



Ontogeny and phylogeny: both are essential to human-sensitive behaviour in the genus *Canis*

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In responding to Hare et al. (2010), we wish to start by outlining our substantive areas of agreement. We do not disagree that pet domestic dogs have a remarkable sensitivity to human actions, gestures and intentional movements. We also agree with Hare et al. that the most likely reason why the wolves tested in Udell et al. (2008a) were so responsive to human pointing gestures was because these animals were 'highly socialized [and] [t]his socialization probably gave [these] subjects significant experience responding to actions similar to human pointing, whether the animal handler was aware of this type of exposure or not' (Hare et al. 2010, page e6). In that paper we argued that 'that environment and development affect a social animal's ability to react in situation appropriate ways to the social cues of other individuals' (Udell et al. 2008a, page 1772).

The crux of our disagreement with Hare et al. (2010) is our belief that socialization and experience are essential for all canids to respond to hetero- and conspecific cues. Since at least the 1920s scientists have recognized that heredity alone is insufficient to fully explain a phenotype. Phenotypes can only be characterized as the outcome of

a complex interaction between heredity, development and environment (Gottlieb 2002). Unfortunately development and environment receive short shrift in the domestication hypothesis as presented by Hare et al. (2010). To be clear, we do not deny an influence of heredity or domestication on the social behaviour of domestic dogs, we simply do not agree that a hypothesis based on genetic inheritance alone is viable without consideration of the interacting developmental and environmental variables that are necessary for the expression of any phenotype. Our response is organized to match Hare et al.'s (2010) commentary. First, we respond to their review of the literature on the sensitivity of dogs, wolves and foxes to human cues. Second, we discuss their reanalysis of our data comparing the performance of wolves and dogs in responding to a human pointing gesture (Udell et al. 2008a). Third, we consider the data on dogs living in a shelter reported in Hare et al. (2010). Fourth we comment briefly on Hare et al.'s response to Wynne et al.'s (2008) reanalysis of Riedel et al.'s (2008) data on the development of following human points in dog pups, before concluding with some general comments on the roles of ontogeny and phylogeny in the expression of complex interspecies social behaviours.

PROBLEMS WITH HARE ET AL.'S REVIEW OF THE LITERATURE

The most common form of test of a dog's ability to use cues given by humans involves a human pointing at one of two

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containers. Choice of the pointed-to container will be rewarded with a small piece of food; choice of the other container is not rewarded. In many cases the target container is pre-baited, containing the food reward before the beginning of the trial. Given that dogs are renowned for their sense of smell (e.g. Oxley & Waggoner 2009), an obvious initial question in considering the results of such studies is whether the dogs under test might not simply identify the baited container by smell alone.

Hare et al. (2010) claim that prior studies of dogs' responsiveness to human communicative behaviours have included 'controls [that] rule out the use of olfactory cues; (Cooper et al. 2003; Hare & Tomasello 2005; Miklósi & Soproni 2006)' (page e1). In fact, none of the three studies, nor the vast majority of other studies on this issue, have reported controls for olfactory cues. Indeed, even the new data presented by Hare et al. (2010) in their commentary included no controls for odour cuing. The absence of controls for the possibility that canids are identifying the baited container in these experiments by smell is especially worrisome in light of the fact that Szeteci et al. (2003) demonstrated that dogs can utilize odour cues when they are available in tasks of this type. We previously found that a wolf could locate an accessible piece of food in one container by odour, consistently approaching the container with accessible food, even if another container was present that contained the same amount of food buried under several centimetres of stones (Udell et al. 2008a).

