental session.

The nine gesture types were divided over three sessions, each consisting of thirty total experimental trials, or ten trials of each of three gesture types. Breaks of at

least an hour and no longer than two days were given between sessions. The duration varied based on an individual's immediate interest in food, determined by willingness to eat the food if freely presented, and scheduling within the testing facilities. All gesture were given from a forward facing orientation, in a standing position, were moved into place in view of the subject, and remained in place until the subject made a choice unless otherwise noted. The nine gestures (Figure 2-2) were defined as follows:

- Dynamic proximal point: While kneeling, E1 extends her ipsilateral arm toward the target container and maintains a point with her finger 10 cm from the target
- Bow: While standing between the response objects, E1 orients and lowers her head and torso over the target container and stares at it
- Body orient: E1 turns and orients towards the target container
- Asymmetric point: E1 steps behind the incorrect container but points to the target container with her ipsilateral arm and hand (distal point, > 50 cm from target)
- Head turn: E1 turns her head only and stares at the target container
- Back-turn distal point: With her back turned to the subject, E1 extends her ipsilateral arm toward the correct container and maintains a point with her finger more than 50 cm from the target
- Cross-body distal point: E1 extends her arm across her body toward the cross-lateral target container. She maintains a point with her finger more than 50 cm from the target
- Foot point: E1 stands on one foot while pointing at the target container with her ipsilateral foot
- Elbow point: E1 tucks her fist against her chest, near her armpit, while sticking her elbow out towards the ipsilateral target container

To reduce the potential for order effects across gesture types, different gesture orders were created and each point type was assigned a number. Gestures were divided into three session groups A, B, C. Session group A consisted of the dynamic proximal point (1), bow (2), and body orient (3). Session group B consisted of the

asymmetric point (4), head turn (5), back-turn distal point (6). Session group C consisted of cross-body distal point (7), foot point (8), and elbow point (9). Gesture Orders were as follows, Order 1: B 4, 6, 5; C 7, 9, 8; A 1, 3, 2 Order 2: C 8, 9, 7; B 5, 6, 4; A 1, 3, 2 Order 3: A 1, 3, 2; B 4, 6, 5; C 9, 7, 8. Order 1 was randomly generated and orders 2 and 3 were pseudorandomly generated to ensure counterbalancing of gesture order. Subjects were randomly assigned to a gesture order group (Table 2-1) with matching numbers of dogs and wolves experiencing each order type.

Control Trials

For each session the tenth and twentieth experimental trials were followed by one control trial and the thirtieth trial was followed by two control trials. This resulted in four control trials per experimental session, and twelve control trials total for each dog and wolf over the full three sessions of testing. On control trials a to-be-rewarded container was still determined, but the experimenter remained in a neutral position throughout the subject's approach and indication of choice. In other words, through the whole duration of a control trial the experimenter stood motionless, equidistant from the two response objects in a forward facing orientation looking straight ahead, and did not present an experimental gesture. However, the presentation of food still followed a correct choice just as in experimental trials. This was done to assess whether other extraneous cues could explain above chance performance in addition to, or in the absence of, the intended gesture. Wolves averaged 5.57 (Range, 4:7) control trials correct out of 12, and dogs averaged 6 control trials correct out of 12 (Range, 4:8). No individual performed greater than would be expected by chance on control trials (Binomial test, $p \geq 0.19$), suggesting that success on the task during experimental trials could be

attributed to the gesture under test and not extraneous cues present in the absence of the gesture.

Statistical Analysis

One sample t-tests were used to determine if dogs or wolves as a group performed significantly better than would be expected by chance on a particular gesture type. To determine if an individual subject performed above chance when using a particular gesture binomial tests were conducted; success was measured as eight or more trials correct out of ten ($p \leq 0.05$).

A two-factor ANOVA was used to compare the mean performance of dogs and wolves across gesture types and the performance of subjects when presented with the different forms of gestures. This test was followed up with t-tests, using a corrected alpha, to determine where significant differences existed when applicable. To determine if differences existed in the number of individual dogs and wolves meeting the success criterion on the task, Fishers exact tests were conducted for each gesture type. All tests were two-tailed and had an alpha of 0.05 unless otherwise noted.

Results

As a group, wolves successfully utilized six of the nine gesture types to locate the target object reliably (one-sample t tests, $t(6) > 2.40$, $p < 0.05$); these were the dynamic proximal point, bow, body orient, asymmetric point, back-turned distal point, and foot point. Dogs as a group utilized five of the nine gesture types (one-sample t-tests, $t(6) > 2.91$, $p < 0.05$); dynamic proximal point, bow, body orient, back-turned distal point, and cross-body distal point. In each of the gesture conditions at least one individual wolf and one individual dog was successful in using the gesture at above chance levels (binomial tests, $p < 0.05$) with the exception of the head turn and elbow pointing gestures. For

these conditions no individual wolf reliably located the target using the provided stimulus (binomial tests, $p > 0.05$), however two out of seven dogs were able to utilize the head turn and three were able to use the elbow point. Average performances and number of individual successes for each gesture type can be found in Figure 2-3.

Overall there was no significant difference between the performance of the socialized wolves and pet domestic dogs on the human guided task (Two-factor ANOVA, $F(1,12) = 3.73$, $p = 0.08$), there was however a strong effect of gesture type (Two-factor ANOVA, $F(8, 96) = 8.29$, $p < 0.0001$) and the interaction between gesture and canid type (Two-factor ANOVA, $F(8, 96) = 2.95$, $p < 0.005$) on performance. As a group dogs outperformed wolves on two of the nine gesture types: Cross-body distal (t-test, Bonferroni-corrected alpha = 0.006, $t(12) = 3.55$, $p = 0.004$) and back-turned distal ($t(12) = 3.47$, $p = 0.005$). At the individual level, however, dogs only significantly outperformed wolves in the back-turned distal condition (Fishers exact test, $p = 0.03$).

To test for generalization of response across gesture types, the average number of trials correct in a given condition was compared to the total number of experimental trials that the subject had experienced prior to the start of the condition. In other words, were subjects more successful in condition X if they had previously experienced 40 trials (utilizing gestures A, B, C, and D) than on condition Y after experiencing only 20 trials (A, B) independent of gesture type? A positive correlation was found between the number of previous trials and performance on the task ($R= 0.7$), suggesting that learning across conditions may have influenced performance on later gesture types. However, performance was generally high across most gesture types and gestures

often utilized different distinct parts of the human body; both of which could have limited the degree of possible improvement over trials.

Discussion

In any comparative endeavor there is a chance that some species or groups will receive more attention than others, possibly resulting in larger subject numbers, a greater diversity of stimuli, or wider range of methods tested and utilized. When this occurs it is often tempting to point towards the many examples of success found in a focal species to support predictions of unique capabilities or diverged cognitive skills. Resulting comparisons rest on the assumption that all other animals were treated equally when in practice this is often not the case. For canines this has resulted in claims that dogs are more like humans than are wolves in terms of certain social skills (Hare et al., 2002; Miklósi et al., 2003). However when wolves are human-socialized (Gácsi, Gyori et al., 2009; Udell, Dorey et al., 2008; Virányi et al., 2008) and are tested in a more equivalent manner to pet dogs (Udell, Dorey et al., 2008) they often perform well on human guided tasks (Gácsi, Gyori et al., 2009; Udell, Dorey et al., 2008). Furthermore the findings of this study unequivocally demonstrate that human-socialized wolves have the capacity to succeed on a wide range of gesture types beyond traditional points made with the human arm and hand.

Dogs were also successful in utilizing most of the nine gesture types in the object choice task. While their average performance was moderately better than that of the wolves on two-thirds of the point types, they only performed significantly better than wolves as a group when the gesture type was a back-turned distal point or cross-body distal point. Since wolves have been shown to match and even outperform domestic dogs on tasks requiring the use of a distal point in some cases (Udell, Dorey et al.,

2008), it would be interesting to further assess the importance of an experimenter turning her back or crossing her arm over her body in this type of task.

While testing conditions for both subspecies were kept as similar as possible, it is important to note two potential relevant factors in this study that may have influenced performance: (1) Wolves were necessarily tested outdoors, whereas dogs were tested indoors. (2) Since the dogs were pets and also enrolled in a doggie daycare their total exposure to humans on a daily basis was much greater than that of the wolves. In fact it was likely greater than that of many dogs tested in previous studies as well.

The outdoor-indoor difference in testing location was chosen for this study because Udell, Dorey et al. (2008) found that pet dogs tested outdoors showed a substantial decrement in performance in comparison to those tested indoors. When Udell, Dorey et al. (2008) tested dogs and wolves with a momentary distal point the most comparable groups were pet dogs tested indoors and wolves tested outdoors. This may be because the majority of pet dogs tested live and interact with humans primarily indoors, whereas the wolves live and interact with humans primarily outdoors. Therefore while it is possible that distractions inherent to an outdoor testing environment could lead to a decrement in performance for wolves, these two testing locations promised to provide the most functionally equivalent starting point for comparing performance across gesture types in this study based on past findings.

It should also be noted that the population of dogs utilized in this study, while denoted as pets, could in fact represent a distinct subgroup of pet dogs. Many pet dogs spend hours of each day alone while their owners go to work, run errands, or engage in other dogless activities. However the dogs in this study were regulars at a doggie

daycare that provided around the clock contact and supervision by humans. It is possible that these dogs were even more prepared to succeed on human guided tasks given this additional exposure. Differences of this type may account for some of the variation between individual dogs on human guided tasks. They might also account for a proportion of the differences in performance seen between wolves and dogs in this study, and possibly previous studies, as different durations and types of interaction experienced with human caregivers prior to testing might be an important variable in such experiments.

Another important aspect of these findings is the large amount of variability in performance; not only within and between subspecies, but within individual subjects as well. While a species' or subspecies' capacity to utilize a particular gesture can be demonstrated by a single individual's success on the task, this is not in practice sufficient to reliably predict the performance of other individuals in the presence of the same stimulus, or the same individual in the presence of a different human stimulus. While both dogs and wolves demonstrated the capacity to successfully utilize most gesture types, there was at least one individual dog and wolf for each gesture type that failed to locate the target at above chance levels. Previous studies have shown that individual responsiveness to human gestures is readily modified by life experience (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008; Elgier, Jakovcevic, Mustaca, & Bentosela, 2009; Udell et al., 2010a) therefore, it is likely that much of this variation is due to prior individual experiences and learning history.

Measuring the performance of domestic dogs and wolves across diverse gesture types provides information about the range of human stimuli that can be utilized by

individuals of each subspecies in an object choice task. However this approach is limited for several reasons. First, the presentation of stimuli that differ dramatically in form and location on the human body makes it difficult to identify the common topographical properties that predict the relative salience of different stimuli under test. Second, while the degree of individual variation and the trend towards improvement across gesture types (possibly due to generalization) suggests the influence of proximate variables, more research is needed to confirm that the salience of specific human gestures can be predicted by stimulus topography, individual learning history, or interactions between the two. In this respect, canine point-following behavior may tie into an established literature on stimulus control that dates back more than a century (Thorndike, 1898; Skinner, 1953). The following five experiments were designed to provide a controlled and systematic assessment of stimulus topography and proximate variables serving as likely contributors to canid success in human guided tasks. To allow for a more controlled and systematic analysis of relevant proximate variables, only variations on the basic point made with the human arm and hand were used and domestic dogs served as the model subspecies under test from this point forward.

Table 2-1. Subject name, canid type, age, sex, breed, and testing order

Subject	Canid Type	Age (Yrs)	Sex	Breed	Testing Order
Kalani	Gray Wolf	5	F	~	3
Ruedi	Gray Wolf	5	M	~	2
Renki	Gray Wolf	5	M	~	3
Ayla	Gray Wolf	5	F	~	2
Marion	Gray Wolf	9	F	~	1
Woton	Gray Wolf	4	M	~	1
Wolfgang	Gray Wolf	4	M	~	2
Delta	Domestic Dog	7	F	Basset hound	1
Jaxx	Domestic Dog	2.5	M	Labrador retriever	3
Black Jack	Domestic Dog	1	M	Labrador retriever	2
BJ	Domestic Dog	1.5	M	Jack Russell Mix	2
Moose	Domestic Dog	1.5	M	Labrador retriever	2
Buster	Domestic Dog	6	M	Beagle	3
Lucky	Domestic Dog	9	F	Labrador retriever	1

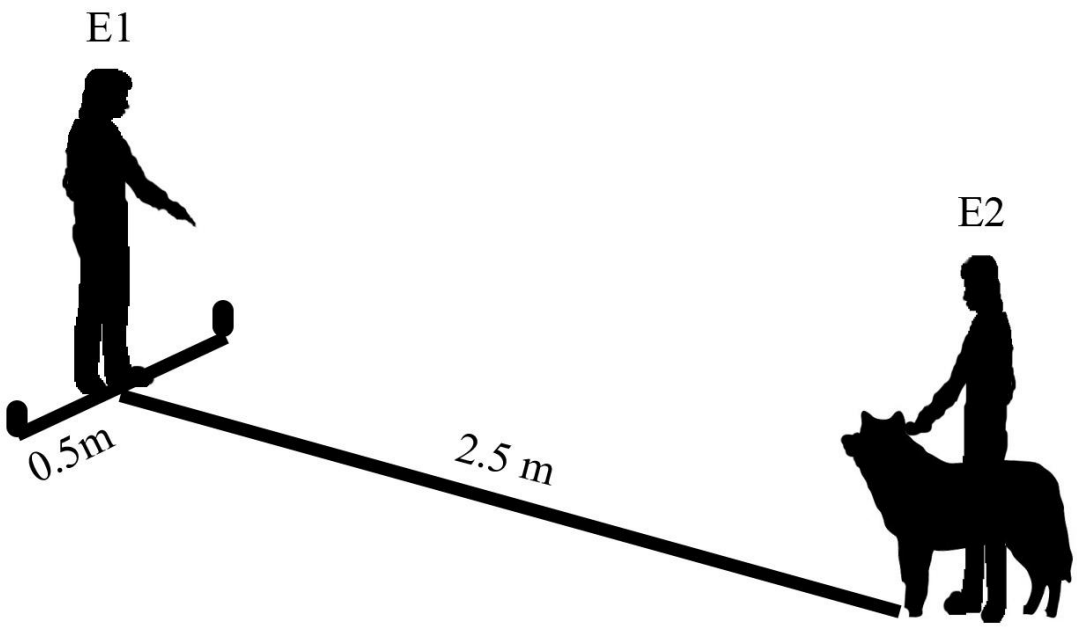


Figure 2-1. Testing Layout

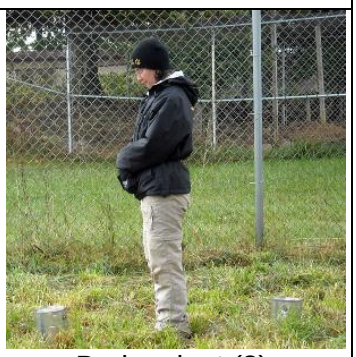
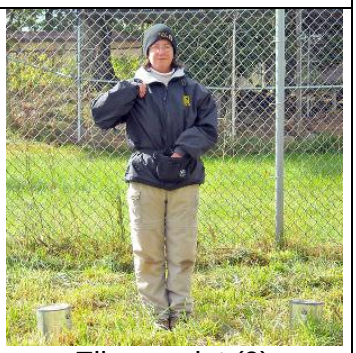
Session	Gesture Types		
A	Dynamic proximal point (1)	Bow (2)	 Body orient (3)
B	Asymmetric point (4)	Head turn (5)	Back-turn distal point (6)
C	Cross-body distal point (7)	Foot point (8)	 Elbow point (9)

Figure 2-2. Images of each of the nine gesture types used in Experiment 1, along with session and number designations.

