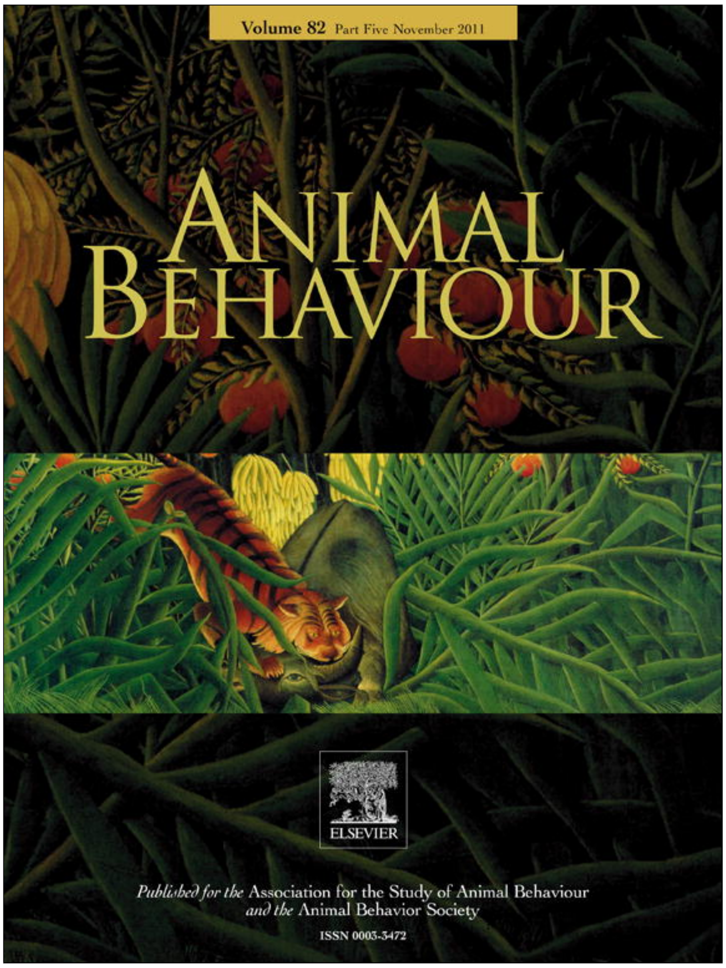
Volume 82 Part Five November 2011
ANIMAL BEHAVIOUR
ELSEVIER
Published for the Association for the Study of Animal Behaviour
and the Animal Behavior Society
ISSN 0003-3472

Animal Behaviour 82 (2011) 1043–1050

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Human-directed gazing behaviour in puppies and adult dogs, *Canis lupus familiaris*

Chiara Passalacqua [a,*], Sarah Marshall-Pescini [a], Shanis Barnard [b,1], Gabriella Lakatos [c,2], Paola Valsecchi [b,1], Emanuela Prato Previde [a]

[a] *Sezione di Psicologia, Dipartimento Scienze e Tecnologie Biomediche, Università di Milano*
[b] *Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma*
[c] *Eötvös Loránd University, Department of Ethology*

ARTICLE INFO

Article history:
Received 23 December 2010
Initial acceptance 7 February 2011
Final acceptance 28 July 2011
Available online 10 September 2011
MS. number: 10-00881R

Keywords:
breed difference
Canis lupus familiaris
development
dog
gaze
human-directed communication

Recent evidence indicates that dogs' sociocognitive abilities and behaviour in a test situation are shaped by both genetic factors and life experiences. We used the 'unsolvable task' paradigm to investigate the effect of breed and age/experience on the use of human-directed gazing behaviour. Following a genetic classification based on recent genome analyses, dogs were allocated to three breed groups, namely Primitive, Hunting/Herding and Molossoid. Furthermore, we tested dogs at 2 months, 4.5 months and as adults. The test consisted of three solvable trials in which dogs could obtain food by manipulating a plastic container followed by an unsolvable trial in which obtaining the food became impossible. The dogs' behaviour towards the apparatus and the people present was analysed. At 2 months no breed group differences emerged and although human-directed gazing behaviour was observed in approximately half of the pups, it occurred for brief periods, suggesting that the aptitude to use human-directed gazing as a request for obtaining help probably develops at a later date when dogs have had more experience with human communication. Breed group differences, however, did emerge strongly in adult dogs and, although less pronounced, also in 4.5-month-old subjects, with dogs in the Hunting/Herding group showing significantly more human-directed gazing behaviour than dogs in the other two breed groups. These results suggest that, although the domestication process may have shaped the dog's human-directed communicative abilities, the later selection for specific types of work might also have had a significant impact on their emergence.

