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**Exploring breed differences in dogs (*Canis lupus familiaris*): Does exaggeration or inhibition of predatory response predict performance on human-guided tasks?**

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**Abstract:** Domestic dogs' (*Canis lupus familiaris*) responsiveness to human action has been a topic of scientific interest for almost two decades. However, are all breeds of domestic dog equally prepared to succeed on human-guided object choice tasks? In the current study we compared three breeds of dog with distinct predatory motor pattern sequences still under direct selection pressure today based on their traditional working roles. Airedale Terriers (hunting dogs) are bred for a fully intact predatory sequence, matching the wild-type form. Border Collies (herding dogs) are bred for an exaggeration of the eye-stalk-chase component of the predatory sequence. Anatolian Shepherds (livestock guarding dogs) are bred for the inhibition of the full predatory sequence. Here we asked if and how these opposing selection pressures corresponded with each breed's tendency to track and follow a human point to a target in an object-choice task. Our results suggest that the presence or exaggeration of key components of the predatory sequence may in fact predict superior initial performance on pointing tasks when compared to a breed selected for its inhibited predatory response. This is the first time relative success on a pointing task has been tied to a known heritable behavioral mechanism (breed specific motor patterns). However, we also demonstrate that breed-specific differences can sometimes be overcome with additional experience. Thus an individual's performance on human-guided tasks is still best predicted by a combination of genetic and lifetime factors. Broader implications for the understanding and investigation of canine social cognition are discussed.

**Key Words:** Breed, dog, *Canis lupus familiaris*, pointing, social, cognition, predatory motor patterns, genes

The idea that dog breeds should differ in social demeanour and intelligence is heavily disseminated in popular media (Coren 2006). While it is known that some breeds differ in developmental rate (Scott & Fuller 1965), motor pattern presentation (Coppinger & Coppinger 2001) and approach avoidance response (Plutchik 1971), it has been more difficult to empirically demonstrate consistent breed differences in other areas, including social cognition and gesture responsiveness (Dorey et al. 2009; Pongrácz et al. 2005). Though there have been some exceptions (Vas et al. 2005; Jakovcevic et al. 2010; Buttelmann & Tomasello 2012), it is possible that breed differences in social cognition are not as pronounced as popularly thought. On the other hand, only a small percentage of studies are specifically designed to analyse breed differences. Many negative reports come from post-hoc analyses, based on small numbers of included breeds, which may not provide sufficient power to detect true differences even if they exist (Dorey et al. 2009).

The human-guided object-choice task has been extensively used as a measure of canine social cognition (for a review see Udell et al. 2010a). In this task, an experimenter points to one of two containers where the dog can obtain food upon approach. Several studies have reported breed-group differences on this task. For example, Wobber et al. (2009) and Gacsi et al. (2009a), found that ‘cooperative’ breeds followed the experimenter’s point to the target significantly more often than ‘independent’ breeds. However, one possible setback to this approach is the subjective nature of breed stereotypes. In other words, how do we know whether a particular breed should be labelled cooperative or independent? In fact, in Gacsi et al. (2009a) Siberian Huskies were placed in the independent worker group – and were ultimately deemed less socially sensitive (less accurate on the pointing task) - while in Wobber et al. (2009)

Siberian Huskies were placed in the cooperative worker group- and were found to be more socially sensitive. Cultural expectations about which breeds should be considered cooperative (or independent) might result in differential treatment, and thus differential performance. However this may have little to do with inherent differences between individual breeds. Helton and Helton (2010) point out another potential setback: the failure to account for physical (or biologically determined) explanations first. In fact, breeds with some morphological traits (larger size, frontally placed eyes) tend to outperform other breeds on pointing tasks (Gacsi et al. 2009a; Helton & Helton 2010). This is likely due to superior visual acuity and depth perception. Yet, to date, relatively few studies have considered the influence of specific breeding criteria on socio-cognitive task performance; none have considered behavioural breeding criterion.

While many pet and show-class dogs are bred on the basis of morphology, some working-class breeds still undergo stringent behavioural selection. For example, selection for the presence or absence of behaviours related to the predatory motor sequence (Coppinger & Schneider 1995; Coppinger & Coppinger 2001). In wolves, the full canine predatory motor sequence: **orient > eye > stalk > chase > grab-bite > kill-bite > dissect > consume**, is reliably triggered by the movement of prey. However the organization of the predatory sequence has become relaxed in dogs- due to a shift in niche from hunter to scavenger (Coppinger & Coppinger 2001). Importantly, there are similarities between behaviours associated with the predatory motor sequence and those required of dogs in many socio-cognitive tasks. For example, pointing tasks involve tracking the movement of a human arm, or other body part, in space (orient, eye) and approaching (stalk, chase) the location of this movement for the opportunity to consume food. Therefore, we

hypothesize that dogs that are bred to exhibit the full portion of the predatory sequence most related to pointing tasks [**orient** >> **eye** >> **stalk** >> **chase**] should outperform those selected for the inhibition and loose organization of this sequence.