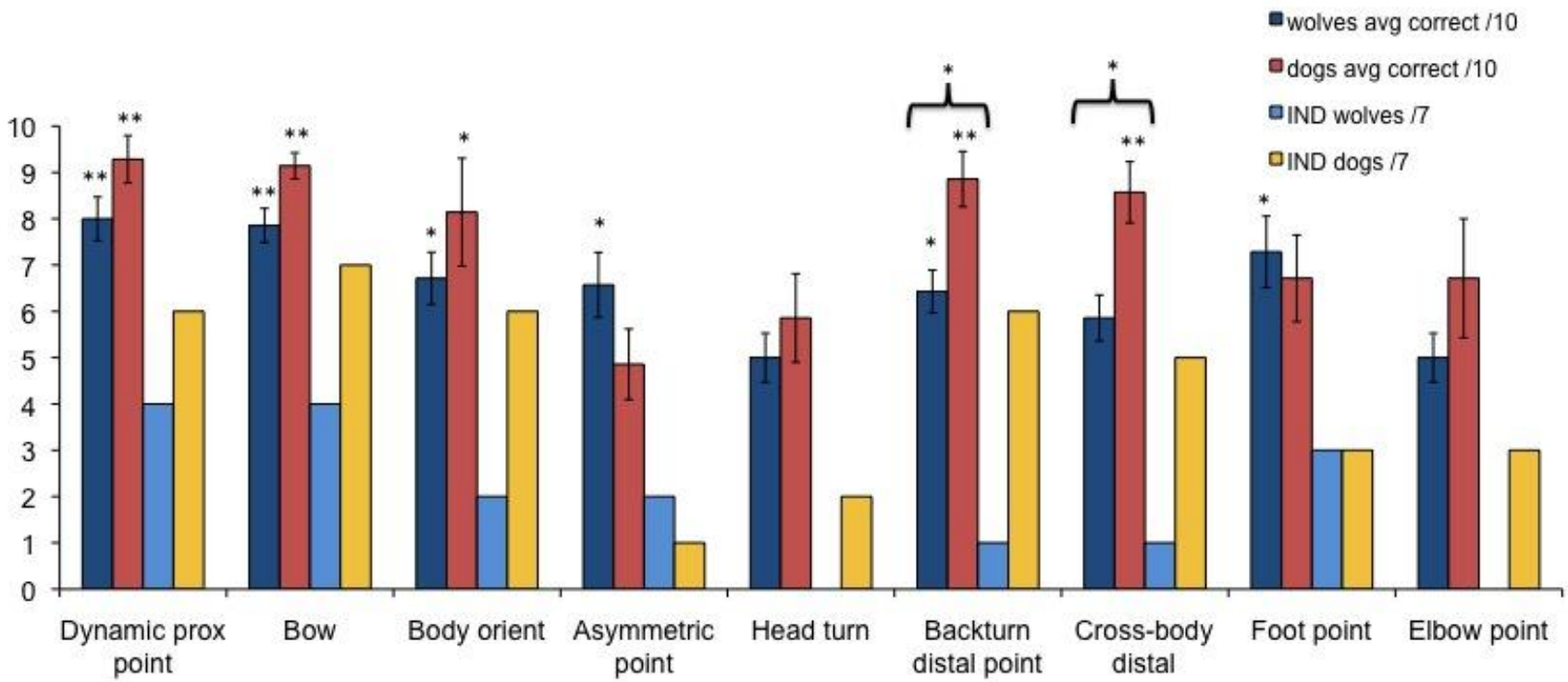


Figure 2-3. Mean performance and individual successes on the human-guided object choice task across the nine gesture types utilized in Experiment 1. The average number of trials correct (out of ten) for each gesture is indicated by the dark blue bars for wolves and red bars for dogs. The number of individuals in each group (out of 7) to successfully utilize a given gesture is illustrated by the light blue bars for wolves and the gold bars for dogs. An individual success was measured as eight or more trials correct out of ten (binomial test, $p < 0.05$). * Indicates $p < 0.05$, ** indicates $p < 0.001$. A * over a bracket represents a significant difference between dogs and wolves on a gesture type (t-test, Bonferroni-corrected, $p < 0.005$). Error bars represent SEM.

CHAPTER 3
STIMULUS PROPERTIES AND GENERALIZATION: POINT FOLLOWING PERFORMANCE ACROSS NINE POINTS GIVEN WITH THE HUMAN ARM AND HAND

Before the origins and mechanisms underlying dogs' responsiveness to human pointing can be fully understood a more fundamental question needs to be addressed: What constitutes a human point? In 2006, Miklósi & Soproni compiled 24 studies where non-human animals were required to utilize a point in an object choice task. Based on the description of stimuli used in these studies, the authors broke the basic pointing gesture into three temporal categories (static, dynamic, or momentary). Each of these categories could be broken down further into five spatial designations (at target/ touching, proximal, distal, cross body, or asymmetric) and then divided again into three attentional state categories (No gazing, gazing at target, gazing at subject, gaze alternation). As a result, over 60 different point-type topographies were possible given the dimensions introduced by different experimenters (Udell et al., 2010b). In other words, a Human Point cannot simply be taken as a unified term for a single gesture; in practice it is much more characteristic of a stimulus class. What is unknown is whether specific stimuli within the class serve the same function in terms of predicting the behavior of dogs, or for that matter humans, in response to the gesture. The lack of methodological consistency, and failure to standardize what is meant by "a point", makes comparisons across species, subspecies, or even across studies with the same species problematic. However determining whether different forms of human point have the same function, in terms of predicting the behavior of an onlooker, is critical to claim that human points have inherent communicative meaning.

Individual variation across different point and gesture types (Chapter 2; Gácsi, Kara et al., 2009; Udell, Dorey et al., 2008) suggests that dogs may not be responding to the human point as a unified stimulus. Therefore, some dimensions of human pointing might be more salient than others, and different populations or individuals may be watching and responding to different elements of human action. Furthermore, some individual point types, especially those possessing more salient stimulus properties, might predict more accurate performance across a wider range of subjects or populations in contrast to point types that possess only a few or none of the stimulus properties that prove to be the most salient to dogs.

This could have additional implications for the probability of generalization and learning within the human home or even during experimental testing. While there is evidence that additional exposure to the same human point type can improve canid performance on an object choice task (Udell, Giglio et al., 2008; Udell et al., 2010a; Virányi et al., 2008), it is unknown whether exposure to stimuli with common topographical properties might allow dogs to generalize their response to novel point types or a more difficult point that they were initially unresponsive to. If this is the case, methodologies that insert probe trials of more difficult point types into a string of salient point types, or methodologies that progressively increase stimulus complexity within testing, might overestimate dogs' spontaneous responsiveness to those point types (Lakatos et al. 2009; Soproni et al., 2002).

It has also been suggested that dogs "appear to understand the communicative nature of the pointing gesture" and are not simply responding to stimuli previously associated with reinforcement (Riedel et al., 2008, p.1013). This has raised questions

about whether dogs might also understand the intentionality of human movements during the production of communicative gestures (Riedel et al., 2008; Topal et al., 2009). The question of whether dogs perceive human points to be communicative and/or intentional in nature relates to a broader literature on Theory of Mind, or the capacity to take the internal knowledge state of others into consideration when behaving in their presence. In a review and critique of non-human primate theory of mind research, Heyes (1998, p. 102) defined the phenomenon this way: "An animal with a theory of mind believes that mental states play a causal role in generating behavior and infers the presence of mental states in others by observing their appearance and behavior under various circumstances". A large range of loosely related methodologies and behaviors has been associated with Theory of Mind. As a result the phenomenon has been difficult to operationalize and has received substantial criticism (Heyes,1998; Schlinger, 2009). However, some of the more carefully defined predictions associated with this area of study, for example an individual's attention to stimuli that predict the action or inaction of others under certain conditions, may still provide useful insight into canine social behavior.

Perspective taking tasks have been considered among the most promising for the study of Theory of Mind and related forms of social cognition (Heyes, 1998), and dogs have demonstrated success in using human cues of attentional state to solve a variety of these tasks. For example, when a dog has been told "leave it" in the presence of food it is less likely to approach or eat the forbidden item while its owner is watching. Once the owner is not looking or has an obstructed view, however, most dogs readily eat the food (Bräuer, Call & Tomasello, 2004; Call, Bräuer, Kaminski & Tomasello, 2003). In

contrast to the forbidden food task, begging tasks require a subject to beg from an attentive individual to obtain food while ignoring individuals with obscured vision. Pet domestic dogs have been equally successful on this task (Cooper et al., 2003; Gácsi, Miklósi, Varga, Topál, & Csányi, 2003). Furthermore, human attentional state has been found to predict whether or not a dog will follow certain basic obedience commands. In a study by Fukuzawa, Mills, and Cooper (2005) dogs who reliably responded to the commands “sit” and “come” when given by an attentive human, showed declines in performance when the human’s eyes were obscured by tinted sunglasses. Furthermore, when the human experimenter gave the two commands from behind a screen, dogs responded to the “come” command, a command often given when a dog is out of sight or far away, but not to the “sit” command, a command that would typically be presented when a dog is in sight at close proximity (Fukuzawa et al., 2005).

While some have noted the potential importance of experimenter gaze in object choice tasks (Miklósi & Soproni, 2006; Udell et al., 2010b), it is important to directly test whether a salient cue of experimenter inattention, similar to those used in begging and forbidden food tasks, would alter a pet dog’s response in the presence of a human point. If pointing can be regarded as inherently communicative then a human turning her back to the subject should reduce the salience of the pointing gesture substantially. In other words, experimenter orientation should result in a conditional discrimination where a human point is only followed IF the experimenter is oriented towards the subject. However, if point following is a response made in the presence of compound stimulus consisting of multiple salient properties, then attentional state alone should have less influence on overall performance.

In Experiment 2, I assess whether different forms of human point, made with the extended arm and finger, can be considered functionally equivalent stimuli—predicting consistent performance independent of stimulus topography—or if different forms of human point predict differing levels of following behavior by domestic dogs depending on stimulus form, which would suggest that different point types are functionally different stimuli.

Experiment 2: Does Performance and Perceived Task Difficulty Vary with Point Topography?

Experiment 2 was designed to provide a systematic comparison of different forms of the basic human pointing gesture by manipulating stimulus properties along the dimensions of movement/duration and distance (Figure 3-1). While prior studies have looked at differences in pet dog performance on object choice tasks in the presence of different gesture types (Miklósi et al., 1998; Soproni et al., 2001, 2002; Udell, Giglio et al., 2008; Udell et al., 2010b) and two meta-analyses have pointed out the importance of understanding the functional differences between point types (Dorey et al., 2009; Miklósi & Soproni, 2006), a systematic experimental manipulation of stimulus properties making up a basic human point with the extended arm and hand had not yet been achieved.

Methods

Experimenter Questionnaire

An invitation to participate in an online questionnaire was sent by email to 17 researchers currently publishing within the field of canine cognition. Out of this group, 11 individuals completed the questionnaire; all were familiar with the testing procedures typical to canine object-choice tasks. The primary purpose of the questionnaire was to

establish an independent rank order of predicted point type difficulty, which would determine the testing orders for dogs in Experiment 3. Because Experiments 2 & 3 were carried out simultaneously, performance scores from Experiment 2 could not be used for this purpose. Average rank and rating scores were also compared with each other and with the performance of domestic dogs on each point type in Experiment 2 to determine the degree of consistency between dependant and independent reports of point-type difficulty and whether such reports correspond with actual behavioral trends. The instructions for rating individual points were as follows:

> Please indicate how well you think pet dogs should follow different types of human points, either from your own experience or based on your expectations about how dogs should perform.

Each point type and definition (Table 3-1) could then be independently rated in difficulty from easy, 1, to difficult, 5, using the following provided guidelines:

1. Should be selected for a point that you think is very easy to follow, where all pet dogs would be expected to score perfectly
2. For a moderately easy point where more than half the dogs would be expected to perform above chance
3. For a slightly more challenging point where only half the dogs might score above chance
4. For a moderately difficult point where more than half the dogs would NOT be expected to perform above chance
5. A difficult point where only exceptional dogs would perform above chance

These instructions were followed by the presentation of each individual point type-definition pair with radial buttons ranging from one to five below the text. Following the independent point difficulty rating, were instructions to rate the point types in difficulty from easiest to most difficult (1-9) in relation to the other point types. The following instructions were provided:

Rank order the nine different types of point from (1) Easiest to (9) Most difficult. Use each rank number once (no ties). Definitions of points same as given above.

Pet Dog Performance

Subjects

Seventy-two pet dogs reported in good health comprised the study. All subjects had been residing in their current home for at least 4 months. All dogs were naive to the task at the time of testing. Additional subject information can be found in Table 3-2. To eliminate the possibility of generalization across point types, each subject only participated in one condition out of the nine possible point type conditions tested. See Table 3-1 for included point-type definitions. Therefore each condition required eight experimentally naive dogs. Dogs were randomly assigned to a condition before testing began.

Testing materials and layout

Two empty paint cans (15 cm diameter, 22 cm tall) with lids tightly fastened served as response objects. During experimental testing food was not present in or on either can until the subject made a correct response. This was done to control for the possibility that smell given off by hidden food could guide the dog's response independent of experimental stimuli. Although sham baiting, or smearing/false baiting both choice objects with food prior to testing, has commonly been used to address this potential confound in the past (Miklósi et al., 1998; Riedel et al., 2008) at least one study has demonstrated that sham baiting alone is an insufficient olfactory control for some canine subjects (Udell, Dorey et al., 2008). Another study demonstrated that dogs are capable of using olfactory cues to locate hidden food in an object choice task (Szetei, Miklósi, Topál, & Csányi, 2003) although dogs may sometimes continue to favor

visual human stimuli to olfactory cues. Given this demonstrated potential for olfactory cueing during object choice tasks, eliminating the practice of pre-baiting the target location ensures the absence of this possible confound.

The cans were placed 0.5 m on either side of the experimenter (E1) and remained there throughout testing. At the start of each trial an assistant (E2) held the subject 2.5 m back from the centerline of the experimenter (Figure 3-2). All distances were measured prior to testing and marked with masking tape on the floor.

During testing dogs were rewarded with a preferred type of commercially available dog treat. To ensure food motivation and absence of fear in the experimental setting, dogs were required to readily eat this treat from the experimenter's hand prior to testing to be included in the study. The correct container or target was determined pseudorandomly before sessions, subject to the constraints that no one location was designated correct more than three times in a row and each location was correct for 50% of the trials.

Pretraining

All testing began with pre-training to familiarize the dog with the response objects and associate the tops of the cans with the presentation of food. Pre-training consisted of the experimenter (E1) calling the dog's name to gain its attention. He then placed a treat on top the designated paint can in view of the dog. The dog was allowed to approach the can and consume the treat. Experimental trials began after a subject successfully completed four pre-training trials (2 trials for each can). A maximum of eight pre-training trials were given. Dogs then immediately moved on to experimental testing.

Experimental testing

During experimental trials the dog was held 2.5 m back from the empty cans by the assistant; the experimenter called the dog's name to gain its attention. The experimenter then administered the designated stimulus (one of the nine possible point types) indicating the previously determined target can. The assistant released the dog which was then allowed to approach one of the two cans. A choice was recorded when the dog's muzzle came within 10 cm of either can or when the dog touched the can with any part of its body. If the dog chose the correct can, the experimenter placed a treat on top of the correct can for the dog to consume. To minimize any effects of delay between the subject's response and receipt of food, the experimenter also marked a correct response by saying "good dog" while placing the treat on the can. If the dog chose the incorrect can, the assistant called the dog back and the next trial began. If the dog did not come within 10 cm of either can within one minute of being released, the assistant called the dog back and a 'no choice' was recorded. In addition to choosing the non-target container, no choice responses were considered incorrect responses in our analysis. If during testing the dog made three incorrect responses in a row, two additional pre-training trials were given, one to each can, to insure motivation. Loss of motivation, as indicated by failure to approach a can and take the food during these pretraining trials, resulted in a suspension of testing. No dog ever failed a test of motivation during testing. Each subject experienced a total of ten experimental trials, only witnessing a single assigned point type.

Control trials

A control trial followed every two experimental trials, with an additional control trial at the end of testing. In total each subject received six control trials. Control trials were

carried out in an identical way to experimental trials, except after calling the dog the experimenter remained in a neutral position (no point offered). This position was held until the subject made a choice or until one minute had passed indicating that the trial had timed out. The correct response or target can for control trials was determined with the same stipulations as the experimental trials. As in experimental trials, subjects received food on top the target can for correct choices and did not receive food if an incorrect response was made. This was done to detect the presence of extraneous stimuli that could be controlling the dog's behavior beyond the designated point in experimental trials. Dogs did not perform above chance in the absence of a pointing stimulus, with a mean of 1.99 (95% CI, 1.73-2.25) control trials correct out of six, suggesting that point following performance was not significantly influenced by other available stimuli within the experimental setting. In fact performance on control trials was slightly below chance as dogs sometimes refused to make a choice in the absence of an overt discriminative stimulus.

Statistical analysis

The results of the expert questionnaire were analyzed, first for correspondence between the two questionnaire measures - rating and ranking - and then to determine if these measures correlated with actual pet dog performance. Performance analysis was based on correct responses. An individual was considered successful on the task if it made eight or more correct responses out of ten trials (binomial test, $p \leq .05$). A one sample t-test was used to determine if a group of eight dogs performed better on a point type than would be predicted by chance. To determine if differences in performance existed across point types a single factor ANOVA was utilized. Performance between point types differing in designated point dimensions (movement/duration and distance)

were then compared using corrected t-tests. All statistical tests were two-tailed and had alpha set at 0.05 unless otherwise noted.

Results and Discussion

Performance Across Point Types

Each group of dogs was successful in following its assigned point type at above chance levels (one sample t-tests, $t(7) \geq 6.00$, $p < 0.0005$) with the exception of the static distal point group ($t(7) = 2.27$, $p = 0.06$) and the momentary distal point group ($t(7) = 0.34$, $p = 0.75$). Mean performance scores and number of individual successes for each group can be found in Figure 3-3. When comparing group performances for the different point types, a highly significant difference in the average number of correct responses between the nine point types was identified (Between-subject single-factor ANOVA, $F(11, 84) = 8.03$, $p < 0.000001$).

Stimulus Dimensions

The original prediction was that the source of differences between groups would be related to the stimulus dimensions of movement/duration, and distance (as measured between the end of the stimulus and target container), therefore two additional analyses were conducted.

Movement/duration could be broken into three categories based on the point-types utilized in this study: Dynamic (movement, point in place at time of choice), Static (no movement, point in place at time of choice), and Momentary (movement, point no longer in place at time of choice). Using corrected two-sample t-tests (corrected alpha, 0.02), a significant difference between pet dog performance on dynamic versus momentary points was found ($t(46) = 2.70$, $p = 0.01$), with dogs making more correct choices on average when presented with dynamic points. There was no significant difference

between momentary and static points (t (46) = 1.19, p = 0.24) or between dynamic and static points (t (46) = 1.82, p = 0.08).

The distance between the end of the pointing finger and the target could also be broken into three categories: Tap/touch (direct contact made with the target), proximal points (10 cm from target), and distal points (50 cm from target). Using corrected t-tests (corrected alpha, 0.02) a significant difference was found in pet dog performance when comparing distal points with proximal points (t (46) = 4.21, p = 0.0001) and distal points with tap/touch (t (46) = 4.25, p = 0.0001). In both cases dogs had a lower average number of correct responses when presented with a distal point than with alternative points coming closer to the target. There was no difference between tap/touch and proximal points (t (46) = 0, p = 1.00).