Hare et al. (2010) argue that wolves can only follow human communicative gestures when they are explicitly trained to do so, whereas dogs have a spontaneous ability to follow points, and they cite Agnetta et al. (2000), Hare et al. (2002) and Virányi et al. (2008) to support that claim. Furthermore, they claim that this dependency of wolves but not of dogs on explicit training has been demonstrated in wolves 'reared in identical conditions with a group of dogs for the purpose of comparing their social skills with humans' (page e1). We do not accept this as an accurate summary of the prior studies on wolves. Both Agnetta et al. (2000) and Hare et al. (2002) tested the ability of adult wolves to follow the pointing gesture of a human towards a baited food container where the human stayed outside the animal's enclosure. To further add to the difficulty of the task, the wolves tested in Agnetta et al. had to move between three cages to get to the locations of the containers. In both studies, the wolves, on average, were not successful in following the human point to find food, although individual results were not presented. We have already demonstrated (Udell et al. 2008a) that the ability of dogs to follow a human point through a fence is substantially limited. Thus, it is reasonable to assume that the presence of the fence barrier, which was not used by Agnetta et al. (2000) and Hare et al. (2002) in their studies on dogs, accounts for the poor performance of the wolves on these tests.

Virányi et al. (2008) come closer to achieving a balanced comparison of dogs and wolves. Virányi et al. (2008), unlike Agnetta et al. (2000) and Hare et al. (2002), reared their wolf and dog pups from birth, and they tested the animals before maturity (at 4 months old) as well as at 7 months old. While dogs followed a momentary distal point at 4 months of age, wolf pups performed at chance levels. At 7 months, and after extensive experience with the task, wolves began to perform at the level of naïve dogs. Unfortunately, the wolf pups, but not the dog pups, were removed from human homes between 2 and 4 months of age and thereafter reared at a private 'wolf farm' where they were visited by their human rearers for only half a day, twice per week. The fact that the experiences of the wolves involved considerably less human contact after 2 months of age than did those of the dogs means that this study cannot achieve its purpose of a direct comparison of wolf and dog pups raised under identical conditions.

We do not doubt that the vast majority of wolves do not follow human points. Our demonstration that a subgroup of wolves can

follow human points without explicit training, recently replicated by Gácsi et al. (2009), demonstrates that the potential to develop responsiveness to human cues exists in nondomesticated canids. No number of demonstrations of wolves that fail to follow human points would contradict this finding.

Hare et al. (2010) cite Hare et al.'s (2005) study of Balyaev's foxes and control wild-type foxes as further evidence that wild-type canids are incapable of following human pointing gestures. Balyaev's foxes were bred for over 40 generations for tolerance of humans, including reduced flight distance to human approach (Trut 1999). Hare et al. (2005) tested Balyaev's and wild-type control foxes for their ability to follow a human point to locate food hidden in one of two containers. Importantly, both groups of foxes scored significantly above chance; however, the Balyaev's foxes attained a higher level of performance than the wild foxes (although only on a one-tailed statistical test). We have drawn attention elsewhere (Udell et al., in press) to the fact that matching the Balyaev's and wild-type foxes by chronological age introduces a confound into the comparison. One of the major impacts of the artificial selection for tameness in Balyaev's foxes is a lengthening of the critical window for socialization (Trut et al. 2004). Thus, the finding that Balyaev's foxes follow human points at a marginally higher level than do nonhuman-socialized wild-type foxes is probably due to their developmental trajectories, including differences in developmental stage at the time of testing, and not simply a function of their phylogenetic histories (for a thorough review of this confound see Udell et al., in press).

Hare et al. (2010) further argue that 'dogs develop their ability to use human communicative cues, such as pointing cues or gaze cues, as young puppies regardless of rearing history' (page e1). Hare et al. (2002) tested dog pups ranging in age from 9 to 26 weeks, some of which had lived in human families, while others had 'lived their entire lives with littermates in a kennel and so had been exposed to humans for only a few minutes each day for husbandry purposes' (page 1635). Hare et al. (2010) reported that even the youngest age group (9–13 weeks) of pups experiencing 'minimal' human contact were successful at following a human pointing gesture to find food at above-chance levels, scoring an average of 15 of 18 trials correct. However, one important problem with Hare et al.'s (2010) interpretation of these data is that it was simply not the case that the kennel-reared pups had experienced only minimal human contact. The pups were obtained from Pik a Pup kennels in Holliston, Massachusetts, U.S.A. This establishment breeds dogs for placement as pets in human homes. They describe their pups as 'a new family member who will give unconditional love for years to come' (<http://pikapup.com/index.php>), and report that both employees and customers interact with the pups on a daily basis.