### **Experiment 1: Breed Differences in Point-Following Performance**

In experiment 1, we predicted that Border Collies, a breed that has undergone behavioural selection for the exaggeration of the [**orient** >> **eye** >> **stalk** >> **chase**] component of the canine predatory sequence, should perform as well, if not better than, other breeds on pointing tasks given their increased sensitivity to moving stimuli and heightened motivation to chase. We predicted that Airedale Terriers would also perform well on this task. On the other hand, we predicted that Anatolians would be at a disadvantage on traditional pointing tasks due to a reduced motivation (or an increased threshold) for tracking/chasing moving objects in space, independent of their socio-cognitive abilities.

### **Methods**

#### *Subjects*

Thirty-six experimentally naive dogs identified as purebreds from working lines were enrolled in this study: 12 Border Collies (A herding breed with a hypertrophied, or exaggerated, eye, stalk and chase: **orient** > **EYE** > **STALK** > **CHASE**), 12 Airedale Terriers (a hunting breed with full replication of the wild-type sequence: **orient** > **eye** >

**stalk > chase**), and 12 Anatolian Shepherds (a livestock guarding breed, for which any predatory behaviour is considered a ‘fault’ and selected against, with an inhibited sequence: (orient) (eye) (stalk) (chase) ). Fourteen of the dogs were male, 22 were female, with a mean age of 4.7 years [Range: 8 months- 11 years]. All dogs were required to be in good health and were at least four months of age (For developmental considerations relating to pointing task participation before four months of age see: Wynne et al. 2008; Dorey et al. 2010). All dogs were from working (not show) lines, however none of them had ever been employed in their traditional working role. Instead, to be included in this study, all dog were required to have a known lifetime history where they were treated as a pet. A trained unfamiliar experimenter tested all dogs individually, indoors, as described below.

*Ethical note.*

All subjects were volunteered by their owners and remained in their care throughout the study. Owners were not asked to food deprive their dogs or engage in any other activity that might compromise their well-being. This study was conducted under ethical approval from the University of Florida (IACUC# E325).

*Testing Layout*

Two one-gallon metal paint cans (15 cm diameter, 22 cm tall), with lids tightly fastened, served as the response objects. These cans were placed 0.5 m on either side of an experimenter, so that when pointing the experimenter’s finger came no closer than 50 cm to the lid of the correct can. An assistant stood 2.5 m away, measured from the

midline between the cans, facing the experimenter; this is also where the dogs began each trial.

No food was present in or on either can until and unless the subject made a correct response (touching or coming within 10 cm of the can with its snout). The correct container was determined pseudorandomly before sessions, with the stipulation that no one location was correct more than twice in a row and each location was correct for exactly 50% of the trials. Preferred food items (dog treats and small bits of meat) were placed on the chosen can as soon as a correct response had been made. These items were chosen based on owner report and confirmed by a dogs eagerness to consume the food item when given by the experimenter (in comparison to other available food items). Willingness to approach the testing cans to obtain this food was confirmed by the following test of motivation.

### *Test of Motivation*

Owners were not asked to food deprive their dogs; therefore tests of food motivation were conducted prior to participation. The experimenter held up a piece of food in the dog's view and called its name to gain its attention. She then placed the food on top one of the cans. The assistant released the dog allowing it to approach the can and eat the food. To proceed to experimental testing the subject had to approach the can and consume the food (which was in full view of the dog) four times in a row. This was to ensure motivation, and willingness to respond when the location of the food was known. Likewise, if during testing a dog made three incorrect responses, or failed to choose on

three consecutive trials, this test of motivation was repeated twice, once on each can. Five dogs of the original 36 failed this test of motivation (one Border Collie, two Airedale Terriers and two Anatolian Shepherds) and were dropped from the study prior to completion. None of the remaining 31 dogs ever failed a test of motivation.

### *Experimental Testing*

Experimental testing began immediately after the initial test of motivation. At the start of a trial, the subject, which was standing next to the assistant, was called by the experimenter until it oriented towards her. From a standing position, the experimenter extended her ipsilateral arm and hand into a Momentary Distal point in the direction of the target container while the subject watched. The tip of the experimenter's finger was held 50 cm from the target can for two full seconds and then retracted back to a neutral position. The subject was then released by the assistant to make a choice. The subject was given up to one minute to make a choice. If the subject chose the correct can first (prior to visiting the other can), this was recorded as a correct response and the experimenter praised the dog verbally ("good") while placing food on top the can for the dog to consume. Any other response was considered incorrect, and no food or praise was provided to the dog. The assistant then called the dog back to immediately begin the next trial. Praise and a small low-value treat (e.g. piece of dog food) were provided by the assistant to maintain call-back compliance. Each dog experienced a total of 10 experimental (pointing) trials.