Expert Report

Expert reports of perceived point type difficulty were compared to subject performance on the task. Independent expert ratings were positively correlated with their dependant ranking of point type difficulty (Pearson's correlation coefficient, R = 0.99). These measures were also highly predictive of subject performance (Pearson's correlation coefficient, rating x performance, R = 0.94; rank x performance, R = 0.93). See Table 3-3.

Experiment 3: Does Experience and Order of Exposure Matter?

Experiment 3 was designed to investigate how experience and generalization during the course of testing might affect object choice task performance. Improved performance on novel point types, sharing some but not all stimulus properties with previously experienced point types, would identify a potential confound common to traditional within-subject pointing tasks. As in Experiment 2, dog subjects witnessed an

experimenter pointing at one of two containers; if the dog approached the pointed-to container the trial was scored as correct. However in Experiment 3 each subject received ten trials of all of the nine different point types (90 trials total). Eight of the subjects experienced the point type conditions in the order of increasing rank difficulty (Easy to Difficult); the other eight experienced the point types in order of decreasing rank difficulty (Difficult to Easy).

Methods

Subjects

Sixteen additional pet dogs reported in good health comprised the study. All subjects had been residing in their current home for at least 4 months. All dogs were naive to the task at the time of testing. Additional subject information can be found in Table 3-4.

Each subject experienced the full series of nine point types, as defined in Experiment 2 (Table 3-1). This was broken down into three sessions of three point type conditions each. Breaks between sessions were determined by participant availability but were never shorter than one day and never longer than two weeks. Half of the subjects experienced the point type conditions in the order of increasing rank difficulty (Easy to Difficult), half experienced the point types in order of decreasing rank difficulty (Difficult to Easy). Point type difficulty was based on the expert (not experimental) rankings from Experiment 2. Before testing began, dogs were randomly assigned to their respective conditions with one exception: if two dogs from the same household participated in the study each was assigned to a different condition to avoid potential confounds between condition assignment and living environment.

Testing Materials, Layout, Pretraining, and Experimental Trials

Materials, layout, pretraining, and experimental trials were identical to those in Experiment 2, with the following exceptions: As in Experiment 2 subjects experienced four pretraining trials at the beginning of each session to familiarize the dog with the response objects and associate the tops of the cans with the presentation of food. Since subjects in Experiment 3 were required to complete three point-type conditions per session (a total of 30 experimental trials, compared to 10 in Exp 1) an additional two pretraining trials, one to each side, were conducted after the first and second conditions of each session to ensure the dog was still food motivated before proceeding to the next condition. No subject failed a test of motivation within the course of a session.

Each subject received a total of 90 experimental trials over the course of testing; 10 trials per point type condition.

Control Trials

A control trial followed every ten experimental trials, resulting in three control trials per session and nine control trials per dog. Control trials were carried out in an identical way to experimental trials, except after calling the dog the experimenter remained in a neutral position (no point offered) until the subject made a choice or until one minute had passed. The correct response/ target can for control trials was determined with the same stipulations as the experimental trials. As in experimental trials, subjects received food for correct choices and did not receive food if an incorrect response was made. This was done to detect the presence of extraneous stimuli that could be responsible for controlling the dog's behavior beyond the designated point in experimental trials. Dogs did not perform above chance in the absence of a pointing stimulus, mean of 3.44 (95%

CI, 2.71-4.17) control trials correct out of 9, suggesting that point following performance was not influenced by other available stimuli within the experimental setting.

Statistical Analysis

Performance analysis was based on correct responses. An individual was considered successful on the task if it made eight or more correct responses out of ten trials (binomial test, $p \leq 0.05$). A one sample t-test was used to determine if a group of eight dogs performed better on a point type than would be predicted by chance. A two-factor within subject ANOVA was used to determine if there were significant differences in performance across point types and between the two subject groups (Difficult to Easy; Easy to Difficult). For each group, we also compared the performance between point types differing in designated point dimensions (movement/duration and distance) using corrected t-tests. All statistical tests were two-tailed and had alpha set at 0.05 unless otherwise noted.

Results and Discussion

Performance Across Point Types

Dogs in the Easy to Difficult condition were successful on each of the nine point types as a group (one sample t-tests, $t(7) > 4.50$, $p < 0.003$). At the individual level at least half the subjects performed significantly above chance (binomial tests, $p \leq 0.05$) on each point type. Dogs in the Difficult to Easy condition were successful on eight of the nine point types as a group (one sample t-tests, $t(7) > 3.25$, $p < 0.01$), failing to reach above chance performance only on the momentary distal point (one sample t-test, $t(7) = 1.67$, $p = 0.14$). No dog in the Difficult to Easy condition was individually successful on the momentary distal point (binomial tests, $p > 0.05$), and fewer than half

of the subjects in this condition were successful on the momentary proximal point (Figure 3-4).

Experience and Learning

A significant difference was found between the mean performances of dogs in the Easy to Difficult condition compared to dogs in the Difficult to Easy condition, with the former outperforming the latter on the series of object choice tasks (Two-factor within subject ANOVA, $F(1,14) = 5.97$, $p = 0.03$). There was also a highly significant difference in performance between point types ($F(8,112) = 15.3$, $p < 0.0001$), as well as a significant interaction between condition and point type ($F(8,112) = 5.66$, $p < 0.0001$). Because dogs were least successful on the momentary distal point in Experiment 2 we predicted that the effect of experience would be most apparent for this point type, therefore we directly compared the average performance of dogs experiencing this point first (Difficult to Easy condition) with dog who experienced this point last (Easy to Difficult condition). A highly significant difference was found between the mean performance of dogs experiencing eight simpler point type conditions prior to encountering the momentary distal point and those without prior experience (t-test, $t(7) = 4.72$, $p = 0.0006$).

Stimulus Dimensions

As in Experiment 2, two additional analyses were conducted to compare the salience of our focal stimulus dimensions (movement/duration, and distance) based on the performance of pet dogs on the object choice task. This was done separately for the two subject groups because prior analyses indicated that order of point exposure influenced the performance of dogs; especially in the presence of the most difficult point

types. We wanted to determine if each group's overall pattern of response across stimulus dimensions was different as well.

As in Experiment 2, movement/duration could be broken into three categories based on the point types utilized in this study: Dynamic, Static, and Momentary. Using corrected two-sample t-tests (corrected alpha, 0.02), we found no significant differences between Dynamic, Static and Momentary points for dogs in the Easy to Difficult condition ($t(46) \leq 2.28$, $p \geq 0.03$). On the other hand, dogs in the Difficult to Easy condition chose the correct target significantly more often when the pointing stimulus was Dynamic as opposed to Static ($t(46) = 3.37$, $p = 0.002$) or Momentary ($t(46) = 4.13$, $p = 0.0002$). No significant difference was found between Static and Momentary points ($t(46) = 1.66$, $p = 0.11$).

Distance between the point and the target could also be broken into three categories: Tap/touch, proximal points, and distal points. Using corrected t-tests (corrected alpha, 0.02), we found no significant differences between tap/touch, proximal and distal points for dogs in the Easy to Difficult group ($t(46) \leq 2.02$, $p \geq 0.03$). However dogs in the Difficult to Easy condition performed significantly better on tap/touch stimuli ($t(46) = 5.21$, $p < 0.0001$) or proximal points ($t(46) = 3.73$, $p = 0.0005$) when compared with distal points. No significant difference was found between tap/touch and proximal points ($t(46) = 1.17$, $p = 0.24$)

Experiment 4: Human Attention and Object-choice Tasks

In Experiment 4, three of the point types from Experiments 2 and 3 (dynamic tap, static proximal point, momentary distal point) were revisited with the addition of a third dimension: attentional state. In the case of the current study, attentional state can be operationalized in terms of human orientation. An experimenter facing the subject

during a trial was considered attentive, whereas an experimenter facing away from the subject was considered inattentive.

An experimenter's attentional state has often been considered an important factor in object choice tasks (Miklósi & Soproni, 2006), however the complete removal of attention during the presentation of a point had not yet been attempted in this experimental context. In the broader literature, pet dogs have been recognized for their ability to discriminate between a person looking towards them and one looking away or with obscured vision; maximizing their chances of obtaining reinforcement by modifying their behavior in the presence of attentive and inattentive audiences (Bräuer et al., 2004; Call et al., 2003; Cooper et al., 2003; Gácsi et al., 2003). This kind of selective responding based on human attention has been used to suggest that dogs recognize the communicative intent of others; a trait used to draw a parallel with behavior components thought to be important to Hominine evolution (Topal et al., 2009).

Consequently, from a higher-level communicative perspective, the presence of a cue that is traditionally used to signal that the experimenter is not aware of the dog would be expected to reduce responsiveness to typically salient gesture types. In other words, if dogs differentially respond to human points based on cues of communicative intent, inattention on the part of the experimenter should change the context of the point, removing the perceived cooperative or instructional function. As a result dogs should be less likely to utilize such stimuli in object choice tasks. On the other hand, point following behavior in dogs may occur as a response to a salient discriminative stimulus independent of assumptions about communicative intent. In this case the attentional state of the experimenter may act as one of many stimulus dimensions that

contribute to the overall salience of a specific point type, or could be entirely unimportant within the context of an object choice task. If this is true, the experimenter's attentional state alone should not be a strong predictor of success or failure on this task.

Methods

Subjects

All subjects were pet domestic dogs reported to be in good health at the time of testing. All subjects had been residing in their current human's home for at least 4 months. Additional subject information can be found in Table 3-5.

Subjects were divided into two groups: Experience and no experience. The experienced group was made up of eight dogs that had previously participated in Experiment 3, and as a result had experience with all nine point types used in that study. Individual dogs were recruited for Experiment 4 as soon as they completed Experiment 3, independent of performance, until the target number of eight subjects was reached. Like in Experiment 3, subjects in this group experienced all point types utilized in Experiment 4. Twenty-four naive subjects were included in the no experience group. Because each dog in the no experience group only received one of the three possible point types during testing this resulted in eight dogs per condition/point type.

Testing Materials, Layout, Pretraining, and Experimental Trials

Materials, layout, pretraining, control and experimental trials were identical to those in Experiment 3, with the following exceptions:

Only three point type conditions were included in Experiment 4: Dynamic tap, static proximal point, and momentary distal point. These conditions were selected because each point possessed different combinations of the stimulus dimensions

investigated in Experiments 2 and 3 (Figure 3-1), together representing a comparatively easy, moderate, and difficult form of the pointing stimulus.

The most significant change to the methods in Experiment 4 was the shift from forward facing to backwards facing point presentations. During experimental and control trials, the testing layout depicted in Figure 3-2 was utilized, however E1 faced away from the dog, looking towards a back wall for the duration of testing. As in the first two experiments, E1 called the dog to obtain its attention before the start of a trial. Since E1 could not see the dog from this position, the assistant, E2, began the trial by saying "point" to indicate that the dog had oriented towards the experimenter. Once the point had been presented the dog was released. The assistant was also responsible for alerting the experimenter once the dog had made a choice: "Yes" indicating a correct response, "No" indicating an incorrect response, and "Time" indicating that the one minute timeout period had passed and no choice had occurred. Scoring was based on the same choice criterion described in Experiments 2 and 3. The experimenter only provided the food reinforcer to the dog if the assistant indicated a correct choice. This was done to ensure that a prompt and consistent response was made to the dog's behavior during testing, even if it occurred outside of the experimenter's field of vision.

Dogs in the experience group were given ten experimental trials for each of the three back-turned point types in the following order: Dynamic tap, static proximal, momentary distal. Dogs experienced these three point types within one 20-30 minute session on a single day. In total, dogs in this group received 30 trials of back-turned points following the 90 trials of forward-facing points from Experiment 3.

Dogs in the no experience group were naive to the task when testing began and were randomly assigned to a single back-turned point type. Each dog in this group received only ten experimental trials.

Control Trials

Control trials were carried out in an identical way to experimental trials, except after calling the dog the experimenter remained in a neutral position (no point offered) until the subject made a choice or until one minute had passed. The correct response or target can for control trials was determined with the same stipulations as the experimental trials. As in experimental trials, subjects received food for correct choices and did not receive food if an incorrect response was made. This was done to detect the presence of extraneous stimuli that could be responsible for controlling the dog's behavior beyond the designated point in experimental trials. Overall, dogs in the experienced group did not perform better than would be expected by chance when no pointing stimulus was present, with a mean of 4.13 (95% CI: 3.24-5.02) out of 12 total. Dogs in the no experience group also performed below chance levels on control trials with a mean of 2.08 (95% CI: 1.57-2.59) out of 6, suggesting that point following performance was unlikely influenced by other available stimuli within the experimental setting.

Statistical Analysis

Performance analysis was based on correct responses. An individual was considered successful on the task if it made eight or more correct responses out of ten trials (binomial test, $p \leq 0.05$). A one sample t-test was used to determine if a group of eight dogs performed better on a point type than would be predicted by chance.

A two-factor ANOVA (one within, one between) was used to determine if there were significant differences in performance across back-turned point types and between the two subject groups (experience, no experience). The mean performance scores of experienced and inexperienced dogs for the back-turned momentary distal point condition were also independently compared using a t-test. Based on the outcome of Experiment 3, and the point types ranking as the most challenging point, it was predicted that regardless of overall performance across point types the momentary distal point would be the strongest independent indicator of performance change attributed to prior experience.

Lastly, the mean scores of dogs with no prior experience for each back-turned point type were compared to the mean scores of dogs with no prior experience on the same point types in the forward facing orientation (from Experiment 2) to evaluate the independent function of attentional state in the context of an object choice task. All statistical tests were two-tailed and had alpha set at 0.05 unless otherwise noted.

Results and Discussion

Dogs in the experienced group performed above chance on all three of the back-turned point types (one-sample t-tests, $t(7) \geq 7.17$, $p < 0.001$). Individually, out of eight dogs, a total of seven successfully used the dynamic tap, six dogs used the static proximal point, and six dogs used the momentary distal point to locate the target at above chance levels (binomial tests, $p \leq 0.05$). Dogs with no prior experience were also successful in using the dynamic tap and static proximal point as a group (one sample t-tests, $t(7) > 13.75$, $p < 0.001$) but did not perform above chance on the task in the back-turned momentary distal point condition (one sample t-test, $t(7) = 0.31$, $p = 0.77$) (Figure 3-5). Individually, out of the eight dogs for each condition in the no experience

group, all eight performed above chance (binomial tests, $p \leq 0.05$) on the back-turned dynamic tap and static proximal point conditions, while only two dogs performed above chance (binomial tests, $p \leq 0.05$) on the back-turned momentary distal point condition.

Differences in dogs' average performance by point type (Two-factor ANOVA, $F(2,28) = 19.1$, $p < 0.0001$) and in interactions between point type and prior experience (Two-factor ANOVA , $F(2,28) = 8.32$ $p = 0.001$) were identified, however no significant difference was found between groups (experience vs no experience) when point types were pooled (Two-factor ANOVA, $F(1,14) = 3.03$ $p = 0.10$). However, when the mean group performances were compared for the back-turned momentary distal point alone, the group of dogs with prior experience performed significantly better on the object-choice task than the naive dogs (t-test, $t(7) = 3.21$, $p = 0.008$).

To assess performance differences predicted by the orientation of the experimenter alone, the mean performances of inexperienced dogs witnessing a dynamic tap, static proximal point, and momentary distal point in Experiment 2 (forward facing) and Experiment 4 (back-turned) were compared using a two-factor between-subject ANOVA. Although differences between point types were found ($F(2, 42) = 33.10$, $p < 0.0001$) with the worst performance corresponding with the presentation of a momentary distal point, a significant difference was not found between the performance of dogs in the forward-facing versus back-turned group ($F(1, 42) = 0.064$, $p = 0.80$). A significant interaction effect between point type and experimenter orientation was also lacking ($F(2,42) = 0.192$ $p = 0.82$).

General Discussion

The results of this study suggest that different forms of a human point, even those utilizing the same portions of the human arm and hand, can act as functionally different

stimuli in the context of an object choice task. Specific stimulus properties of human points, including the duration and distance of a point, alter the salience of these point types, predicting different levels of success for pet dogs. These findings suggest that human stimuli, and different versions of the basic human pointing gesture, cannot be used interchangeably if valid comparisons are to be made within or across different studies, species, or breeds.

Although our findings suggest that the specific stimulus properties of a human point influence object choice task performance, the next step is to ask why some properties might be more effective predictors of success than others. For example, in the current study a stimulus presented at a further distance from the target (distal point) might make it difficult or impossible for dogs to view both the stimulus and point at the same time during the stimulus presentation. Momentary points additionally eliminate the dog's ability to view the discriminative stimulus at the time of choice. While the dog may be able to see the human point and the target separately, it may not perceive any physical connection between the point and the target in either or both of these cases. This could add a memory component to the task, adding an extra layer of complexity, or requiring an additional strategy to perform with high accuracy. It is interesting to note that while the combination of the momentary and distal components led to the most challenging point type across all three experiments, dogs were successful in utilizing a range of other point types possessing either the momentary or distal component in other combinations. Therefore predicting the degree of salience associated with a pointing stimulus may not be as easy as calculating the sum of its parts.

In Experiment 3, dogs in the Easy to Difficult group displayed a clear trend of improved performance on more difficult point types, in comparison to the less experienced subjects in the Difficult to Easy group. The effect of prior experience was most pronounced for the momentary distal point condition, where dogs with prior experience outperformed inexperienced dogs on the task at both the group and individual level. As in Experiment 2, dogs in the Difficult to Easy condition of Experiment 3 showed the most difficulty in utilizing a momentary distal point in the object choice task, however this group also showed a decrement in performance when presented with static points.