Dog pups not socialized to human company are rare in modern Western societies where the majority of dogs have a close bond to humans (New et al. 2004). Since dog pups imprint easily on humans during their long critical window for social development (up to 16 weeks: Coppinger & Coppinger 2001), and are usually exposed to people during their first 4 months of life, it is actually quite difficult to rear a dog that is not socially imprinted on humans. No responsible breeder would intentionally rear such animals, and it is unlikely that rearing unsocialized dogs would be tolerated by animal experimentation ethics committees in the Western world today. Fifty years ago, Scott & Fuller (1965) reared a small number of completely unsocialized dogs and reported that these animals '... later react toward [humans] with extreme fear and hostility' (page 176).

We have already commented on the results obtained by Riedel et al. (2008) in Wynne et al. (2008). Since Hare et al. (2010) raise issues with our reanalysis of Riedel et al.'s (2008) data, we dedicate

a separate subsection to this study below. Suffice it to say here that this study offers clear evidence that dogs' ability to follow human cues improves with age (Wynne et al. 2008).

REANALYSIS OF UDELL ET AL. (2008a): WOLVES ARE STILL MORE SKILLED THAN DOGS

Hare et al. (2010) raise several questions about the methodology by which we compared the performance of wolves and several groups of dogs in their ability to follow human points in Udell et al. (2008a).

Their first criticism is that 'Unlike Hare et al. (2005) and Virányi et al. (2008), none of the subjects [in Udell et al. 2008a] were reared for the purposes of the experiment' (page e2). While it is true that Virányi et al. (2008) reared their wolves for the purpose of their experimental test, this is the exception in the literature, not the rule. In a recent review, we analysed the performance of dogs following human points from 14 published papers (Dorey et al. 2009). In none of these papers were the dogs specifically raised by the experimenters; rather, they were all pets volunteered for testing by their owners.

Furthermore, the fox and dog subjects in Hare et al. (2005), and the wolf and dog subjects in Hare et al. (2002) were also not reared for the purpose of the experiments. The wolves Hare et al. (2002) used resided at Wolf Hollow, an educational establishment not dissimilar from Wolf Park where the wolves tested in Udell et al. (2008a) were living. The wolves were reported to be adults at the onset of the experiment, and there is no evidence that they were reared specifically for Hare et al.'s experiment. The dog subjects used in Hare et al. (2002) were pets and dogs intended to be sold as pets: none was reported to be reared by the experimenters for the purpose of the experiment. The foxes tested by Hare et al. (2005) were part of the stock of the Balyaev fox farm at the Russian Academy of Sciences, Institute for Cytology and Genetics, and were also not reared for Hare et al.'s (2005) experiments (see Supplementary Material in Hare et al. 2005). Despite the fact that none of the canids was reared for the purpose of these experiments, Hare et al. (2010) did not hesitate to use these data as support for the domestication hypothesis.

If what Hare et al. (2010) really meant was that the foxes and wolves tested by Hare et al. (2002, 2005) were reared in a research facility that raised their animals in a specific and known way, although not actually reared for the purpose of the experiment, then the same is true of the wolf subjects used in Udell et al. (2008a).

It appears that the crux of Hare et al.'s (2010) critique is not really about special rearing of animals for testing, but rather concerns the degree of socialization and experience with humans that our wolf subjects may have received compared to that of previously tested undomesticated canids. Hare et al. (2010) state: 'In fact, we suspect that, given their use in public education programmes, the wolves that Udell and colleagues tested probably had received previous training and were highly socialized. *This socialization probably gave their subjects significant experience responding to actions similar to human pointing, whether the animal handler was aware of this type of exposure or not.* Udell et al. (2008a) cannot rule out this type of simple exposure explanation for the success of their adult wolves based on the current data' (page e6, emphasis added).