### *Control Trials*

Control trials were identical to experimental trials in every way, except that after calling the dog to gain its attention the experimenter did not point (however the assistant still released the dog as if she had). The experimenter stood in her neutral starting position for a full minute or until the dog made a choice. As in experimental trials, a correct can was chosen prior to testing and both the assistant and experimenter knew which can would result in reward if approached. If a dog made a correct choice during a control trial it was given food and praise by the experimenter just as in experimental trials. This was done to control for any unintentional cues that could be given off by the experimenter independent of the pointing gesture. A total of six control trials were conducted; one after every two experimental trials and two after the last experimental trial.

### *Statistical Analysis*

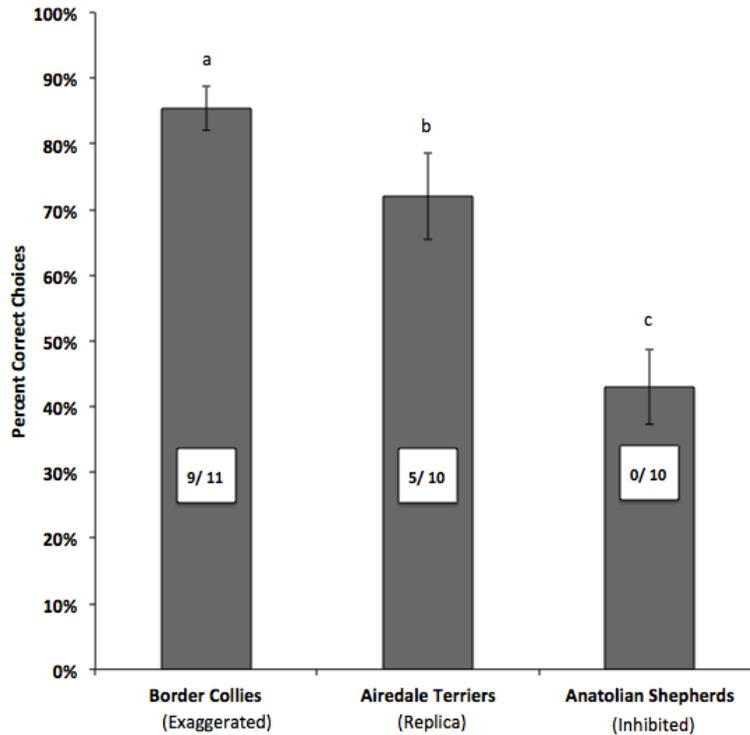
The experimental data were normally distributed for each group according to the Kolmogorov-Smirnov test, therefore a one-way ANOVA was used to analyze breed differences on the pointing task. Tukey HSD tests were used to further determine the source of these differences, and one-sample t-tests were used to determine if individual groups performed better than would be expected by chance. A Fishers Exact test was used to determine if there were differences in the number of individuals performing above chance between breeds. Individual successes (above chance performances) were

defined as eight or more correct responses out of 10, reaching binomial significance ( $p \leq 0.05$ ). All statistical tests were two-tailed and had alpha set at 0.05 unless otherwise specified.

## Results and Discussion

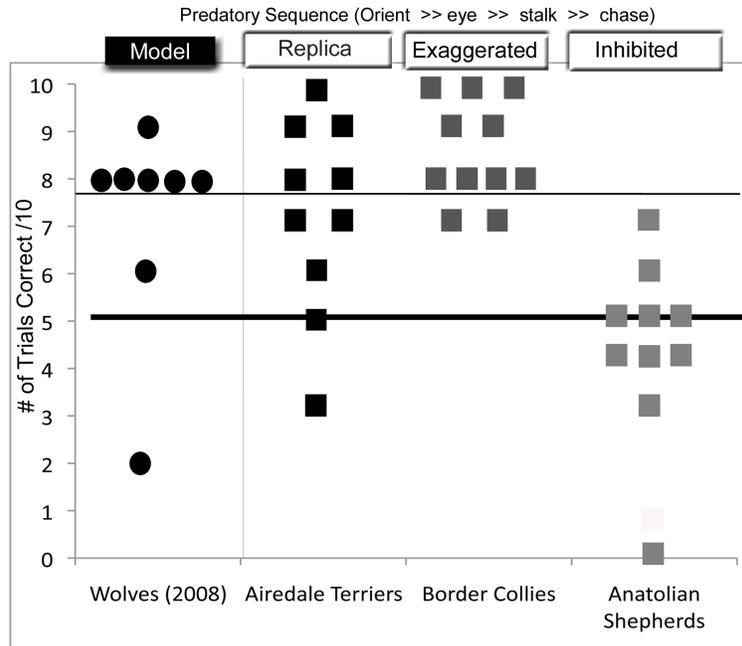
Mean performance on control trials was not better than would be expected by chance for any breed group: Out of 6 control trials, Border Collies ( $\bar{X} \pm SE = 2 \pm 0.6$  correct), Airedale Terriers ( $\bar{X} \pm SE = 2 \pm 0.6$ ) and Anatolian Shepherds ( $\bar{X} \pm SE = 1.7 \pm 0.4$ ), suggesting that above chance performance on experimental trials was dependent on the pointing gesture, and could not be attributed to other factors within the experimental setup.