Importantly, dogs in the Easy to Difficult condition performed equally well across point type dimensions, failing to show a decrement in performance when a point type possessed a momentary, static, or distal component. Because dogs in this group experienced a total of 20 pointing trials before encountering a point with a static component, 30 trials before a momentary component, and 60 trials before a distal component, generalization across different point types appears to have improved this group's overall performance. Exposure to the task, even when utilizing points containing some but not all of the stimulus properties present in the most difficult points, was enough to place individuals with this experience at a significant advantage. Generalization across stimuli during the course of experimental testing, even after only a small number of trials, appears to be sufficient exposure for these experienced dogs to succeed on all point types, even where the occurrence of spontaneous success for naive dogs is rare. Therefore within-subject research intended to survey the domestic dog's spontaneous success on human-guided tasks (Soproni et al., 2001; Virányi et al.,

2008) should carefully consider the likelihood of generalization across human stimuli or the effects of experience across trials.

It should be noted, however, that generalization within the course of an experiment may be less likely in studies utilizing stimuli that differ greatly from one another (Miklósi et al., 1998; Udell, Giglio et al., 2008). For example, conditions utilizing a momentary distal point towards a target followed by a condition using a head turn. While it is possible that subjects may still learn something about the task—including the desired topography of response or even to attend to human movement more generally—a drastic shift in stimulus form or location could potentially decrease performance on the task. For example, a dog may still attend to the experimenter's neutrally placed hand when the solution is to be found by looking at the experimenter's head. In Experiment 3, the solution could always be found by looking at the experimenter's arm and hand, with stimulus topography changing only slightly across conditions.

Lastly, the results of Experiment 4 suggest that the attentional state of the experimenter did not significantly influence pet dog performance in the context of the human-point-guided object choice task. Dogs with no prior experience were likely to succeed on the dynamic tap and static proximal point conditions and fail on the momentary distal point condition independent of experimenter orientation. This suggests that dogs may not rely on cues of cooperative intent or intentionality when responding to human points.

An important outcome of this study, especially given the findings of Experiment 3, is the demonstration that a certain history of experience, related to, but not specifically including exposure to momentary distal points, can prepare pet dogs to outperform

naive dogs on an object choice task utilizing this stimulus. This implicates a learning mechanism for the development of this behavior, and not a fixed capacity to utilize specific stimulus properties in this case. However, it is possible that other foundational stimulus properties are necessary for a dog to utilize a human point as a stimulus, for example, adequate stimulus size given an individual's visual acuity (Udell, Giglio et al., 2008), or sufficient contrast with a given background (Lakatos et al., 2007). It is also possible that the degree to which certain stimulus properties are functionally necessary or important varies by dog breed or population.

Udell, Dorey et al. (2008) noted that one population of domestic dogs, dogs living in an animal shelter, performed poorly on a human guided task requiring the use of a momentary distal point. Unlike the successful wolves and pet dogs tested indoors, not a single shelter dog followed the human point at above chance levels. Although shelter dogs could conceivably represent a distinct biological population, whose abnormal health or cognition resulted in abandonment, the findings of the current study suggest that such results might be influenced by the stimulus type under test and exposure to relevant stimuli within their current environment. In other words pet dogs and shelter dogs could belong to different social populations that experience different levels and types of exposure to human stimuli. This in turn might make different human stimuli initially more or less salient to each group, however such differences should be reduced with additional exposure to the task. The following two experiments ask (1) whether shelter dogs are universally unresponsive to human pointing, or if they can successfully use more salient forms of the gesture, and (2) if shelter dogs become more proficient in following a momentary distal point with additional experience.

Table 3-1. Point type definitions

Point Type	Definition
Static touch	The experimenter touches the target container with one finger while the dog's view of the testing area is blocked. The dog is then allowed into the testing area while the experimenter maintains his touching position until the dog makes its choice.
Dynamic tap	The experimenter extends his arm toward the target container while the dog watches and continually taps the container with one finger until the dog makes its choice.
Momentary tap	The experimenter extends his arm toward the target container while the dog watches and taps four times on the top of the container with one finger. The experimenter then returns to a neutral position and the dog is released to make its choice.
Static proximal point	The experimenter begins pointing towards the target container, with his finger 10 cm from the container, while the dog's view of the testing area is blocked. The dog is then allowed into the testing area and the experimenter maintains his pointing position until the dog makes its choice.
Dynamic proximal point	The experimenter extends his arm toward the target container while the dog watches and maintains a point with his finger 10 cm from the container until the dog makes its choice.
Momentary proximal point	The experimenter extends his arm toward the target container while the dog watches and maintains a point with his finger 10 cm from the container for 4 seconds. The experimenter then returns to a neutral position and the dog is released to make its choice.
Static distal point	The experimenter begins pointing towards the target container, with his finger 50 cm from the container, while the dog's view of the testing area is blocked. The dog is then allowed into the testing area and the experimenter maintains his pointing position until the dog makes its choice.

Table 3-1. Continued

Point Type	Definition
Dynamic distal point	The experimenter extends his arm toward the target container while the dog watches and maintains a point with their finger 50 cm from the container until the dog makes its choice.
Momentary distal point	The experimenter extends his arm toward the target container while the dog watches and maintains a point with their finger 50 cm from the container for 4 seconds. The experimenter then returns to a neutral position and the dog is released to make its choice

Table 3-2. Subject information for Experiment 2

Name	Age (yrs)	Sex	Breed	Point type condition
Bodie	2	M	Beagle	Dynamic Distal Point
Buster	6	M	Beagle	Dynamic Distal Point
Citta	2	F	Beagle mix	Dynamic Distal Point
Jackson	7	M	Golden retriever	Dynamic Distal Point
Jasmine	2.5	F	German shepherd	Dynamic Distal Point
Necco	4	M	Border collie	Dynamic Distal Point
Noel	8 mth	F	Boxer mix	Dynamic Distal Point
Penny	2	F	Terrier mix	Dynamic Distal Point
Ben	4	M	Labrador retriever	Dynamic Proximal Point
Bingo	12	M	Mix	Dynamic Proximal Point
Candi	10	F	Chow mix	Dynamic Proximal Point
Dottie	1.5	F	Dachshund	Dynamic Proximal Point
Kilo	?	M	Great Pyrenees	Dynamic Proximal Point
Mima	2.5	F	German shepherd	Dynamic Proximal Point
Penny Lane	3	F	Boston terrier	Dynamic Proximal Point
Zuni	2	not recorded	Chi	Dynamic Proximal Point
Booker	3	M	Cockapoo	Dynamic Tap
Dakota	4	F	Boxer	Dynamic Tap
Lada	2.5	F	Pitbull	Dynamic Tap
Marley	7	M	Bernese mountain dog	Dynamic Tap
Nikita	11	F	German shepherd	Dynamic Tap
Otis	4	M	Cairn terrier	Dynamic Tap
Prince	2.5	M	Shar-pei mix	Dynamic Tap

Table 3-2. Continued

Name	Age (yrs)	Sex	Breed	Point type condition
Tug	1.5	M	Basset hound	Dynamic Tap
Black Jack	1	M	Labrador retriever	Momentary Distal Point
Delta	7	F	Basset hound	Momentary Distal Point
Jack	3	M	Shepherd mix	Momentary Distal Point
Jaxx	2.5	M	Labrador retriever	Momentary Distal Point
Marlin 1	1.5	M	Border collie mix	Momentary Distal Point
Molly	4	F	Hound mix	Momentary Distal Point
Sasha	11	F	Chow	Momentary Distal Point
Tigger	2	M	Mix	Momentary Distal Point
Autmn	1	F	Labrador retriever mix	Momentary Proximal Point
Bailey	5	F	Labrador retriever mix	Momentary Proximal Point
Bejhe	4	M	Shih tzu	Momentary Proximal Point
Gigi	9 mth	F	Labrador retriever	Momentary Proximal Point
Landis	6 mth	M	Lab mix	Momentary Proximal Point
Lucky	9	F	Labrador retriever	Momentary Proximal Point
Marlin 2	7	M	Labrador retriever	Momentary Proximal Point
Moon	1	M	Labrador retriever	Momentary Proximal Point
Ananda	5	F	Collie mix	Momentary Tap
Aro	1.5	M	Pug	Momentary Tap
Ellie	4	F	Labrador retriever	Momentary Tap
Lily	1.3	F	Hound mix	Momentary Tap
Lou	3	M	Labrador retriever mix	Momentary Tap
Patty	2.5	F	Anatolian shepherd mix	Momentary Tap
Pie	3.5	F	Flat coat retriever	Momentary Tap
Timbo	4	M	Dachshund	Momentary Tap

Table 3-2. Continued

Name	Age (yrs)	Sex	Breed	Point type condition
Bella	4	F	Miniature pincher	Static Distal Point
Butch	10	M	Mix	Static Distal Point
Clyde	9	M	Doberman pincher	Static Distal Point
Cody	3	M	Lab-beagle mix	Static Distal Point
Harvin	2	M	Lab-basenji mix	Static Distal Point
Higgins	1	M	English bulldog	Static Distal Point
Lucy	1	F	Chihuahua	Static Distal Point
Pretzel	2	M	Boston terrier	Static Distal Point
Bam bam	4	M	Goldendoodle	Static Proximal Point
Bo	7	M	Labrador retriever	Static Proximal Point
Brodie	8 mth	M	Australian shepherd mix	Static Proximal Point
Kima	2.5	F	Mix	Static Proximal Point
Loki	1	M	German shepherd	Static Proximal Point
Nuisance	10	F	Mix	Static Proximal Point
Pete	6	F	Retriever mix	Static Proximal Point
Tracker	8	M	Australian shepherd	Static Proximal Point
Diesel	?	M	Australian shepherd	Static Touch
Duke	5	M	Lab-pitbull mix	Static Touch
Hank	9 mth	M	Redbone coonhound	Static Touch
Moose	1.5	M	Labrador retriever	Static Touch
Rocky	1	M	Goldendoodle	Static Touch
Rubert	?	M	Mix	Static Touch
Sydney	2	F	Cattledog mix	Static Touch
Wesley	7	M	Lab-pointer mix	Static Touch

Table 3-3. Point type expert rank, rating, and subject performance rank

	Expert Score		Performance
Point Type	Rank (/9)	Rating (/5)	Rank (/9)
Dynamic tap	1	1.09	1
Dynamic proximal point	2.5	1.45	2
Static touch	2.5	1.64	4.5
Momentary tap	4	1.82	4.5
Static proximal point	5	2.18	3
Momentary proximal point	6	2.45	6
Dynamic distal point	7	3.00	7
Static distal point	8	3.27	8
Momentary distal point	9	3.36	9

Table 3-4. Subject information for Experiment 3

Name	Age (yrs)	Sex	Breed	Condition
Arthur	7	M	Australian shepherd	Easy to Difficult
Sadie	3	F	Lab-Rottweiler mix	Easy to Difficult
Rocky H.	8	M	Beagle-German shepherd	Easy to Difficult
Hannah	3	F	Lab-boykin spaniel mix	Easy to Difficult
Rumor	2	F	Glen of Imall terrier	Easy to Difficult
Balfour	2.5	M	Glen of Imall terrier	Easy to Difficult
Meara	5	F	Glen of Imall terrier	Easy to Difficult
Mango	5	F	Beagle	Easy to Difficult
Cole	2	M	Labradoodle	Difficult to Easy
Rocky M.	5	M	Boxer	Difficult to Easy
Bretzl	3	F	Glen of Imall terrier	Difficult to Easy
Beckett	9 mth	M	Glen of Imall terrier	Difficult to Easy
Addie	6	F	Beagle	Difficult to Easy
Jager	1	M	German shorthair pointer	Difficult to Easy
Tyler	9	M	German shepherd mix	Difficult to Easy
Madison	6	F	Mix	Difficult to Easy

Table 3-5. Subject information for Experiment 4

Name	Age (yrs)	Sex	Breed	Condition
			Experience (from Exp 2)	
Arthur	7	M	Australian shepherd	All Points
Sadie	3	F	Lab-Rottweiler mix	All Points
Rocky H.	8	M	Beagle-German shepherd	All Points
Hannah	3	F	Lab-boykin spaniel	All Points
Meara	5	F	Glen of Imall terrier	All Points
Cole	2	M	Labradoodle	All Points
Rocky M.	5	M	Boxer	All Points
Beckett	9 mth	M	Glen of Imall terrier	All Points
			No Experience	
Gollum	3	M	Pitbull	Dynamic Tap
Gus	9 mth	M	Bullmastiff	Dynamic Tap
Jackson 2	1.75	M	Labrador retriever	Dynamic Tap
Jade	7.5	F	Great Dane	Dynamic Tap
Jo Jo	?	M	Maltese mix	Dynamic Tap
Lexi	1.5	F	Border collie mix	Dynamic Tap
Lilly	1.1	F	Labrador retriever	Dynamic Tap
Sasha 2	7	F	Labrador retriever	Dynamic Tap
Abbie	3	F	Beagle- Chihuahua mix	Momentary Distal Point
Betsy	6 mth	F	Husky	Momentary Distal Point
Bowser	6	M	Pitbull mix	Momentary Distal Point
Chloe	5	F	Boxer	Momentary Distal Point
Milli	6	F	Great Dane-rottweiler mix	Momentary Distal Point
Smiegel-Beagle	3	M	Pitbull	Momentary Distal Point

Table 3-5. Continued

Name	Age (yrs)	Sex	Breed	Condition
			No Experience	
Styx	8 mth	F	Shar pei-Australian shep.	Momentary Distal Point
Tomko	6 mth	M	Pitbull	Momentary Distal Point
Cabo	?	M	Unknown	Static Proximal Point
Cash	2.5	M	Toy poodle	Static Proximal Point
Ellie Sanchez	6	F	Pitbull-hound mix	Static Proximal Point
Famous	2	F	Pitbull	Static Proximal Point
Phantom	2	M	Pitbull	Static Proximal Point
Stanford	5.5	M	Chihuahua mix	Static Proximal Point
Sugar	1.5	F	Boxer	Static Proximal Point
Zaya	6 mth	F	Pitbull	Static Proximal Point

		Movement/Duration		
		Dynamic	**Static**	**Momentary**
Distance	**Touch/Tap:**	**Dynamic Tap**	Static Touch	Momentary Tap
	Proximal (≤ 10cm):	Dynamic Proximal	**Static Proximal**	Momentary Proximal
	Distal (≥ 40cm):	Dynamic Distal	Static Distal	**Momentary Distal**

Figure 3-1. Point type conditions identified by combinations of relevant stimulus dimensions. All nine point type conditions were utilized in Experiments 2 and 3. Black boxes indicate point types also tested in Experiment 4 where attention was removed during stimulus presentation.