We do not disagree that the wolves we tested were more successful than those tested in prior studies because they had been more effectively socialized to humans. This was precisely our point in Udell et al. (2008a). Discussions with the wolves' caregivers assured us that the wolves tested had not experienced explicit training on following points, but we consider it highly likely that

their daily experiences with humans had led them to attend to the movement of human hands in anticipation of food and other rewards. We also agree that this attentiveness to human limb movements is likely to occur in environments where canids have daily interactions with humans, whether the handler is aware of it or not. Research and education facilities where wolves are effectively socialized to humans and continue to receive daily interaction with humans throughout their lives, just like dogs living in human homes, are candidates for such exposure.

Hare et al. (2010) are also concerned about our use of response objects (closed paint cans) that did not conceal food prior to the subject making a choice. As we stated in Udell et al. (2008a): 'This method was adopted because preliminary studies with wolves indicated that they could detect even small pieces of pre-hidden food in a container by smell alone' (Udell et al. 2008a, page 1769). We have already discussed the paucity of controls for odour cuing in the extant literature. Since our methodology was consistent across all groups, differences in performance between canid types cannot be explained by our use of this methodology.

Two other criticisms were raised about our methodology: (1) the use of a clicker; and (2) the use of warm-up trials. A clicker is a device that simply makes a consistent 'click' sound, much like the sound of opening a soda can. This sound was a tool to reduce the effects of reinforcer delay since food was not immediately accessible as it is in the traditional methodology. None of the subjects in our experiment received prior training on the experimental task with or without the use of a clicker. Our use of the term 'naïve' was intended to convey that no such training had taken place.

Second, our use of warm-up trials to familiarize the subjects with the response objects and to test for motivation is not 'unlike all previous studies' (Hare et al. 2010, page e2). Such warm-up trials have been used since the first experiment of this type conducted with dogs (Miklósi et al. 1998). The experiment on shelter dogs reported in Hare et al.'s (2010) critique itself includes similar warm-up trials. The only identifiable difference from our warm-up procedure and that of other researchers is that we placed food on top of the response objects during warm-up trials rather than in or under the response object. Since the purpose of warm-up trials is simply to test for food motivation and to familiarize subjects with the condition of eating food from the experimental containers, we can see no reason to place food inside the containers during warm-up trials if food is never going to be found inside the containers during testing.

Hare et al. (2010) raise several issues concerning our data analysis. In Udell et al. (2008a) we defined a correct choice as the subject 'touching or coming within 10 cm of [the correct can] with its snout' (page 1769). Failure to make a correct response during an experimental trial was scored as an incorrect response. Hare et al. (2010) argue that the only valid incorrect response is touching the opposite can, and that all other responses should be coded as nonparticipation and excluded from statistical analyses. We were fully aware of the possibility of nonparticipation when designing our study. In fact, as Hare et al. (2010) mention, unlike most studies, we included a specific test of motivation in our methodology to ensure that, regardless of point following performance, subjects were motivated to participate in the task. None of the subjects reported in Udell et al. (2008a) failed a test of motivation at any point in the study. When a participating subject did not approach either can during a trial, it often performed an alternative behaviour used to solicit food in their home environment, such as begging from the experimenter or barking at her. However, when we report that each subject experienced 10 trials and got some number of those trials correct, we mean what we say: the stimulus (the human's hand movement) was presented 10 times and the subject had 10 opportunities to respond; on some number of those

opportunities, the subject responded to the container that the human pointed to and the subject was reinforced. All of our statistical analyses were performed on the basis of the number of correct responses out of a total of 10 trials per subject; there were no 'do-overs,' selectively dropped trials, or any other variations from our stated procedure.