A significant difference was found between the three breed groups (One-way ANOVA,  $F(2,28) = 16.17, p < 0.0001$ ). Tukey HSD post-hoc tests showed that there was a significant difference between the mean performances of Border Collies and Anatolian Shepherds, with the former outperforming the later (Tukey HSD,  $p < 0.01$ ). There was also a significant difference between the performance of Airedale Terriers and Anatolian Shepherds (Tukey HSD,  $p < 0.01$ ), again with the former outperforming the latter. Border Collies also performed better than Airedale Terriers on average (Tukey HSD,  $p < 0.01$ ). Border Collies (one-sample t-test,  $t(10) = 10.42, p < 0.0001$ ) and Airedale Terriers (one-sample t-test,  $t(9) = 3.31, p = 0.009$ ) both performed significantly above chance on average, while Anatolian Shepherds did not perform better than would be expected by chance (one-sample t-test,  $t(9) = 1.17, p = 0.27$ ; Fig. 1).



**Figure 1.** Breed differences in point following performance. Grey bars show mean percent correct choices (points followed) +/- SEM for each breed. Border Collies (a) and Airedale Terriers (b) performed significantly above chance as a group,  $p < 0.01$ , Anatolian Shepherds (c) did not,  $p = 0.27$ . Significant differences were found between a & b ( $p < 0.01$ ), b & c ( $p < 0.01$ ) and a & c ( $p < 0.01$ ). White boxes show the number of individuals performing above chance on the task for each breed.

A significant difference in the number of individuals from each breed performing above chance ( $> 8/10$  correct) on the task was also found (Fisher's Exact,  $p = 0.007$ ; Fig. 2); Border Collies had the most individual successes, Anatolian Shepherds had the least.



**Figure 2.** Individual performance on the momentary distal pointing task by breed (and predatory sequence type). Each square represents the final performance score of a single dog on this task (/10 trials). These results can be compared to the individual performance of wolves represented as circles (at left) as reported in (Udell et al. 2008b). The thick line at center represents chance performance (5/10 trials correct), the thin grey line marks the threshold for above chance performance at the individual level ( $\geq 8/10$  trials correct).

Additional analyses were conducted to assess whether differences in approach inhibition could be detected between breeds. If the poor point following performance of Anatolians was related to inhibited predatory response (an inhibited response to moving stimuli), we would expect the form of incorrect responses to reflect this. In other words, we would expect such differences to indicate a significantly higher rate of “no-choice” responses (where neither can was selected), as opposed to active selection of the incorrect can alone. While some individuals from all breeds occasionally choose not to approach either can, Anatolians displayed the highest average levels of approach inhibition during experimental trials (Percent of experimental trials: Anatolians 47%, Airedales 18%, Border Collies 7%; One-way ANOVA,  $F(2, 28) = 15.62, p < 0.0001$ ). Post-hoc tests

confirmed significant differences between Anatolians and the other breeds (Tukey HSD,  $p < 0.01$ ); a significant difference was not found between Airedales and Border Collies. However it is important to note that on 89% of these “no-choice” trials, Anatolians still approached the experimenter, actively participating by entering the testing area even on trials where they failed to follow the directional movement on the point to the target. These same Anatolians also displayed high levels of motivation to approach and consume visible food from the cans in tests of motivation. Interestingly, while most dogs (e.g. Udell et al. 2013; Airdales and Border Collies in the current study), show lower rates of approach to a can in the *absence* of stimulus movement, i.e. during control trials (Airedales: Experimental (18%), control (42%); Border collies: Experimental (7%), control (27%)), on average Anatolians displayed significantly higher levels of response inhibition after the *presentation* of a pointing stimulus/movement (47%) when compared to control trials where there was no pointing stimulus/movement (32%) (Paired  $t$ -test,  $t(9) = 2.45$ ,  $p = 0.04$ ).