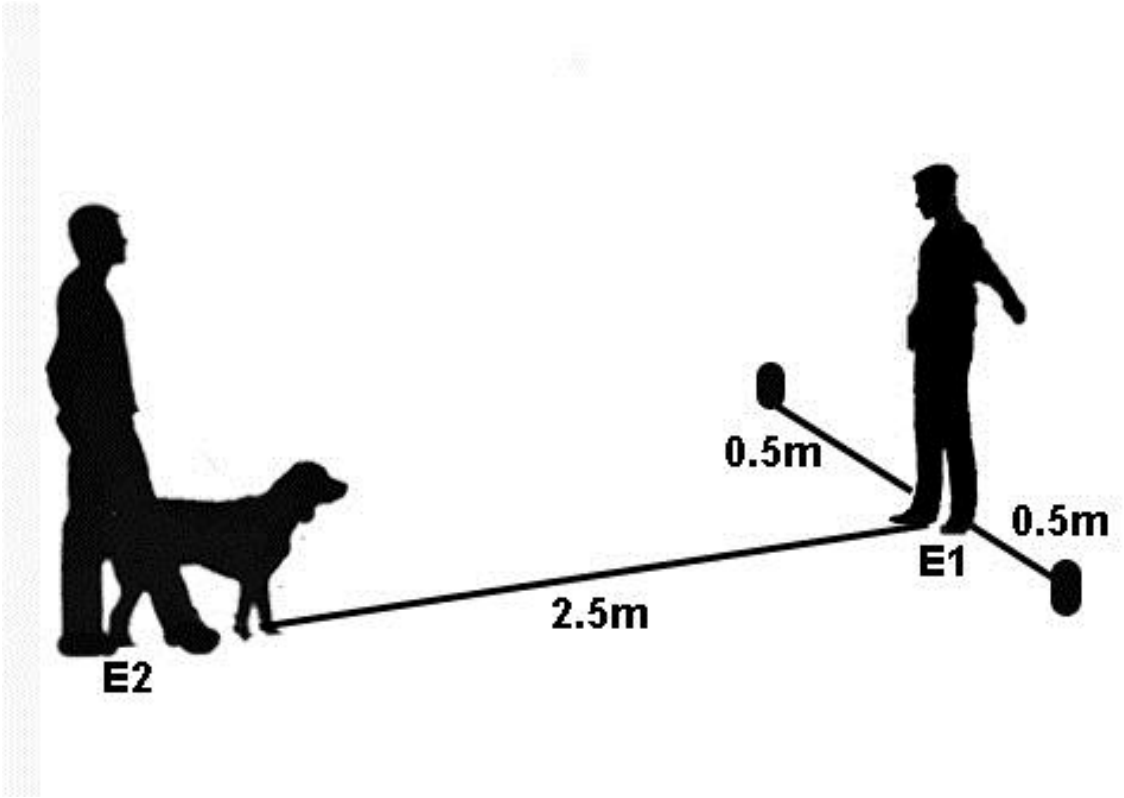


Figure 3-2. Testing Layout

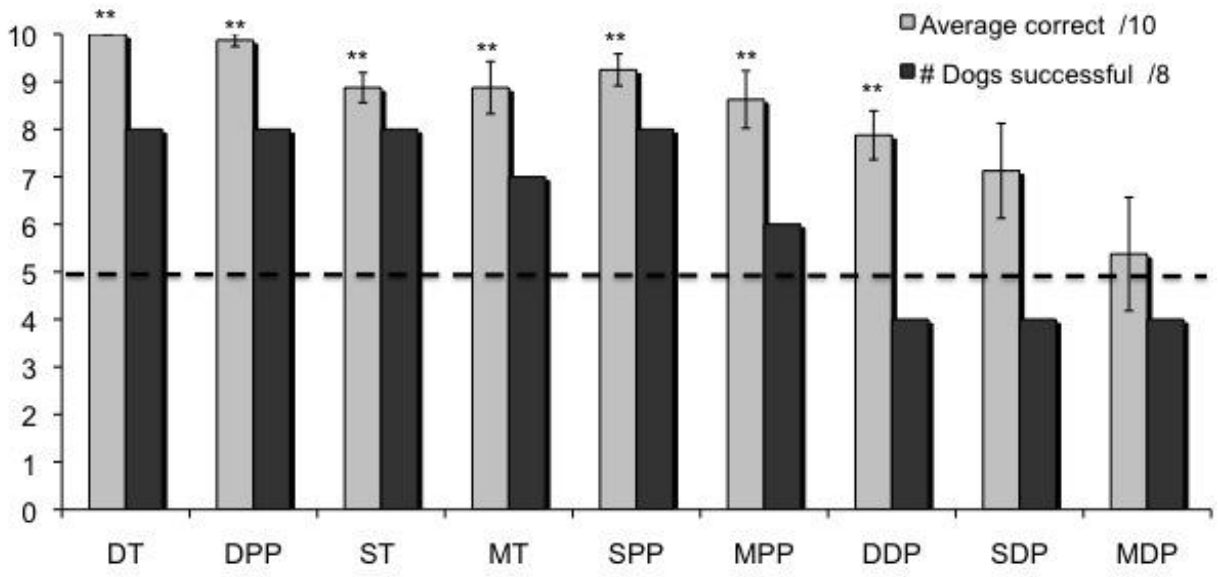


Figure 3-3. Mean number of correct responses and number of successful individuals across point types in Experiment 2. Point types are abbreviated as follows: DT (Dynamic tap), DPP (Dynamic proximal point), ST (Static touch), MT (Momentary tap), SPP (Static proximal point), MPP (Momentary proximal point), DDP (Dynamic distal point), SDP (Static distal point), MDP (Momentary distal point). Error bars represent +/- SEM. ** indicates one sample t-test, $t(7) \geq 6.00$, $p < 0.001$. Individuals were considered successful with a point type if they made eight or more correct responses out of ten (binomial test, $p \leq 0.05$). Dashed line at chance.

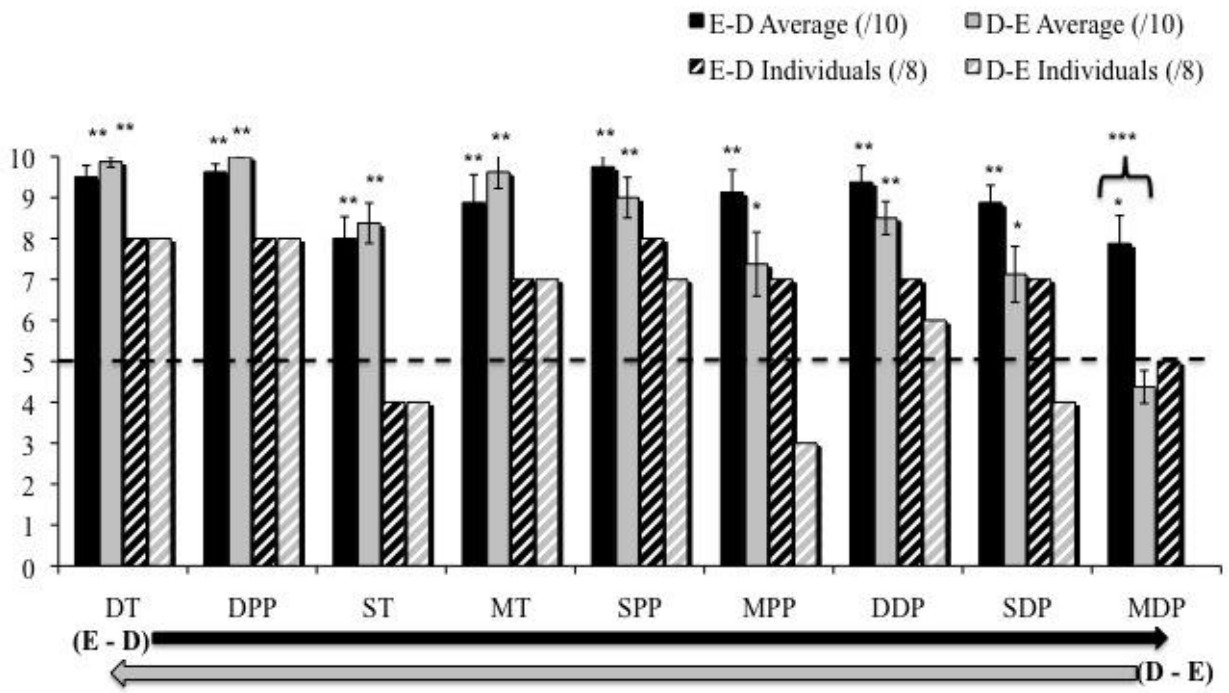


Figure 3-4. Mean number of correct responses and number of successful individuals across point types in Experiment 3. Point types abbreviations are the same as Figure 3-3. Dog subjects in the Easy to Difficult (E-D) condition experienced all point types in order from left to right. Dog subjects in the Difficult to Easy (D-E) condition experienced all point types in order from right to left. Error bars represent +/- SEM. ** indicates one sample t-test, $t(7) \geq 6.00$, $p < 0.001$; * indicates one sample t-test, $t(7) \geq 3.25$, $p < 0.05$. *** Located over the momentary distal point bracket indicates a significant difference between groups (t-test, $t(7) = 4.72$, $p < 0.0006$). Individuals were considered successful if they made eight or more correct responses out of ten on a point type (binomial test, $p \leq 0.05$). Dashed line at chance.

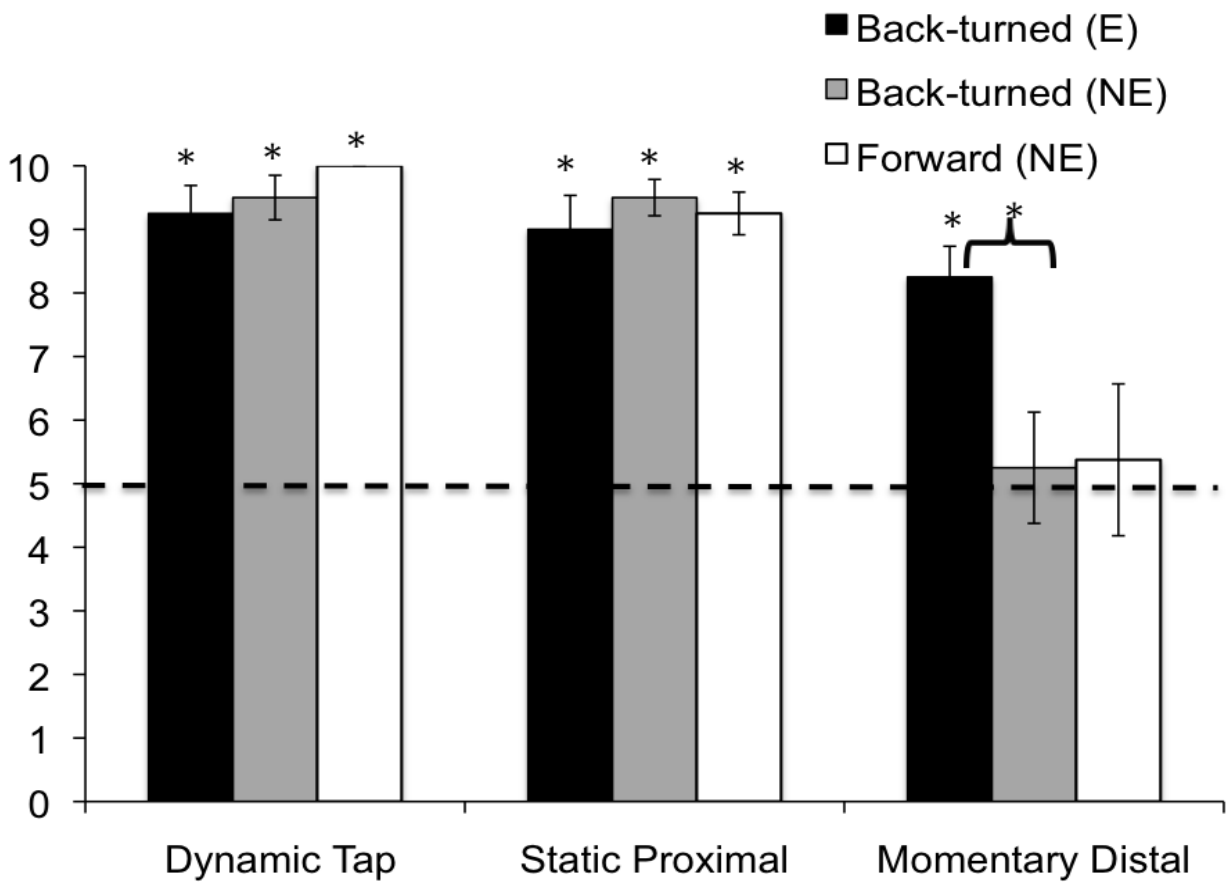


Figure 3-5. The influence of attentional state and experience on pet dog perfomance across three point types. The grey bars show the average number of trials (out of 10) where naive (NE) dogs in the back-turned condition made the correct response. This performance was compared to dogs with prior experience in object choice tasks (E) participating in a back-turned variation for the first time, black bars, and the perfomance of naive dogs from Experiment 1 on the forward-facing version of this task, white bars. * indicates $p < 0.05$ as determined by one-sample t-tests. * over brackets indicates $p < 0.05$ as determined by a two-sample t-test. Error bars represent SEM. Dashed line is at chance.

CHAPTER 4
SHELTER DOG PERFORMANCE ON POINTING TASKS: STIMULUS TOPOGRAPHY AND EXPERIENCE[1]

As mentioned previously, the great majority of subjects in studies of the origins of domestic dogs' human-compatible social cognition have been pet dogs living in human homes (Udell et al., 2010b), with human oriented working dogs representing the remainder of the subject pool (Miklósi et al., 1998; Marshall-Pescini, Valsecchi, Petak, Accorsi, & Previde, 2008). Even within this population, specific breeds and breed groups are over represented and others not represented at all (Dorey et al., 2009). While pet and working dog populations might be the standard forms of domestic dog in the Western world, whether in terms of population numbers or the ease of acquiring potential subjects, free roaming or "village dogs" are reported as "the most abundant dog category in underdeveloped areas of the world" (Ortolani, Vernooij, & Coppinger, 2009, p. 211). Ortolani et al. (2009) demonstrated that when approached by a human, the most common response made by village dogs in four Ethiopian villages was to flee (52%). An additional 11% responded to the approaching human with aggression. Only 4% of the surveyed population approached the human non-aggressively. Such populations have not been tested on human guided object-choice tasks, but with only a 4% non-aggressive approach rate it would be hard to imagine that the performance of this group of dogs would look the same as that achieved by pets living in the Western world if such a test could be carried out at all. Free roaming dogs fill a different niche

[1] Portions of this chapter were previously published by the author as part of the following scientific journal article: Udell, M. A. R., Dorey, N., Wynne, C. D. L. (2010). The performance of stray dogs (*Canis lupus familiaris)* living in a shelter on human guided object-choice tasks. *Animal Behaviour,* 79, 717–725.

than do pets; their behavioral responses must be modified to fit the environmental pressures they face in their lives.

Village dogs in underdeveloped nations, however, are not the only population of domestic dogs with life experiences distinct from those of pets. Even within the United States, six to eight million dogs can be found in shelters each year (Humane Society of the United States, 2008): that is roughly 11 percent of the U.S. domestic dog population (American Veterinary Medicine Association, 2007). Despite their prevalence in the countries where the majority of the current research is conducted, domestic dogs living in shelters are heavily underrepresented in research investigating responsiveness to human social cues. Unlike pet dogs and hand-reared wolves, shelter dogs identified as strays were found to be unsuccessful at following a human experimenter's momentary distal point to a target location to obtain food (Udell, Dorey et al., 2008). This finding suggests that shelters are a good place to look for context or life experience variables that lead to success or failure of individual dogs on these tasks. This would not only include variables that might set shelter dogs apart as a population, including possible genetic and ontonogenic differences, but also variables which might be a product of recent experience, living environment, or testing environment. Evidence of differences in the behavior of populations within a subspecies of animals, is important when attempting to draw comparative conclusions between species and subspecies of animals.

The purpose of the current study was to explore the reasons for shelter dogs' poor performance in following human pointing gestures. Experiment 5 compares shelter dogs' ability to spontaneously follow a momentary distal point with their performance on

a simpler dynamic proximal point. In Experiment 6, shelter dogs that were unable to spontaneously follow a momentary distal point were trained to do so in two different conditions. These experiments thus test variables that contribute to the differences in performance between dogs residing in a shelter and those living in human homes. Furthermore they assess if and how individuals who initially fail to follow human points are able acquire this ability during their lifetime.

Experiment 5: The Effect of Point Topography on Shelter Dog Performance

Different forms of human pointing may be more or less salient to a dog based on topographical features apparent to the dog during an experimenter's presentation of the cue (Chapter 3; Dorey et al., 2009; Miklósi & Soproni, 2006; Udell, Giglio et al., 2008). It is possible that stray dogs residing in a shelter may have experience with, and thus be more sensitive to, some features of human pointing, while lacking sensitivity to others (Udell et al., 2010a). On the other hand, it is possible that the capacity for canine responsiveness to human gestures is a general and inherited trait requiring little or no exposure to humans during the dog's lifetime (Hare et al., 2002; Riedel et al., 2008). If this were the case, shelter dogs failing to use one form of human point in an object-choice task would be predicted to fail in using others as well, possibly indicating a subset of domestic dogs lacking the capacity for, or the behavioral phenotype associated with, responsiveness to human gestures. In Experiment 5 seven dogs residing in a local shelter were presented with two forms of human point alternating in order to determine if stimulus topography is an important variable for these subjects in an object-choice task.

Methods

Subjects

Seven dogs classified as strays, housed at a local animal shelter, were used in this study (Table 4-1). All dogs were at least four months old, had been checked by a veterinarian, were in good health, and had been cleared for adoption. The only other requirement was that the dogs had to be willing to approach the experimenter and eat from her hand. This was to ensure the absence of potential stress or fear that might have prevented responding in the presence of the newly introduced experimenter. Such behavioral characteristics are consistent with dogs socialized to humans during their sensitive period of social development (Scott & Fuller, 1965), although the specific details surrounding a subject's early life were unknown.

Materials

Two cylindrical metal empty unmarked paint cans (15 cm diameter, 22 cm tall), with lids tightly fastened, served as the response choice objects. No food was present in or on either container until and unless the subject indicated a choice of the correct can by touching or coming within 10 cm of it with its snout. This was done to eliminate the possibility that the dogs could be learning to sniff out available food in the target container. Although many studies pre-bait the correct container during an object-choice task, Udell, Dorey et al. (2008) and Szetei et al. (2003) have reported that some canids are able to detect a prebaited container by smell alone, introducing the potential for a confounding olfactory cue. However, pet dogs have been shown to perform equally well on an object-choice task even when the container is not prebaited (Udell, Dorey et al., 2008), thus this methodology was used to place full control in the point type used and to eliminate extraneous variables.

The correct container was determined pseudorandomly before sessions, subject to the constraints that no one location was designated correct more than three times in a row and each location was correct for 50% of the trials. Food reinforcers included: Pet Botanics® dog food rolls, Publix® Jerky Sticks, Publix® Bacon Wavy Treats, and Purina® Little Bites dog food.

Pretraining

The animal was separated from conspecifics and brought into an indoor garage space that served as the testing area where it could be visually separated from other dogs and kennels within the facility. Figure 4-1 shows the configuration of the testing area. An assistant (E2) stood at a distance of 2.5 m from the midline between the cans with the subject until the experimenter (E1) was ready to proceed. At the start of a trial the subject was called by the experimenter until it oriented towards her. The experimenter next held up a piece of food in the subject's view and placed it on top of one of the two cans. The subject was then released and allowed to approach the can and eat the food. To proceed to experimental testing the subject had to approach the can with food first and consume the food four times within eight possible trials. This was to ensure motivation and willingness to respond prior to testing. All of the subjects passed this initial criterion and moved on to participate in experimental trials.

Experimental Testing

In Experiment 5, subjects were exposed to two different types of human pointing during experimental trials, a momentary distal point and a dynamic proximal point, as well as control trials where no point was issued. The definitions for each point type were as follows:

Momentary distal point: From a standing position, the experimenter's ipsilateral arm and hand were extended into a traditional point in the direction of the target container while the subject watched. The tip of the experimenter's finger was 50 cm from the closest edge of the target container at full extension. After a two second presentation the experimenter's arm was retracted back to a neutral position before the subject was allowed to make a choice.

Dynamic proximal point: From a kneeling position, the experimenter's ipsilateral arm and hand were extended into a traditional point in the direction of the target container while the subject watched. At full extension the tip of the experimenter's finger was 10 cm from the target can. The experimenter then maintained this point until the end of the trial.