While Hare et al. (2010) assert that their reanalysis of our data used a 'more conventional method of examining separately (1) participation (making a choice or not) and (2) the level of correct choices (choosing the cup indicated by a point instead of the one ignored)' (page e3), they provide no references for prior use of this method, and we are not aware that it has ever been used previously. Furthermore this is not the method they used for scoring or analysing their own experimental data in the shelter dog study provided within their critique. Instead, the method Hare et al. used was selective repetition of trials when their subject failed to make one of two desired responses. According to Hare et al. (2010, page e4) 'If a dog did not clearly touch one of the two cups within 25 s (i.e. the dog became distracted or unmotivated), the trial was repeated'. No behavioural definitions or tests for distraction or lack of motivation are provided. Thus, it seems the experimenter had the option of deciding, 25 s into a trial, whether the dog was responding in a desirable way. If not, the data were removed from the analysis and the dog was given another chance to view the human point before making a choice. While an overall percentage of these redone trials is given, the authors provide no indication of which trials for which individuals were redone, or what circumstances justified the selective removal of data beyond the failure to obtain a desired response from the dog. Yet, according to Hare et al. (2010, page e3), 'in previous studies the exclusion or repetition of no-choice trials has been the standard'. Again, no citations are offered, but one can only assume that this is the standard method used by Hare and colleagues in prior experiments even though published methods do not mention it.

The analysis presented in Udell et al. (2008a) accurately summarized the full data set collected in that study. Even after Hare et al.'s (2010) reanalysis, wolves and pet dogs tested indoors still performed significantly above chance on an object-choice task using a momentary distal point without the use of additional odour cues or the repetition of trials during testing. Furthermore, Hare et al.'s reanalysis also leaves untouched our finding that shelter dogs did not succeed on the human-guided object-choice task. Thus, our conclusion that 'domestication alone cannot account for canids' sensitivity to human social cues involved in following a point' (Udell et al. 2008a, page 1772) is not impacted by Hare et al.'s reanalysis.

While Hare et al. argue that their reanalysis shows that 'there is no evidence from the data of Udell et al. (2008a) that adult wolves outperform adult dogs using a human pointing gesture' (Hare et al., 2010, page e4), that is simply because they chose to avoid all mention of individual performance. Udell et al. (2008a, page 1770) reported that 'more individual wolves (six of eight subjects) followed the point on eight or more of 10 trials (binomial test: $P = 0.05$) more often than did domestic dogs [home unfamiliar group] (three of eight subjects)'. According to Hare et al. (2010, page e3) participation reanalysis 'Post hoc comparisons (Bonferroni tests) revealed that the dog home unfamiliar group participated significantly more often than the other three dog groups, but did not differ from the wolf group ($P < 0.05$ for all significant tests)'. Therefore individual comparisons between the dog home unfamiliar group and wolves remain valid even under this new criterion. Despite equal levels of contact with the two response objects, more individual wolves used a human point to perform above chance on the human-guided task than did pet domestic dogs. In fact, even adding the number of successful individuals from all of

the domestic dog groups in Udell et al. (2008a) together ($N = 32$), only seven domestic dogs were individually successful on the task (22%). Of the eight wolves tested, six were individually successful using the same point (75%). Thus, our overall conclusion that 'wolves outperform dogs in following human social cues' remains an accurate portrayal of the findings presented in Udell et al. (2008a, page 1767).

Lastly, Hare et al. (2010) suggest that dogs tested in a more distracting environment (e.g. outdoors or in an unfamiliar location) may perform worse on an object-choice task than they would in a familiar environment. We agree entirely. In fact we said so in our original article: 'Pet dogs reared in comparable conditions can perform differently from each other in different testing environments (indoors versus outdoors and fence versus no fence)' (Udell et al. 2008a, page 1771). No prior study has considered testing environment as an important variable. We suggested in Udell et al. (2008a) that environmental considerations were probably relevant considerations in prior research conducted with wolves and dogs: 'Wolves in the study by Hare et al. (2002) and in the studies by Virányi et al. (2008) were tested under different conditions from their own domestic dog comparison groups, and thus, interfering or distracting aspects of the wolves' testing environment may not have been accounted for' (Udell et al. 2008a, page 1772). It is gratifying to find other researchers taking an interest in this important variable.