These results support our hypothesis: breeds selected for the maintenance (Airedale Terriers) or exaggeration (Border Collies) of the **orient >> eye >> stalk >> chase** component of the predatory sequence outperformed individuals bred for the absence or inhibition of this sequence (Anatolian Shepherds) on the momentary distal pointing task. Airedale Terriers, which show a replication of the wolf’s predatory sequence, were not only successful on average, but performed much like wolves, tested in a prior study with comparable methods (see Udell, Dorey & Wynne, 2008), on this task at the individual level (see Figure 2). Border Collies, which show an exaggeration of this sequence, performed significantly better than both the Airedale Terriers and Anatolian

Shepherds. Anatolians, bred for inhibition of this sequence, did not follow the experimenter's point at above chance levels. Furthermore, the behavior of Anatolians in experimental trials appeared to be consistent with an *inhibited* response in the presence of movement. This suggests that performances on pointing tasks may be influenced by more than social cognition alone; they may also be influenced by breed specific biological predispositions, including differences in the organization of motor patterns associated with food getting (predatory) responses or differences in motivation. Lifetime experience may also play a significant role in the behavior of these individuals, a point that will be discussed further in the general discussion. These findings do however raise the question of whether poor performance on the pointing task necessarily implies inferior or altered 'socio-cognitive capacity' in Anatolians (and possibly other livestock guarding breeds), or whether poor initial performance could be interpreted as the interaction between a byproduct of a known *behavioral inhibition* of the predatory response and individual experience?

## **Experiment 2**

In experiment 2 we asked whether Anatolian Shepherds, which performed at chance levels on the point following task in experiment 1, were capable of following human points reliably with additional experience. If poor performance could be described as a byproduct of behavioral inhibition, as opposed to a cognitive deficit or lack of motivation, we predicted that Anatolians would be able to overcome this initial inhibition with repeated exposure to the task-specific contingencies.

## **Methods**

### *Subjects*

We were able to re-recruit six of the original Anatolian Shepherd participants for a follow-up study, five that had completed testing and one that had initially failed a test of motivation during experiment 1. This group consisted of four females and two males with a mean age of 2.8 years (Range: 8 months - 6 years). All individuals were purebreds from working lines, living as pets. Subjects were tested individually, in the same location and by the same experimenter as in experiment 1.

### *Ethical note.*

All subjects were volunteered by their owners and remained in their care throughout the study. Owners were not asked to food deprive their dogs or engage in any other activity that might compromise their well-being. This study was conducted under ethical approval from the University of Florida (IACUC# E325).

### *Testing Layout & Test of Motivation*

Both the testing layout and motivation test were identical to experiment 1. Only one dog failed a test of motivation during experiment 2 (after 5 experimental trials), refusing to approach the cans even when food was placed on it in plain sight, and thus was excluded from analysis. This was also one of the dogs that failed a test of motivation in experiment 1.

### *Experimental Testing and Analysis*

Experimental testing was identical to experiment 1, only instead of the experimenter pointing at the correct container for a total of 10 trials, testing continued for up to 60 trials or until an individual dog reached criterion set at eight out of the last 10 trials correct. As in experiment 1, correct responses (approaching the correct can first within one minute) resulted in verbal praise and placement of a preferred food item on top the correct can for the dog to consume. Approach of the incorrect can, or neither can within one minute, resulted in the dog being called back to the start location without food or praise.

The goal was to determine whether individual Anatolian Shepherds could learn to follow an experimenter's point with additional training, using a standard success criterion (see also Udell et al. 2010); this would be the expected outcome if initial failures were due to a modifiable inhibition to follow or approach a moving stimulus, possibly coupled with lack of rewarded experience for engaging in such tasks. However, if individuals failed to follow the experimenter's point over the course of additional trials, this might indicate that breed selection had indeed resulted in a socio-cognitive deficit or the absence of stimulus tracking behavior, making point following inherently more challenging for this group. Therefore the number of successful individuals, and the number of trials required to reach success, were assessed in this experiment. A one-tailed Fisher's Exact test was used to determine if there was a significant improvement in the

number of successful Anatolian's in Experiment 2 (after additional experience) compared to Experiment 1.

## **Results and Discussion**

All five Anatolian Shepherds participating in experiment 2 reached the success criterion in less than the allotted 60 trials. This was a statistically significant improvement from the zero (of 10 Anatolian Shepherds) that performed above chance on this task in experiment 1 (Fisher's Exact test,  $p = 0.0001$ ). In fact all individuals met the success criterion in 30 trials or fewer (average additional trials before success criterion met,  $\bar{X} \pm SE = 15.8 \pm 4.2$ ), suggesting that the poor initial performance of Anatolian Shepherds was more likely due to their known *inhibition* for following a moving stimulus, or lack of experience, than a breed-specific socio-cognitive deficit or lack of motivation. By providing additional training trials, Anatolians were able to overcome this behavioral inhibition and reliably approach the correct can to obtain food.