Control trial: The experimenter maintained a neutral position (standing after sessions 1 and 3, kneeling after sessions 2 and 4) facing forward until the end of the trial.

Each subject received a total of 40 experimental trials, 20 for each point type, and eight control trials. Trials were broken into four testing sessions each consisting of ten experimental trials followed by two control trials. In sessions 1 and 3 the experimenter presented a momentary distal point. In sessions 2 and 4 the experimenter presented a dynamic proximal point. This alternation of point types was intended to control for possible order effects (see discussion). Two (sessions 3 and 4) or four (sessions 1 and 2) pretraining trials were conducted before each session to test for motivation. A break of at least 15 minutes and up to an hour was given between sessions 2 and 3. Short breaks lasting no more than 3 minutes were taken between the other sessions to allow

the experimenters to obtain more treats and prepare for the next set of trials. All experimental trials were completed during the same day for all subjects.

The testing layout for experimental trials was identical to pretraining (Figure 4-1). An assistant stood at a distance of 2.5 m from the midline between the cans with the subject until the experimenter was ready to proceed. No food was present on or in either of the testing cans at the start of a trial. The experimenter called the subject until it oriented towards her. At that time the experimenter presented the session designated point type, and the dog was released to make its choice. Once a dog touched or placed its muzzle within 10 cm of either can, or after one minute, the trial came to an end, was scored, and the assistant called the subject back to start the next trial. A trial was only scored as correct if the subject touched or placed its muzzle within 10 cm of the target can indicated by the experimenter's point, prior to choosing the alternative can.

Statistical Analysis

One sample t-tests were used to determine if a group of subjects approached the target container significantly more than would be expected by chance after witnessing a human experimenter present each point type. Separate one sample t-tests were run for the first and second rounds (first and second ten trials) of each point type in addition to the evaluation of overall performance. This was done to detect any changes in performance patterns that might be due to learning or order effects within experimental trials.

A paired t-test was used to compare the mean number of correct choices out of 20 that shelter dogs made on the object-choice task when presented with the two types of point. The initial mean scores of shelter dogs were also compared using a paired t-test

(round 1: sessions 1 and 2), as were the final scores (round 2: sessions 3 and 4) after shelter dogs had received prior experience with both point types.

Binomial tests were used to determine each dog's individual performance using each point type during each session. A subject's performance was said to be significantly above chance if a dog got 15 or more trials correct out of the full 20 trials ($p \leq 0.04$) or eight or more trials correct out of ten within a session ($p \leq 0.05$). A Fisher's exact test was used to determine if more dogs performed significantly above chance at the individual level during the first or second rounds of testing. Learning within a point type was assessed by comparing performance on the first and last five trials of testing out of the 20 experimental trials for each point type using a paired t-test. All statistical tests were two-tailed and had alpha set at 0.05.

Results

As in Udell, Dorey et al. (2008) shelter dogs did not choose the target container significantly more often than would be expected by chance when presented with a momentary distal point both overall (one sample t-test, $t(6) = 0.52$, $p = 0.62$) as well as in the first (one sample t-tests, $t(6) = 0.29$, $p = 0.78$) and second ($t(6) = 0.63$, $p = 0.55$) rounds of testing. Conversely, shelter dogs were highly successful at using the experimenter's dynamic proximal point to locate the target container at above chance levels (one sample t-test, $t(6) = 16.71$, $p < 0.0001$). This was not only true overall, but for each independent round of testing as well (one sample t-tests, round 1: $t(6) = 10.19$, $p < 0.0001$; round 2: $t(6) = 12.01$, $p < 0.0001$). Shelter dogs did not perform above chance levels on control trials, choosing the target can during only 34% of trials on average (95% CI: 14%-54%).

When the mean numbers of correct choices made by the subjects on the two types of point were compared, shelter dogs experiencing both point types chose the target can significantly more often when presented with the dynamic proximal point (paired t-test, $t(6) = 3.51$, $p = 0.01$). Again when the first and second rounds of testing were analyzed separately, shelter dogs were still found to choose the target can significantly more often in the presence of the dynamic proximal point (paired t-tests, round 1: $t(6) = 3.91$, $p = 0.008$; round 2: $t(6) = 2.44$, $p = 0.05$), although less of a difference between the two point types was detected by the second round of testing (Figure 4-2).

Considering the individual performance of the subjects, (Figure 4-3), three out of the seven shelter dogs performed significantly above chance when presented with the momentary distal point over 20 trials (binomial test, $p \leq 0.04$). However, similarly to Udell, Dorey et al. (2008), performance during the first round of 10 trials was low with only one dog out of seven performing significantly above chance (binomial tests, $p = 0.02$). In the second round, two dogs scored significantly above chance (binomial tests, $p \leq 0.02$). At the individual level shelter dogs were more successful in following a dynamic proximal point, with all seven dogs choosing the correct can at above chance levels (binomial tests, $p \leq 0.003$). When analyzed separately, all but one dog performed above chance in the first round (binomial tests, $p \leq 0.02$), and all dogs performed above chance in the second round (binomial tests, $p \leq 0.05$).

To assess the probability of learning over the course of experimental testing, the first and last five trials of each point type were compared using a paired t-test. There was no significant difference between the mean number of correct responses during the

first and last five trials of testing for either the momentary distal point ($t(6) = 0.48$, $p = 0.65$) or for the dynamic proximal point ($t(6) = 0.54$, $p = 0.61$).

Discussion

Overall there was a clear effect of point type on the performance of shelter dogs in the human guided object-choice task. The same group of dogs that failed to use a momentary distal point consistently chose the correct container when the experimenter displayed a dynamic proximal point. It is unlikely that the shelter dogs performed poorly on the momentary distal point trials due to of lack of motivation, since the same dogs performed almost perfectly on the same task, in the presence of the same experimenter, and for the same food reinforcer, when the point type was substituted with the dynamic proximal point. It is also unlikely that satiation over time could account for this performance, since successful performance on the dynamic distal point followed failure on the momentary distal point in rotating conditions. Furthermore, because each dog had two rounds of testing with each point in an alternating order it is impossible to attribute shelter dogs' superior performance on the dynamic proximal point to order effects alone. However, shelter dogs did appear to improve slightly on the task over additional trials within each point type (Figures 4-2 and 4-3).

Therefore the most probable explanation for this performance is that shelter dogs find some human stimuli more salient than others in the context of an object-choice task. This is an interesting outcome for at least two reasons.

First, these findings demonstrate that dogs residing in a shelter do not possess an "all or nothing" ability to follow human points. Their failure to utilize a momentary distal point did not predict their performance on an object-choice task utilizing a different form of human point. This suggests that comparisons between domestic dog populations

should consider different forms of response in the presence of different human stimuli instead of searching for evidence of a universal inborn capacity to respond to human gestures. Furthermore, this is constant with the differences seen between individual pet dogs and groups of dogs differing in experience level in Chapter 3.

A second reason the present results are intriguing is that similar findings have been reported for a population of human-socialized wolves. Virányi et al. (2008) found that socialized wolves that were initially unsuccessful in using a human momentary distal point could nonetheless follow simpler points to the target location, including a dynamic distal point, momentary proximal point, and touching the target container in an object-choice task. After additional experience with the more difficult momentary distal point, the wolves in Virányi et al. (2008) did show improvement, after a total of 220 trials, all wolves performed significantly above chance on the task.

The most interesting factor when comparing the current population of shelter dogs with the wolves tested in Virányi et al. (2008) is the fact that the wolves in their study, while socialized to humans in early life, were removed from their caretakers and relocated to a ‘wolf farm’ once they reached two to four months of age. Although the caretakers visited the wolves about twice a week, this similarity in performance between Virányi et al.’s wolves and the present shelter dogs, coinciding with separation from a human home, and relocation to a facility with reduced or altered human interaction prior to testing, may suggest circumstances that lead to reduced performance on tasks utilizing more difficult forms of human point, even across species.

Although the comparison of subjects’ scores in the first and last five trials of testing showed no significant differences, this may be because averaging a small subset of

scores is an underpowered method of assessing possible learning within the task. Therefore the experimental procedures and data analysis in Experiment 6 were designed specifically to measure the affects of additional experience on the performance of shelter dogs in an object-choice task utilizing a momentary distal point. This approach addressed an unanswered question about the performance of shelter dogs: Can shelter dogs learn to use a momentary distal point to identify a target location after exposure to additional trial presentations?

Experiment 6: Can Shelter Dogs Learn to Follow a Momentary Distal Point?

Out of a total of 15 shelter dogs tested for their ability to use a momentary distal point in an object-choice task, in two methodologically similar experiments (Experiment 5; Udell, Dorey et al., 2008), only one dog performed above chance within the first ten trials of testing. However, Experiment 5 also indicated that shelter dogs were highly successful when presented with an easier form of gesture, the dynamic proximal point. Thus it is unlikely that stray dogs residing in shelters represent some genetically distinct portion of the population lacking the capacity for sensitivity to human gestures. Two other variables, however, might explain the low performance of shelter dogs in the presence of momentary distal points. The first is context. It is possible that the new testing environment or introduction to the new experimenter creates a level of stress, excitement or distraction that could reduce performance on more difficult forms of object-choice tasks. This could have a constant effect or the effect might wane with time as the subject habituates to the new situation. The second possibility is that the subjects possess inadequate experience with the stimulus properties associated with the more difficult form of point. As mentioned above, the momentary distal point requires a shift in

attention from the experimenter's finger to the target and includes a memory component since the point is no longer in place when a choice is made.

In Experiment 6 it was asked whether additional experience with the momentary distal point would allow shelter dogs that initially failed to meet criterion on the object-choice task, to associate the presentation of the gesture with the location of the target can. To control for possible effects of testing context and excitement in the presence of the new experimenter, half of the subjects were exposed to a Play-Train condition designed to habituate the subjects to these new features of the environment before proceeding to training; the other half began the training phase immediately after baseline.

Methods

Subjects

Sixteen additional dogs classified as strays, housed at a local animal shelter, were used in this study (Table 4-2). All dogs were naive to the task, at least four months old, were in good health, and had been cleared for adoption. The only other requirement, as in Experiment 5, was that the dogs had to be willing to approach the experimenter and eat from her hand, demonstrating that stress or fear levels were not high enough to prevent responding in the presence of the experimenter. One of the subjects, 22B, was not food motivated and thus was dropped. Another subject, 20B, met the criterion for point following in baseline and thus did not proceed to the training phase of the study. In total 14 dogs met the pretesting criterion and completed the training portion of the study.

Materials and Layout

The experimental setup, materials, testing objects, choice definitions, and pretraining trials were identical to those used in Experiment 5.

Baseline Testing

During all experimental trials the experimenter (E1) stood between two empty paint cans on the ground and pointed to one of them for 2 s, while the assistant (E2) stood with the subject 2.5 m away facing the experimenter (Figure 4-1). After 2 s the experimenter returned to a neutral position and looked straight ahead until a choice was made. The point was given from a standing position with the can between 0.5 - 0.8 m away from the tip of the experimenter's finger at full extension, qualifying as a momentary distal point. When a subject chose the correct can, the experimenter dropped a piece of food on the chosen container and allowed the dog to consume it. For an incorrect choice the experimenter remained in a neutral position and no food was presented. Once a choice was made, or after one minute had passed, the assistant called the subject back to the starting location and began the next trial. Ten experimental trials were presented to each subject during baseline. If any individual made three incorrect responses in a row, two pretraining trials were given (one to each side) to ensure that the canid was still motivated to obtain the food when the approach response required to obtain the food was unambiguous. No individual, with the exception of 22B who was disqualified from the experiment during pretraining, ever failed a test of motivation.

Control Trials

In baseline, every two experimental trials were followed by a control trial. During control trials a to-be-rewarded container was still pseudo-randomly assigned, but the experimenter remained in a neutral position throughout the subject's approach and indication of choice. The placement of food on the target can still followed a correct choice. In total six control trials were given during baseline testing.

Continuation Criterion

The criterion for continuing to the training phase was a score of seven or fewer correct trials out of ten in baseline. This was because a score of eight or more correct choices out of ten indicated a performance that was already significantly better than would be expected by chance (binomial test, $p = 0.05$). If this occurred then the subject's behavior could be said to be under the control of the discriminative stimulus (the human point) already and no additional training would be needed. Only one out of the 15 shelter dogs participating in this study performed above chance on the object-choice task during baseline. For the remaining 14 subjects that met the continuation criterion the mean number of correct responses was 4.43 out of 10 (95% CI: 3.53 to 5.33).

From the 14 dogs continuing to the next stage of the experiment, pairs of subjects were yoked together at random. Each yoked pair consisted of one dog that proceeded immediately to the training phase and one dog that experienced an additional control (Play-Train condition) before the initiation of the training phase.

Training Phase

Every subject experienced the training phase as the last stage of testing. For one subject in each yoked pair this phase immediately followed baseline (Group 'Train-only' in Table 4-2). For the 'Play-Train' group this phase immediately followed the Play-Train condition described in the following section.

The procedure for the training phase was almost identical to the baseline procedure. The experimenter stood between the two empty paint cans on the ground and presented a momentary distal point towards one of them for 2 s in full view of the subject located 2.5 m away. After 2 s the experimenter returned to a neutral position

and looked straight ahead until a choice was made. When a subject chose the correct can, the experimenter dropped a piece of food on the chosen container. For an incorrect choice the experimenter remained in a neutral position and no food was presented. The assistant then called the subject back to the starting location. However, in this phase up to 40 additional trials were presented. Criterion for learning was set at four correct choices out of the last five trials. Once this criterion was met, or once the subject had received all 40 additional trials, training ceased and five additional control trials were run to ensure that no unintended cues could account for the subject's improved performance.

Play-Train Condition

The time from completion of baseline testing to the time when a subject met the learning criterion or reached its 40th additional trial was recorded for each dog in the Train-only group. Each subject's yoked partner in the Play-Train group received that amount of additional time to interact with the experimenter, assistant, and the testing environment before proceeding to the training phase. No food or toys were given to the subjects in this phase, nor did the experimenter touch the buckets during this time. Play and petting were permitted as well as free exploration of the testing area by the dog.

If shelter dogs simply needed time to adjust to the environment to succeed on the object-choice task, dogs in the Play-Train group would be expected to be at an advantage, reaching criterion in significantly fewer trials during the training phase. Dogs in this group began the training phase described above immediately following this condition.

Scoring

A trial was scored as correct if the subject touched or placed its muzzle within 10 cm of the target can, indicated by the experimenter's point, prior to coming into contact with the alternative can. An analysis of the nature of the incorrect response was also carried out. Incorrect responses were coded as the selection of the incorrect can (I) or the selection of neither can before the trial timed out (NC), but instead engaging in an alternative behavior. NC responses often included, but were not limited to, approaching and sitting in front of the experimenter, barking or pawing at the experimenter, or investigating other aspects of the testing environment after release. We were interested in quantifying these two types of incorrect responses in order to determine if higher initial levels of NC responses predicted poorer performance over trial presentations, possibly indicating inattention or hesitancy to participate in the task, or if they were simply representative of an alternative form of pre-solution behavior, in which case such subjects would be equally likely to learn to follow the point with additional experience regardless of the topography of incorrect responses.

Statistical Analysis

Binomial tests were used to determine if each dog performed significantly better than chance in baseline, and to determine if more dogs reached criterion in the training phase than would be expected by chance. A one sample t-test was used to determine if shelter dogs as a group performed significantly above chance in baseline. Paired t-tests were used to determine if there were any differences in initial performance or in the mean number of additional trials needed to reach criterion between the Train-only and Play-Train groups. Correlations were used to assess the relationship between a subject's baseline score, the number of no choice responses in baseline, and play

duration (for the Play-Train group only) and the number of additional trials needed to reach criterion in the training phase. All tests were two-tailed and used an alpha level of 0.05.

Results

Overall subjects performed at chance levels during control trials averaging 36% correct (95% CI: 27% to 45%). Only one of the 15 dogs tested in baseline performed significantly above chance on the initial object-choice task (it scored 8/10 trials correct, binomial test, $p = 0.05$). As a group the shelter dogs did not perform above chance on the initial object-choice task (mean = 4.67; one sample t-test, $t(14) = 0.73$, $p = 0.48$).

In the training phase, 12 of the 14 (86%) remaining dogs that participated in training met the learning criterion (binomial test, $p < 0.0001$). In addition, more than half of the dogs that met criterion did so in 15 or fewer training trials (Figure 4-4). The performance of the Play-Train group and the Train-only group was compared to see if the additional play/adjustment time before the testing phase gave the Play-Train group an advantage (Figure 4-5). Even though the dogs in the Play-Train group had a slightly higher average performance on the initial baseline test (Mean baseline score, Train-only group = 3.57, Play-Train group = 5.29), the two groups did not differ significantly in the number of additional trials needed to reach criterion (paired t-test, $t(6) = 0.18$, $p = 0.86$). The number of dogs reaching criterion after the training phase was identical for both groups, six subjects apiece.

Therefore, the majority of shelter dogs that initially failed to use a momentary distal point learned to do so given additional exposure to the stimulus. This finding is similar to that reported for socialized wolves removed from their early rearing environment and caretakers before testing (Virányi et al., 2008), and for pet dogs faced with the

presentation of novel gestures (Udell, Giglio et al., 2008) or point reversals (Elgier et al., 2009). Adjustment to the novel testing environment or experimenters did not result in superior performance on the task. The receipt of additional trials of exposure during the training phase was the best predictor that a shelter dog would meet criterion on the object-choice task.