ENVIRONMENT, EXPERIENCE AND METHODOLOGY MATTER

Hare et al. (2010) present additional data on the ability of dogs at a shelter to follow human points. Unfortunately, Hare et al. tested their shelter dogs on a substantially simpler form of point than that used by Udell et al. (2008a). In the dynamic proximal point used by Hare et al., the human pointing gesture was repeated four times at 20 cm from the target container. While the resting place of the human hand was not specified by Hare et al., dynamic proximal points are typically left in place until the subject makes its choice. The momentary distal point used in Udell et al. (2008a) involved the experimenter gesturing only once, and her hand came no closer than 50 cm to the pointed to container and it was returned to her midline before the canid was released to make its choice (for point type definitions and the importance of carefully defining stimuli used in object-choice tasks see: Miklósi & Soproni 2006; Udell et al., in press). Thus, we see no inherent contradiction between Hare et al.'s finding that approximately one-third of their subjects were successful on a dynamic proximal point and our finding that none of our subjects achieved success in following the more challenging momentary distal point. We have reanalysed Hare et al.'s data from trials on which the human point was presented, and found that 7 of the 22 subjects followed the human gesture at above-chance levels (binomial test: $P < 0.05$). Our own results (M. A. R. Udell, N. R. Dorey & C. D. L. Wynne, unpublished data) indicate that shelter dogs showed an even higher success rate on the dynamic proximal point (six of seven subjects performed at above chance in the first 10 trials; binomial test: $P < 0.05$). This indicates that when different types of points are used, success and failure of different groups of canids will vary correspondingly. In any case, our purpose was not to claim that domestic dogs cannot follow points. Instead, we predict that the ability of canids to follow human pointing gestures depends on their developmental experiences and current environments, resulting in varied levels of responsiveness in different individuals raised and living under different conditions.

An additional concern with Hare et al.'s shelter dog comparison is that of the four 'human communicative cue' conditions presented, only one was in fact human based: the human point and gaze cue just discussed. The other three cues were (1) a block of

wood placed on top of the cup containing food, (2) shaking the cup containing food to produce an audible noise and (3) shaking the empty cup to produce no noise. As defined in a paper authored by Hare and colleagues (Bräuer et al. 2006), these cues were considered 'causal' cues, not 'human communicative' cues. If unconventional methodology was thought to explain the poor performance of shelter dogs in Udell et al. (2008a), this question could have been addressed by a comparison of the specific methodological differences criticized by Hare et al. (2010). This was not done, however, and it is difficult to see how any comparison can be made on the basis of a study utilizing not only a different methodology but also completely different stimuli.

SPECIFIC EXPERIENCES WITH HUMANS MATTER

Hare et al. (2010) revisit our previous critique (Wynne et al. 2008) of the developmental study by Riedel et al. (2008). We are reluctant to simply repeat remarks we have published previously, so we focus instead on a few broader issues in assessing the development of this behaviour.

First, demonstrating the absence of a developmental change in behaviour amounts statistically to affirming the null hypothesis. Statistical hypothesis testing is only suited for analyses designed to reject a null hypothesis. A failure to reject the null hypothesis cannot be used as evidence that the null hypothesis is true, because null hypothesis testing assumes the truth of the null hypothesis a priori.

When Riedel et al. (2008) performed their main analysis of an effect of age on all pointing types, they included the control condition. Since age would not be expected to affect performance on the control trials, this meant that, in the ANOVA, the effect of age entered as an interaction. Interactions necessarily have fewer degrees of freedom than do main effects on the same data set, thereby reducing the statistical power of the test. When Riedel et al. (2008) analysed each point type separately, they likewise reduced the number of observations per cell compared to the analysis that pooled across all point types, and thereby again reduced the power of the statistical test. Even so, Hare et al. (2010) and Riedel et al. (2008) conceded that one point type showed a definite effect of age, and the other was close to customary levels of statistical significance ($P = 0.094$). Although a probability of rejecting the null hypothesis of around 9% would not normally be considered sufficient to actually reject the null hypothesis, it is far from what can be considered strong support in favour of the null hypothesis. The bottom line for the analysis of dog pups' ability to follow points in Riedel et al. (2008) experiment 1 is that their Figure 2 shows very obvious improvements with age.