These data emphasize that failure to engage in behavior may sometimes occur even when the cognitive capacity for success exists. In this case, a predisposed (breed selected) inhibition for chasing moving objects and/or lack of experience may have been sufficient to temporarily mask the ability of one breed of dog, the Anatolian Shepherd, to perform successfully on a human-guided task (point following); even though the potential for success on this socio-cognitive tasks was present. Similarly, it has previously been noted that recent lifetime experiences can also result in initial poor performance on human-guided tasks across breeds, even among individuals that demonstrated the

cognitive capacity to succeed under different conditions or with additional experience. For example, Udell et al. (2010) found that dogs living in a shelter were initially unsuccessful at following a momentary distal point at above chance levels, however with additional trials (often in as few as 15 point repetitions) they could acquire this skill.

## **General Discussion**

The results of experiment 1 supported the prediction that point following tasks, which require dogs to track and follow human movement to a location where they can consume food, may be influenced by breed in some cases. In particular, this study demonstrated that breed-specific predatory motor patterns can serve as an important predictor of success on this task. Terriers which have the most wolf-like predatory sequence typically performed above chance on this task at a rate similar to wolves tested in prior studies (e.g. Udell et al., 2008). Border Collies, which have been bred for a hypertrophied, or exaggerated, eye-stalk-chase component of the predatory sequence, performed above chance on this task at a higher rate than Terriers. On the other hand, Anatolian Shepherds, which were bred for the inhibition of behaviors related to the predatory sequence, initially performed at chance levels on this task; fairing significantly worse than any other group. However, experiment 2 demonstrated that despite their poor initial performance, Anatolians overcame this behavioral inhibition quickly, with some individuals reaching above chance performance in as few as eight additional trials. Therefore Anatolian Shepherds appeared to be displaying a breed-characteristic resistance to the approach of movement (a inhibition intentionally selected for in

livestock guarding breeds), rather than an inherent deficit in social cognition or lack of motivation, when they initially failed to follow human points to the target.

It is important to note that multiple factors may contribute to performance differences between breeds. Even if breed-specific genetic predispositions can account for some of the variability seen between dogs, lifetime experience, physical attributes, or other biological variables may serve to compound this effect (Udell et al. 2010a). For example, it has been suggested that some breeds, including Border Collies, might find access to (or the chase of) moving stimuli inherently reinforcing (Marschark & Baenninger 2002). This may provide additional motivation for following human points (food+ opportunity to chase) compared with breeds that do not find chase inherently reinforcing (food alone). Some breeds or individuals may also be more motivated by food, or certain kinds of food, than others. Physical size and snout shape may influence performance on pointing tasks (Helton & Helton 2010), either directly (i.e. larger breeds often have superior visual acuity) or indirectly (i.e. differential treatment by owners, indoor/outdoor lifestyle, owner/stranger perceptions). While in the current study we controlled for working versus pet history (all subjects were working breeds but lived as pets with no training or use in their working roles), future studies may find value in comparing working dogs and pets from the same breed to better understand the influence of differential lifetime experiences and training history independent of breed (for examples see: Marshall-Pescini et al. 2009; Mariti et al. 2012). In fact, in some cases traits attributed to breed (e.g., aggression towards humans) may be more accurately predicted by the behaviour of a dog's owner (including a personal history or aggression, arrest, etc.) than by any inherent quality of the dog itself (Sacks et al. 2000; Ott et al.

2008; Ragatz et al. 2009). This could suggest that some behavioural traits attributed to pet breeds are heavily influenced by the lifestyle and behavior of the people who tend to seek them out (Gladwell 2006). Breed stereotypes can also alter both dog and owner experiences within the home and in the presence of bystanders (Twining et al. 2000), which may in turn contribute to the development of something like the expected behaviour in a dog of a particular breed, for better or for worse (a self-fulfilling prophecy effect). Even in experimental tests, environment (indoor versus outdoor), testing layout (with or without a barrier between subject and human), gesture type, and order can influence subject performance in many cases (Gasci et al. 2009a; Udell et al. 2008, 2010b, 2012, 2013). Therefore future studies should continue to tease apart the many possible lifetime and biological variables that contribute to canine performance on human guided tasks, as well as the interactions that exist between them.