The number of correct trials in baseline had only a weak relationship to the number of additional trials needed to reach criterion in training ($R^2 = 0.15$). Figure 4-6 suggests, however, an inverted-U-shaped relationship between the number of no choice trials in baseline and the number of additional trials needed to reach criterion in training (polynomial fit: $R^2 = 0.35$). Dogs with zero or four or five no-choice trials in baseline required more training trials to reach criterion than those with no choice scores closer to the mean (Figure 4-6).

General Discussion

The near universal initial failure of shelter dogs to spontaneously follow a human momentary distal point could be explained in many ways. From the point of view of the hypothesis that domestic dogs' sensitivity to human stimuli is a byproduct of domestication, endowing dogs with human-like social cognition from birth (Hare et al., 2002; Hare & Tomasello, 2005), one might predict that members of this sub-population are in shelters because they are genetic anomalies, lacking the capacity to develop the human-oriented social cognition possessed by other domesticated canids. This explanation has been advanced to account for similar failures by socialized wolves (Virányi et al., 2008), and the failures of other non-domesticated species (Hare et al., 2002; Miklósi & Soproni, 2006). However this is not an explanation the current data support. Instead, most shelter dogs showing initial deficits in performance, improve on

human-guided tasks given additional experience. Furthermore, failure to use one type of human stimulus does not predict universal failure on human guided tasks. Therefore experience and the topography of the human stimulus appear to be important predictors of an individual's success on these tasks. These are undoubtedly not the only important variables behind an individual's responsiveness to human gestures (Udell et al., 2010b), but if such differences can account for even a proportion of the difference reported across populations of domestic dogs, it is likely that these same variables can account for a proportion of the difference found between subspecies of canid as well.

The current results cannot directly address the evolution of domestic dogs' social behavior, however our findings do show that the addition of specific experiences during an individual's lifetime can result in improved responsiveness to human pointing, even after initial failure on the task. Therefore the designation *Canis lupus familiaris* cannot itself be considered sufficient to predict success on a human guided choice task.

Studies that provide animals with increasing levels of experience need explicit tests for the possibility of learning and experience. While it may sometimes be possible to detect the effects of learning through statistical procedures (Wynne et al., 2008), this may not always be a sufficiently powerful method. While learning was not detected in Experiment 5 using the traditional method of comparing the first and last subsets of experimental trials, individuals from the same population demonstrated clear learning effects in Experiment 6, which was designed specifically to test for learning. This finding should serve as a reminder that post-hoc statistical tests are not sufficient, nor are the findings from them always equivalent to those obtained in studies designed to empirically evaluate the effect of lifetime variables on the behavior of animals.

There are limitations to the choice of shelter dogs as test subjects. First, their history is often unknown beyond the reports made at their initial collection and health check. Second, the shelter environment might present additional distractions or may result in subjects that are too stressed or excited to participate and succeed on experimental tests. Third, dogs that end up in the shelter might represent some genetically distinct portion of the population that is unrepresentative of domestic dogs as a whole. However these concerns do not outweigh the fact that experimentally inconvenient samples of dog, including shelter dogs, feral dogs, village dogs, and so on, are still members of the domestic dog subspecies; they cannot be ignored if general conclusions about the behavior of domestic dog are to be drawn. The challenge of designing experiments that can be used to test and compare these populations alongside the more convenient pet samples must be faced.

Research with feral dogs or dogs residing in shelters faces some of the same challenges encountered in research on wild species – whether free-roaming or brought into experimental settings. While one can speculate about the origins and previous experiences of the subjects, it is impossible to have experimental control over these variables. Moreover, experiments on pet dogs are not so dissimilar from those on other dog populations as might be supposed. While the report of an owner might be considered knowledge of an individual's background, it is difficult to determine if such reports are unbiased or complete. The types of questions that can be asked using any experimental sample depend on the quality of experimental control that can be applied to that sample. When specific control over early experiences is required, laboratory-reared and -tested individuals might be best, but that does not nullify the need for

research on dogs or other species residing in naturally occurring niches outside of the lab.

More research on the topography, prevalence, and outcome of initial no-choice responses during object-choice tasks is needed. Care should be taken in how such responses are treated and scored. While no-choice responses clearly cannot be scored as correct, the current data suggests that they should not be repeated or thrown out under the assumption that the subject failed to participate during the trial. In fact, dogs with a moderate number of no choice responses during baseline tests were more likely to learn the task in fewer trials during the training phase. While this relationship may seem counterintuitive, a similar performance trend is sometimes noted by animal trainers when first bringing a subject's behavior under stimulus control (Pryor, 1985).

> What is going on, in my opinion, is that at first the subject is learning the cue without really being aware of doing so; the trainer sees only a heartening tendency towards slowly increasing correct performance. But then the subject *notices* the cue, and becomes aware that the signal has something to do with whether it gets reinforced. At that point it attends to the signal rather than offering the behavior. Of course it gives no response and goes unreinforced. When, by coincidence of the trainer's perseverance, it does once again offer the behavior in the presence of the cue, and does get reinforced, the subject 'gets the picture.' From then on it 'knows' what the cue means and responds correctly and with confidence. (Pryor,1985)

This possibility is important for several reasons: (1) It could explain why some subjects may display a moderate level of no choice responses despite adequate motivation, (2) it provides rationale for why individuals that display moderate levels of no choice behavior may actually learn the task faster than individuals who make a 'choice' on every trial, (3) and it suggests that no-choice trials are an important occurrence and represent a valid response that should be counted as choice behavior: Choosing not to choose or the choice to perform an alternative behavior. Therefore the occasional

failure to respond to either target object during an object choice task does not necessarily imply lack of sensitivity to human cues, fear, or inadequate motivation. In fact it could signal that the subject is actively observing available discriminative stimuli present in the environment at the temporary cost of making an unguided overt response with a 50% chance of payoff. This typically leads to a richer schedule of reinforcement, 100%, once the association has been formed. More data are necessary to confirm this trend and to explicate the mechanisms for it.

Scientists are far from identifying all potential variables underlying a specific dog's responsiveness to human gestures, from the interacting evolutionary, developmental, and environmental factors influencing the dog's behavior, to the stimulus properties that make up a specific form of human point (Dorey et al., 2009; Udell et al., 2010b). Cross-species comparative studies have contributed much to our way of thinking about the social behavior of domestic dogs. Yet we still need to be careful that our general claims and predictions consider the many diverse populations of dogs of which pets are only one.

Table 4-1. Name (dogs without names are assigned numbers by the shelter), age, sex, and breed of subjects used in Experiment 5

Name	Age (years)	Sex	Breed
27	0.4	F	Pit-bull Terrier Mix
17	1.5	F	Labrador Retriever Mix
35	3	F	Mix
34	0.5	M	Pointer Mix
20	3	M	Hound mix
41A	1	M	Labrador Retriever Mix
41B	1	M	Labrador Retriever Mix

Table 4-2. Name (dogs without names are assigned numbers by the shelter), age in years, sex, and breed of subjects used in Experiment 6. Dogs were assigned to pairs and each dog within the pair was assigned to the Train-only or Play-Train condition. Condition group and pairings are presented for each subject, with the exception of two dogs that did not meet the conditions for training

Name/#	Age	Sex	Breed	Group	Pairing
16	2	F	Pit-bull mix	Train-only	A
17	1.5	F	Pit-bull mix	Play-Train	A
20	1	M	Labrador retriever	Train-only	B
26	0.6	F	Labrador retriever mix	Play-Train	B
31	3	M	Rottweiler	Train-only	C
32	1	M	Bulldog mix	Play-Train	C
17B	1	M	Labrador retriever mix	Train-only	D
18	1.5	M	Pit-bull mix	Play-Train	D
22	1	M	Beagle mix	Train-only	E
21	0.4	F	Pointer mix	Play-Train	E
57	1	M	Pit-bull mix	Train-only	F
25	2	M	Manchester terrier	Play-Train	F
29	1	M	Catahoula hound mix	Train-only	G
30	1.5	M	Labrador retriever mix	Play-Train	G
20B	2	M	Pit-bull mix	Met initial criterion	
22B	2	M	Rottweiler mix	Dropped prior to testing	

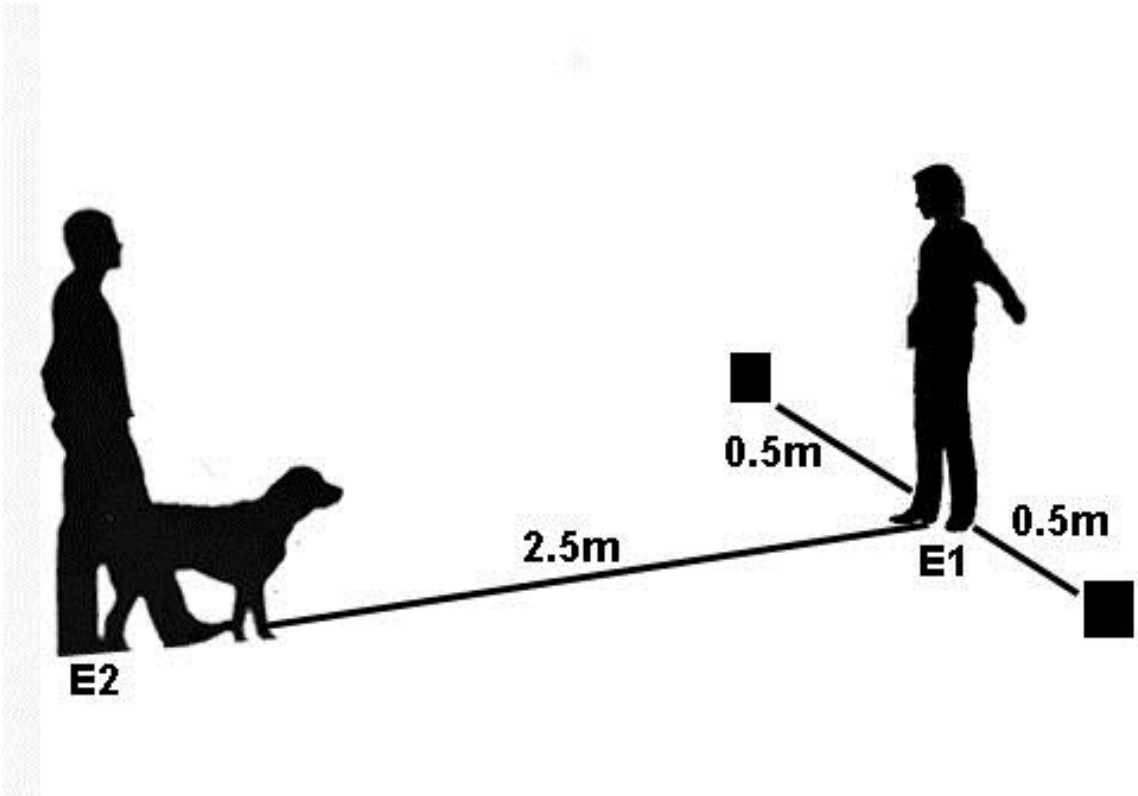


Figure 4-1. Testing layout for Experiments 5 and 6.

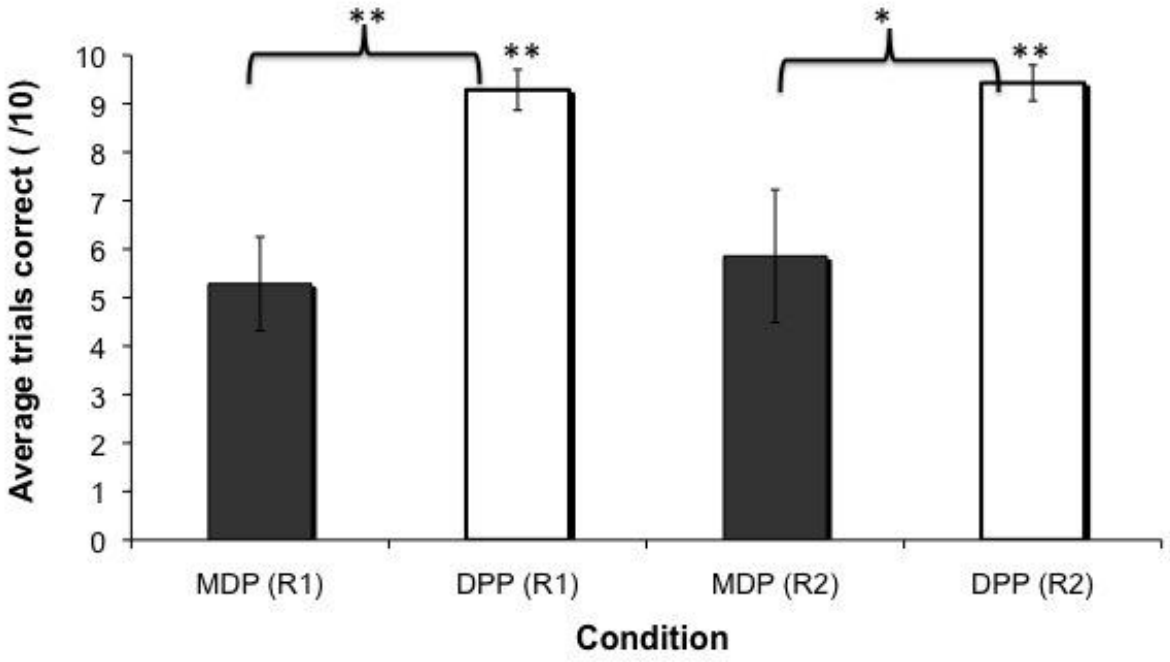


Figure 4-2. Mean number of trials correct on an object-choice task utilizing a momentary distal or dynamic proximal point over two rounds in Experiment 5. Shelter dogs had a significantly higher average score when presented with the dynamic distal point. * denotes $p = 0.05$, ** denotes $p < 0.01$. MDP, momentary distal point; DPP, dynamic proximal point; R1, round 1 or first ten trials of point type; R2, round 2 or second ten trials.

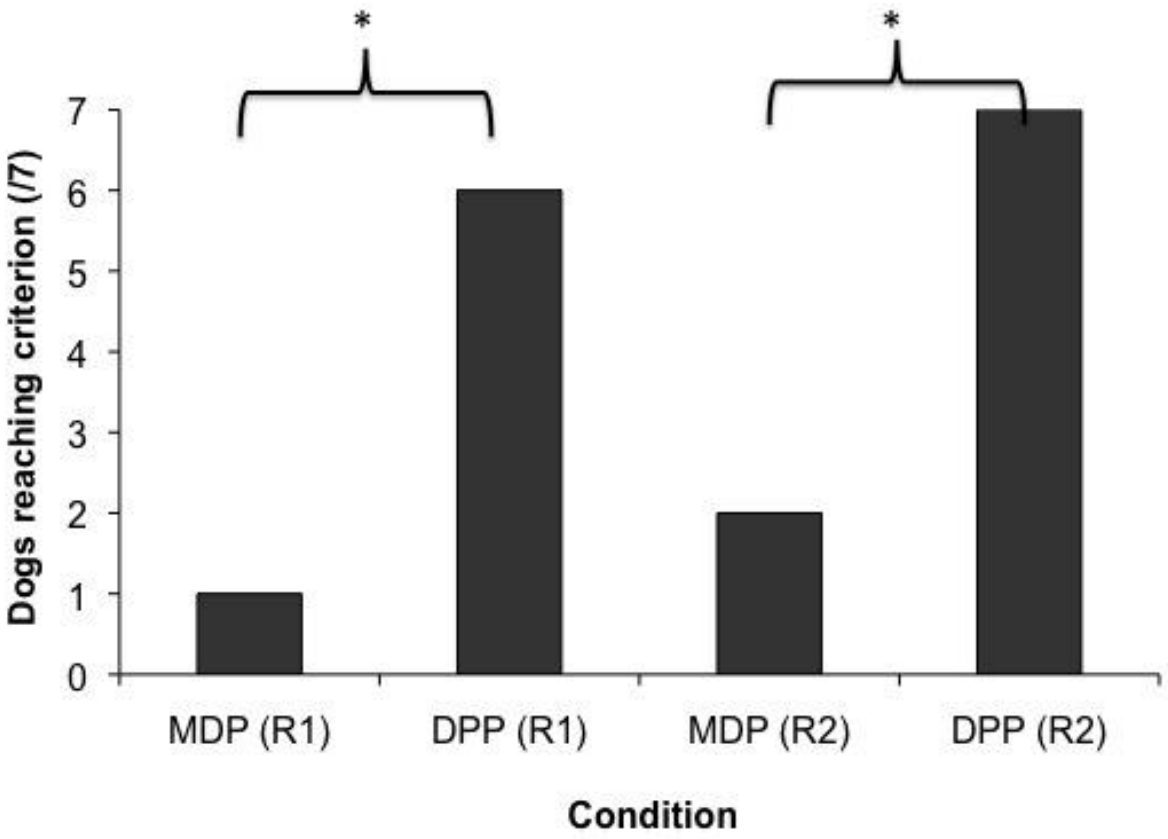


Figure 4-3. Individual performance of shelter dogs on a human guided object-choice task utilizing a momentary distal or dynamic proximal point in Experiment 5. More individual subjects were successful on the object-choice task when using the dynamic distal point than when using the momentary distal point. * indicates a significant difference, fisher's exact test, $p < 0.05$. MDP, momentary distal point; DPP, dynamic proximal point; R1, round 1 or first ten trials of point type; R2, round 2 or second ten trials.