Hare et al. (2010) draw attention to the fact that in Wynne et al. (2008) we did not comment on experiments 2 and 3 in Riedel et al. (2008). We refrained from commenting on these other experiments because the performance of the dogs tested was at such uniformly low levels that they contributed nothing to a discussion of the importance of ontogeny to this ability. If a task is too easy or too difficult, developmental trends will not be identifiable. This says nothing important, however, about the contribution of ontogeny to these behaviours.

GENERAL DISCUSSION

Behaviour develops. This is an uncontroversial statement. Human behaviour develops; wolf behaviour develops; fox behaviour develops and dog behaviour develops. The development of adult social behaviour of humans with other humans depends on interactions with other humans during childhood (e.g. Harwood et al. 2008). An extensive literature documents how the

development of conspecific social behaviour in dogs and wolves depends on appropriate interactions with other conspecifics during development (reviewed in Udell et al., *in press*). Thus, we would consider it at least anomalous if dogs showed the ability to comprehend human social cues, such as pointing gestures, at the earliest testable ages regardless of environmental experiences. After all, no such ability exists in human infants. Ample evidence exists, some by coauthors to the commentary by Hare et al. (2010), that clearly shows that children do not fully develop the ability to follow human pointing gestures until their second year of life (Murphy & Messer 1977; Lempers 1979; Behne et al. 2005; Lakatos et al. 2009).

Although the domestication hypothesis posits that learning does not affect domestic dogs' performance in object-choice tasks, there is ample evidence to the contrary. For example, Bentosela et al. (2008) showed that dogs can learn to attend to human gaze in as few as three trials; Udell et al. (2008b) showed that dogs learn to follow unfamiliar human cues in fewer than 10 trials (reviewed in Udell et al., *in press*). The selective deletion of incorrect responses, which Hare et al. (2010) state is customary in this literature, implies that subjects have more opportunities to learn to follow human gestures than is indicated by published studies. The rapidity with which dogs can learn new human cues, combined with the apparently customary incomplete data reporting in the literature, means that it is unclear how any claims about changes in performance across trials can be made by these authors.

Of course something happened during domestication. We are not suggesting that a dog cannot be distinguished from a wolf. The question is not whether something happened during domestication, but what? There is a substantial literature on how domestication affects development and socialization in canids (reviewed in Udell et al., *in press*). Our assertion that domestication in itself cannot explain domestic dogs' responsiveness to human cues, calls for an acknowledgement that neither phylogeny nor ontogeny occur in isolation. It is the interaction that counts. Domestic dogs are interesting specifically because their evolutionary history and their daily life experiences are uniquely tied to human society; their behaviour is always a product of both. We suggest that the phylogenetic prerequisites for responding to the bodily gestures of companions are present in both wolves and domestic dogs. Socialization to humans during early development allows humans to be viewed as companions, and experience throughout life allows for flexible associations between specific bodily movements of companions and important environmental events. These are the predictions of the two-stage hypothesis (Udell et al., *in press*). According to this hypothesis, domestication changes the timeframe and, subsequently, the socialization intensity during which primary socialization to companions, including humans, needs to take place to have the greatest effect. For nondomesticated canids, such as wolves, this period is shorter and ends earlier than it does in domesticated canids such as dogs.

In this commentary we have restricted our comments solely to those aspects of the literature on canids' abilities to respond to human cues raised by Hare et al. (2010). For a more thorough analysis of the reasons why the domestication hypothesis is untenable see Udell et al. (*in press*).

In conclusion we are gratified to see our raw data put to interesting use by other researchers. Such fresh analysis can move a field forward much more rapidly than when different groups of researchers have to collect equivalent data sets. Our trial-by-trial raw data are available to all interested parties on our website, www.caninecognition.com, and we encourage other researchers to return the courtesy (Dorey et al. 2009).

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