To our knowledge, this study is the first to propose the hypothesis that breed differences in responsiveness to human gestures may be influenced by behavioral mechanisms that have been (and still are) selected for among working breeds- i.e. predatory motor response. Furthermore in experiment 2, we demonstrated that explicit experience can be used to overcome breed-specific predispositions in some cases. Therefore our current findings suggest that differences in point following performance between breeds may not be due to differences in socio-cognitive ability. Instead, taken together, these results suggest that the *interaction* between previously identified genetic predispositions (breed-specific motor patterns) and lifetime experience may serve as an important predictor of canine performance on human-guided pointing tasks.

While the current results provide strong predictors about the behavior of these three working breeds on human guided tasks, these findings may be limited in the sense that only a small percentage of breeds today (and then often only working lines within those breeds) experience intense breeding and genetic selection for specific behavioral traits or motor patterns. The great majority of the world's dogs are not purebreds. Most dogs are mixed-breed or feral type village dogs where such designations are not relevant (Coppinger & Coppinger, 2001). So where does this leave us?

Unfortunately this study will not make it possible to predict the pointing task performance of all dog breeds based on the current data or based on their known predatory sequence; this is because unlike the breeds tested here, many pet breeds 'do not have' a well established/consistent predatory motor sequence shared by all members of their breed. However the current study does suggest that an individual dog's uniquely developed predatory sequence (or lack-there-of) may still influence performance on cognitive tasks; especially those tasks related to tracking movement (orient, eye), goal directed navigation (stalk, chase), grabbing or pulling objects or ropes (grab-bite), tearing into or opening objects (kill-bite/shake, dissect), or any task involving food retrieval or consumption. In other words, relevant components of the predatory sequence may influence canine performance on a wide range of cognitive tasks based on known biological predispositions, although it may be easier to pinpoint and anticipate the effect for individuals from breeds where the predatory response has been shaped and maintained through selective breeding. This could explain a proportion of the individual variability that has been repeatedly identified in studies on canine cognition ((Udell et al. 2008a, 2008b, 2013; Gacsi et al. 2009a). Likewise, other behavioral motor patterns may

also influence the individual performance of dogs. And of course, individual life experiences, including explicit training or employment in a particular working role (Marshall-Pescini et al. 2009), provide another important source of behavioral variation that should not be overlooked. As demonstrated in experiment 2, heritable predispositions and experience both contribute significantly to an individual's behavioral phenotype and performance, a finding that has also been robustly demonstrated in the literature (see Udell et al. 2010a for a review). In any case, these findings suggest that additional care should to be taken when designing and interpreting comparative studies to ensure reported differences are really due to the mechanism in question (i.e. social cognition), and not due to behavioral inhibitions, physical differences or conflicts triggered by other aspects of the experimental design.

Future study of how societal or owner perceptions of breed influence the real or imagined behavioral traits of individual dogs would be interesting and valuable. Differential treatment by owners based on a dog's size, form, breed designation, or behavioral predispositions could influence a dog's behavior on social or problem solving tasks in a multitude of ways. However those interested in heritable breed differences in canine cognition should consider investigating how empirically documented behavioral predispositions or motor patterns selected for within a specific breed (as opposed to hypothetical or subjective breed categories) can influence performance on behaviorally relevant cognitive tasks. The current study suggests that such hypotheses not only have strong predictive value, but can also shed light on the nature of biological mechanisms that may underlie performance on cognitive tasks relevant to the success of dogs in human environments (including the human home) and in various working roles (Udell &

Wynne 2008). This approach will also likely prove pragmatic for those interested in identifying underlying genetic contributors of physical and/or socio-cognitive performance in dogs (Spady & Ostrander 2008).

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## References

- Buttelmann, D. & Tomasello, M. 2012. Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? *Animal Cognition*, 16, 137–145.
- Coppinger, R. & Coppinger, L. 2001. *Dogs: A startling new understanding of canine origin, behavior & evolution*. 1st edn. New York: Scribner.
- Coppinger, R. & Schneider, R. 1995. The evolution of working dogs. In: *The domestic dog: Its evolution, behaviour and interactions with people*, Serpell JS (ed) edn. New York: Cambridge University Press.
- Coren, S. 2006. *The intelligence of dogs: a guide to the thoughts, emotions, and inner lives of our canine companions*. New York: Free Press.
- Dorey, N. R., Udell, M. A. R. & Wynne, C. D. L. 2009. Breed differences in dogs sensitivity to human points: A meta-analysis. *Behavioural Processes*, 81, 409–415.
- Dorey, N. R., Udell, M. A. R. & Wynne, C. D. L. 2010. When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, 79, 37–41.
- Gacsi, M., Kara, E., Belenyi, B., Topal, J. & Miklosi, A. 2009a. The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition*, 12, 471–479.
- Gacsi, M., McGreevy, P., Kara, E. & Adam, M. 2009b. Effects of selection for cooperation and attention in dogs. *Behavioral And Brain Functions*, 5.
- Gladwell, M. 2006. Troublemakers. *The New Yorker*.
- Helton, W. S. & Helton, N. D. 2010. Physical size matters in the domestic dog's (*Canis lupus familiaris*) ability to use human pointing cues. *Behavioural Processes*, 85, 77–79.
- Jakovcevic, A., Elgier, A. M., Mustaca, A. E. & Bentosela, M. 2010. Breed differences in dogs' (*Canis familiaris*) gaze to the human face. *Behavioural Processes*, 84, 602–607.
- Mariti, C., Ricci, E., Carlone, B., Moore, J. L., Sighieri, C. & Gazzano, A. 2012. Dog attachment to man: A comparison between pet and working dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8, 135–145.
- Marschark, E. D. & Baenninger, R. 2002. Modification of instinctive herding dog behavior using reinforcement and punishment. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, 15, 51–68.
- Marshall-Pescini, S., Passalacqua, C., Barnard, S., Valsecchi, P. & Prato-Previde, E. 2009. Agility and search and rescue training differently affects pet dogs' behaviour in socio-cognitive tasks. *Behavioural Processes*, 81, 416–422.