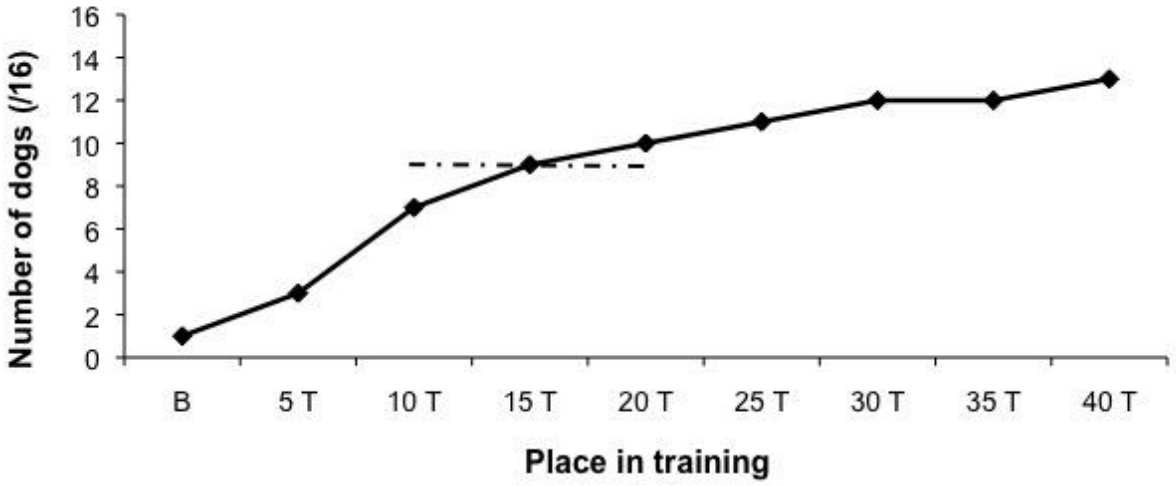


Figure 4-4. Shelter dogs learn to follow a momentary distal point in Experiment 6. Cumulative number of dogs meeting criterion after baseline (initial 10 trials, B) and after 5, 10, 15, 20, 25, 30, and 40 additional training trials (*n* T). At the end of testing all but two dogs had met criterion. The dashed line indicates the point at which half of the shelter dogs had learned to follow the point.

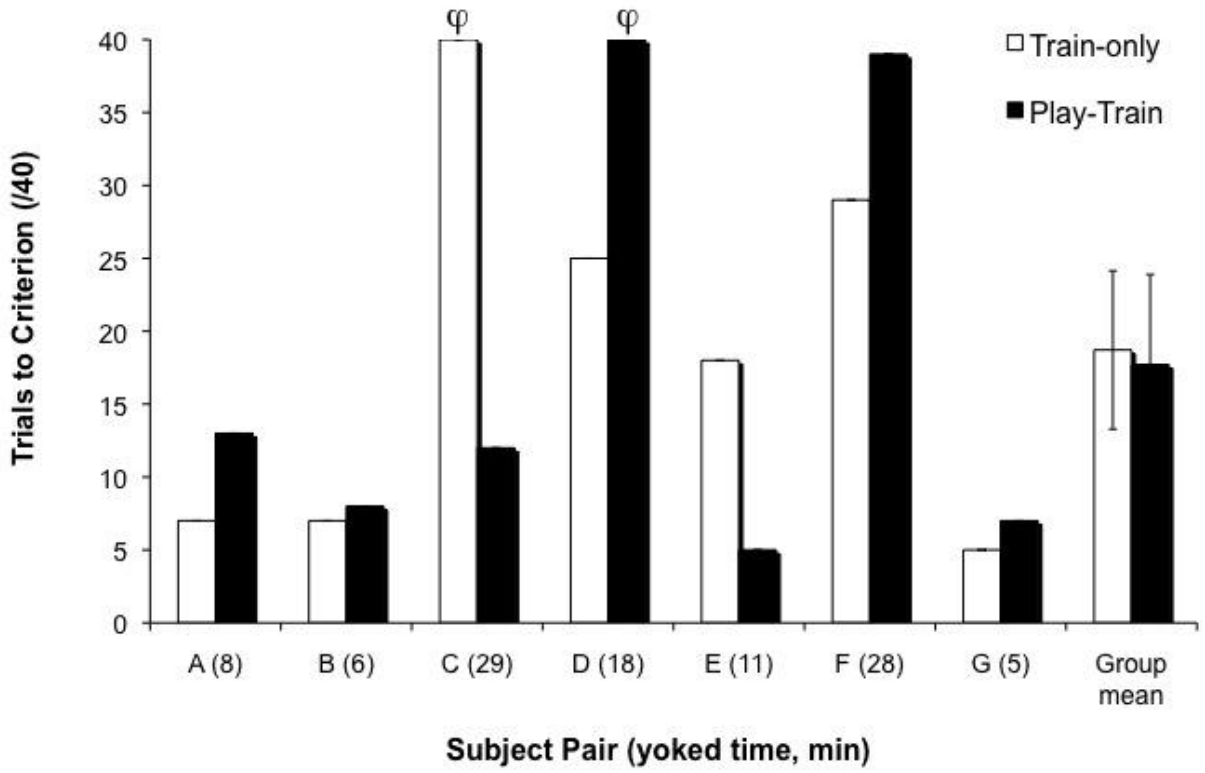


Figure 4-5. Trials to criterion for subjects in Train-only and Play-train yoked pairs. One subject from each group, marked in the figure by φ, completed the maximum number of training trials but failed to reach criterion: subject 31, Group C, Train-only; subject 18, Group D, Play-train.

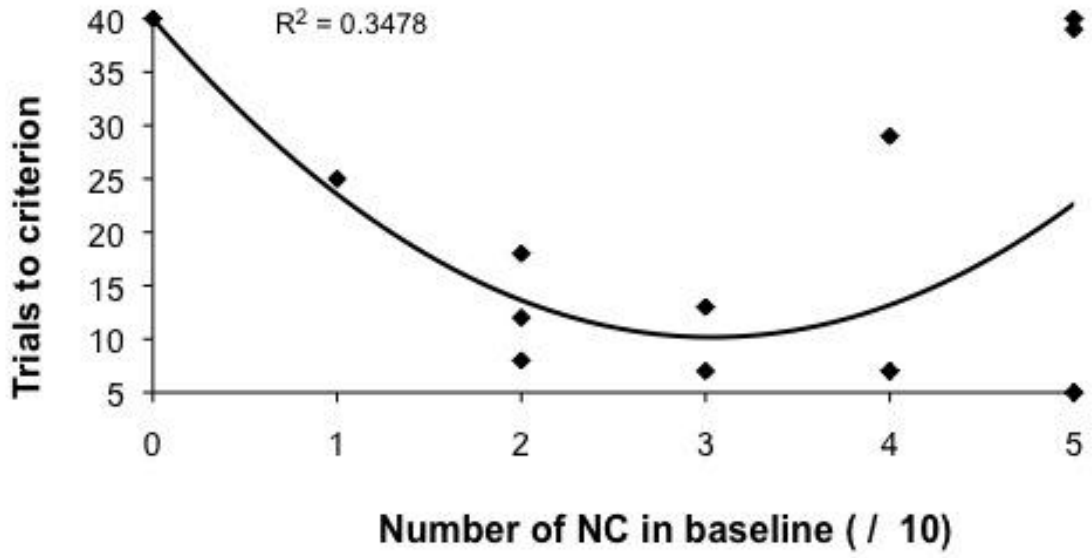


Figure 4-6. Relationship between total number of no-choice (NC) responses in baseline and trails to criterion in training.

CHAPTER 5
CONCLUSIONS

Human Gestures: Form and Function

Experiment 1 confirmed that both pet domestic dogs and human-socialized wolves have the capacity to respond to a diverse range of human gestures. Likewise pet dogs as a group, as well as many individuals, are able to follow numerous forms of human points to a target (Experiments 2 and 3; Udell et al., 2010b). While this data reconfirms that the capacity for responsiveness to human gestures is not unique to domesticated canids (Gácsi, Gyori et al., 2009; Udell, Dorey et al., 2008), and that this holds true even beyond basic points made with the arm and hand, it does not suggest that dogs or wolves have an automatic response to human gestures or that dogs are responding to a universal communicative meaning common to all human points as suggested by Hare and Tomasello (2005). Instead individual subjects show varying levels of success when utilizing different gesture (Experiment 1) or point types (Experiments 2-6) in the context of an object choice task. Even when human stimuli appear to be similar in form, for example variations on the human point made with the extended arm and hand, the function of each stimulus, in terms of the predicted behavioral response of the subject, can vary substantially. Consequently, if a human point holds referential meaning for dogs it is likely the product of an individual's association between the specific topographical properties of that point and the behavioral and environmental changes that are predicted by it. These findings are consistent with the predictions of the Two Stage Hypothesis as described by Udell et al. (2010b).

Experience and Learning

There was clear evidence, especially in Experiments 3, 4 and 6, that the performance of dogs on human guided tasks is influenced by experience with relevant stimuli. Experiment 3 further demonstrated that direct exposure to a specific stimulus under test in not necessary for improved performance on the task; experience with other stimuli sharing some but not all of the same stimulus properties is generally sufficient. Stimulus generalization may explain how canine responsiveness to human gestures develops casually in human based environments, where pointing and gestural stimuli predicting specific environmental opportunities and outcomes may be similar, but are unlikely identical, across presentations. Furthermore, Experiments 5 & 6 demonstrate that a failure to spontaneously utilize a particular gesture does not imply an inherent socio-cognitive deficit or the absence of the capacity to utilize that gesture. Instead dogs from populations that routinely fail to utilize the momentary distal pointing gesture, such as shelter dogs, may learn to utilize the point rapidly if reinforcement is made contingent on a specific response. In fact half the dogs in Experiment 6 began following the point reliably after only 15 additional presentations of the stimulus (25 pointing demonstrations total). These shelter dogs were taken from a population of dogs that had a spontaneous success rate of only 7% across all prior studies conducted (Udell et al., 2010a).

These results are consistent with the broader literature on point following and the use of referential stimuli. There is ample evidence that both human children (Carpenter, Nagell, & Tomasello 1998; Mundy et al., 2007) and dogs (Fox, 1969; Scott & Fuller, 1965) learn and develop the ability to respond to the stimuli of conspecific social companions with age and experience, as well the stimuli of heterospecifics (Bentosela

et al., 2008; Elgier et al., 2009; Dorey, Udell, & Wynne, 2010). In fact, stimulus type predicts the performance of young human children in object-choice tasks as well (Lakatos et al., 2009). Considering the wide variety of gestures that could be made with the human body, and the impact that culture, environment, growth, coordination, and context could have on a human's gesturing behavior, flexibility - including the ability to learn and modify responses to different human stimuli - could provide many short and long term benefits compared with a rigid ability to respond to preprogrammed gesture types. Indeed there is evidence that domestic dogs not only learn about human stimuli, modifying their behavior accordingly, but they can often do so rapidly. For example, Udell, Giglio et al. (2008) demonstrated that individual pet dogs showed evidence of learning to follow new gesture types within the course of ten trials of experimental testing. Elgier et al. (2009) demonstrated that dogs can learn to go to a container opposite the one pointed to after fewer than 50 trials of training and can be conditioned to look at the human face for access to food in as few as three trials (Bentosela et al., 2008). Instead of viewing dogs as programmed during domestication to respond in specific ways to humans and human referential behavior, these findings suggest that dogs may use a more flexible strategy, generalizing across social cues during their lifetime.

Additional Considerations and Future Directions

Identifying the evolutionary origins of a human-like social cognition has been a primary motive for conducting comparative studies on responsiveness to human gestures (Hare & Tomasello, 2005; Miklósi, Topál & Csányi, 2007). Demonstrations that canine responsiveness to human gestures is (1) strongly influenced by proximate mechanisms and (2) shared by both domesticated and non-domesticated members of

the genus do not, however, negate the need for more comparative research on this topic. First it is possible that there are biological prerequisites necessary for the capacity to respond to the visual signals or actions of social companions, whether conspecifics or heterospecifics, that not all species share. Second, the type of responsiveness to stimuli measured in object-choice tasks may require some kind of social relationship between the signaler and subject, even if only one of reduced fear. It is possible that certain species are more biologically predisposed to form such social relationships than others. This could be explained in terms of a species' readiness to accept new social companions (belonging to one's own or another species) as well as the timeframe and effort required for this to be accomplished. Differences in required effort and in the timing and duration of developmental widows for social development are known to occur even within species and subspecies, including canids, through the process of domestication (Trut, 1999; Trut et al., 2004) or even due to inherent variation between individuals and strains (Coppinger & Coppinger, 2001). Therefore the specific role socialization plays in different species' ability to learn about and respond appropriately towards the bodily signals of others, especially heterospecifics, is an important area requiring further study.

On a smaller scale, identifying proximate mechanisms that contribute to the behavioral response a dog displays in the presence of human stimuli is a critical part of understanding and improving our ongoing relationship with domestic dogs. It allows us to move beyond a generalized, and pet centered, perception of what a dog should be, towards a more pragmatic assessment of what domestic dogs are and why individuals behave the way they do under different environmental conditions. Despite the fact that

domestic dogs (*Canis lupus familiaris*) filling many distinct niches exist in large numbers worldwide, including various categories of working, village, stray and feral dogs, their differential behavior towards humans has not been well accounted for by previous socio-cognitive evolutionary claims that downplay the importance of development, environment, and experience. A greater acknowledgement and understanding of relevant proximate factors is the first step in identifying mechanisms that better predict the behavior and success of dogs living in different populations.

In the Western world dogs kept as pets are often reinforced for their close proximity to and vigilance of humans and their behavior. Dogs in homes, as well as in many working roles are expected to gain proficiency with hand signals and voice commands issued by human handlers, and often context specific rules that vary by who is present, their attentional state, and the environmental context of the event (Udell & Wynne, 2008). Some dogs are very good at this, not only avoiding punishment by strategically engaging in forbidden acts when out of view (Bräuer, Call & Tomasello, 2004; Call et al., 2003), but responding towards visibly angry owners with submissive signals even when they have done nothing wrong (Horowitz, 2009). In some cases this gives humans the false sense that dogs understand the moral underpinnings of their behavior, resulting in reduced punishment or even sympathy (Horowitz, 2009). If such behaviors contribute to a dog's success in our society, then a better understanding of the proximate mechanisms involved could have many applications. For example, research has shown that the simple act of providing dogs in a shelter with additional human attention or enticing them to sit at the front of their cage closer to potential adoptees can result in higher levels of adoption (Wells & Hepper, 2000).

Furthermore, while it is still poorly understood what the effects, if any, dog ownership has on the health, happiness, and well being of humans, this is a growing area of interest (McCardle, Mccune, Griffin, & Maholmes, 2010). It seems likely that the perceived quality of interactions between dog and owner strongly influence whatever benefits might be possible, especially given that a dog's relative success in the human home is predicted by such factors. Undesirable behavior in pet dogs, including social behavior, can often be tied back to experiences during development (Scott & Fuller, 1965) or the environment and experiences created by a dog's current owners (Gladwell, 2006). In fact Randall Lockwood, a senior vice-president of the ASPCA, has suggested that even in the most extreme cases, such as dog attacks, the dog's behavior can typically be traced back to "a perfect storm of bad human-canine interactions—the wrong dog, the wrong background, the wrong history in the hands of the wrong person in the wrong environmental situation" (Gladwell, 2006, p. 26). Likewise, my current research suggests that desirable social behavior in dogs, including responsiveness to human gestures, is strongly influenced by an individual's home environment and relevant life experiences with humans. Therefore as the use of dogs in therapeutic, assistant, and other human-oriented working roles increases, efforts should be made to better understand what effect a dog's individual social behavior has on these interactions, which environments, rearing and training methods predict the best behavioral outcomes, and how negative outcomes can be reduced.

Concluding Remarks

My current findings are consistent with the predictions of the Two Stage Hypothesis, in that (1) both domesticated dogs and undomesticated wolves demonstrated the capacity to respond to diverse human stimuli and (2) proximate

variables such as experience and current living environment were important predictors of performance on the human-guided tasks. These findings do not support the claim that domestic dogs are prepared to respond in specific ways to human communicative stimuli. Instead the dogs tested demonstrated flexibility in response that was modifiable over the course of a single testing session, based on a history of reinforcement for a specific response. Furthermore, many dogs rapidly generalized reinforced responses to other discriminative stimuli possessing some but not all of the same topographical properties. Given that prosocial behavior towards humans is not universal, especially in non-pet populations of dogs, flexibility of response may in fact prove to be a better predictor of the domestic dog's success as a subspecies than a single form of social responding.

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BIOGRAPHICAL SKETCH

Monique Udell's fascination with animal behavior began long before any formal training. As an undergraduate student she decided to put her interests to work, conducting both field and laboratory research on animal behavior and volunteering as a keeper at an exotic cat rescue facility. After receiving degrees in both biology and psychology from Stetson University, she decided that her aspirations for graduate school could best be met by studying under Dr. Clive Wynne at the University of Florida.

Upon entering graduate school, Monique began a line of research new to her program, focusing on the social interactions between humans and domestic dogs. Although interest in the adaptations and behavioral traits allowing domestic dogs to thrive within a human environment had been circulating for over a decade, the existing research had almost exclusively stemmed from evolutionary and cognitive perspectives. Her growing exposure to behavior analysis convinced her that a better understanding of canine behavior could be accomplished through the utilization of behavioral methods and interpretations. Heavily influenced by coursework taken with Dr. Jesse Dallery and Dr. Timothy Hackenberg during her first year in the University of Florida's behavior analysis program, these ideas were formalized in a review article written for *JEAB,* coauthored with her research mentor Dr. Clive Wynne. This marked the foundation of the Canine Cognition and Behavior Laboratory, which now consists of students ranging from undergraduates to post docs who wish to study canids from a behavioral perspective.

In 2008 Monique received her Master of Science in psychology from the University of Florida. After obtaining her doctorate, she plans to continue teaching and conducting

research at the college level. She currently lives in Florida with her husband of five years, Chester Udell, and her two ferrets, Dakota and Bear.