Ott, S. A., Schalke, E., Gaertner, V., M, A. & Hackbarth, H. 2008. Is there a difference? Comparison of golden retrievers and dogs affected by breed-specific legislation regarding aggressive behavior. *Journal of Veterinary Behavior: Clinical Applications and Research*, 3, 134–140.

Plutchik, R. 1971. Individual and breed differences in approach and withdrawal in dogs. *Behaviour*, 40, 302–311.

Pongrácz, P., Miklósi, Á., Vida, V. & Csányi, V. 2005. The pet dogs ability for learning from a human demonstrator in a detour task is independent from the breed and age. *Applied Animal Behaviour Science*, 90, 309–323.

Ragatz, L., Fremouw, W., Thomas, T. & McCoy, K. 2009. Vicious dogs: the antisocial behaviors and psychological characteristics of owners. *Journal of Forensic Sciences*, 54, 699–703.

Sacks, J., Sinclair, L. & Gilchrist, J. 2000. Breeds of dogs involved in fatal human attacks in the United States between 1979 and 1998. *Journal of the American Veterinary Medical Association*, 217, 836–840.

Scott, J. P. & Fuller, J. L. 1965. *Genetics and the social behavior of the dog*. 1st edn. Chicago, IL.: University Of Chicago Press.

Spady, T. C. & Ostrander, E. A. 2008. Canine behavioral genetics: Pointing out the phenotypes and herding up the genes. *The American Journal of Human Genetics*, 82, 10–18.

Twining, H., Arluke, A. & Patronek, G. 2000. Managing the stigma of outlaw breeds: A case study of pit bull owners. *Society and Animals*, 8, 25–52.

Udell, M. A. R., Giglio, R. F. & Wynne, C. D. L. 2008a. Domestic dogs (*Canis familiaris*) use human gestures but not nonhuman tokens to find hidden food. *Journal of Comparative Psychology*, 122, 84–93.

Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L. 2008b. Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76, 1767–1773.

Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L. 2010a. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, 85, 327–345.

Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L. 2010b. The performance of stray dogs (*Canis familiaris*) living in a shelter on human-guided object-choice tasks. *Animal Behaviour*, 79, 717–725.

Udell, M., Hall, N. J., Morrison, J., Dorey, N. R. & Wynne, C. D. L. 2013. Point topography and within-session learning are important predictors of pet dogs' (*Canis lupus*

familiaris) performance on human guided tasks. *Revista Argentina de Ciencias del Comportamiento*, 5, 3–20.

Udell, M. A. R., Spencer, J. M., Dorey, N. R., Wynne, C. D. L. 2012. Human-socialized wolves follow diverse human gestures... and they may not be alone. *International Journal of Comparative Psychology*, 25, 97–117.

Udell, M. A. R. & Wynne, C. D. L. 2008. A review of domestic dogs' (*Canis familiaris*) human-like behaviors: or why behavior analysts should stop worrying and love their dogs. *Journal of the Experimental Analysis of Behavior*, 89, 247–261.

Vas, J., Topál, J., Gácsi, M., Miklósi, Á. & Csányi, V. 2005. A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science*, 94, 99–115.

Wobber, V., Hare, B., Koler-Matznick, J., Wrangham, R., Tomasello, M. 2009. Breed differences in domestic dogs' (*Canis familiaris*) comprehension of human communicative signals. *Interaction Studies*, 10, 206–224.

Wynne, C. D. L., Udell, M. A. R. & Lord, K. A. 2008. Ontogeny's impacts on human-dog communication. *Animal Behaviour*, 76, e1–e4.