A number of studies have shown that dogs are capable of understanding many aspects of human communication, including communicative cues such as gazing, pointing and head turning (Miklósi et al. 1998; Soproni et al. 2001; Hare & Tomasello 2005; Miklósi & Soproni 2006) and that they are also capable of using gaze as a communicative cue when requesting a specific out-of-reach object from humans (Miklósi et al. 2000, 2003, 2004). It has been suggested that as a direct consequence of domestication by humans, dogs may have (inadvertently) been selected for the ability to follow human communicative gestures (Hare et al. 2002; Miklósi et al. 2003; Hare & Tomasello 2005). This idea is supported by results showing that: (1) dog pups as young as 6 weeks of age can already use a variety of human communicative cues to locate hidden food (Agnetta et al. 2000; Hare et al. 2002; Riedel et al. 2008; Dorey et al. 2010); (2) compared to other domesticated species dogs show a greater flexibility in their use (Miklósi et al. 2004; Maros et al. 2008; Proops & McComb 2010); and (3) hand-reared wolves, *Canis lupus*, are less skilled or developmentally slower in their understanding of human communicative cues than dogs (Hare et al. 2002; Miklósi et al. 2003;Virányi et al. 2008; Gàcsi et al. 2009a; although see Udell et al. 2008 for wolves outperforming dogs on the comprehension of some forms of pointing in specific situations). Further insight on the evolution of dogs' communication with humans comes from recent work on the New Guinea singing dog, *Canis hallstromi* (Wobber et al. 2009) and Australian dingoes, *Canis dingo* (Smith & Litchfield 2010), both considered to have undergone early domestication with very little subsequent selection and contact with humans. Both dingoes and singing dogs were tested with a range of pointing cues and,

* Correspondence: C. Passalacqua, Sezione di Psicologia, Dipartimento Scienze e Tecnologie Biomediche, Facoltà di Medicina, Università di Milano, Via Fratelli Cervi, 93 20090 Segrate (Mi), Italy.
E-mail address: chiara.passalacqua@unimi.it (C. Passalacqua).
[1] S. Barnard and P. Valsecchi are at the Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma, Via G.P. Usberti 11/A, 43100 Parma, Italy.
[2] G. Lakatos is at the Eötvös Loránd University, Department of Ethology, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary.

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.07.039

although the former performed to some extent better than the latter, their performance lies somewhere in between that of wolves and dogs. Together with evidence that foxes, *Vulpes vulpes*, selected for tameness outperform 'untamed' foxes raised in the same manner in following pointing cues (Hare et al. 2005), these studies seem to indicate a strong role of domestication in dogs' ability to comprehend human gestures.

Although a number of studies have focused on canines' comprehension of human communicative cues, far fewer comparative studies have been carried out on their use of communicative cues (such as gazing) towards humans. The only study thus far has shown that hand-reared wolves are less inclined than dogs to produce communicative signals towards humans, although they do not differ in their problem-solving abilities (Miklósi et al. 2003).

Another valuable way to evaluate the possibility of dogs' sensitivity to human communicative cues being a heritable trait is by investigating breed differences. A number of studies have analysed breed differences in relation to temperament (Scott & Fuller 1965; Wilson & Sundgren 1997; Serpell & Hsu 2005) or problem-solving behaviour (Scott & Fuller 1965; Frank & Frank 1982, 1985; Pongrácz et al. 2005); however, very few have investigated the potential differences relating to interspecific communicative skills. To investigate whether dogs' comprehension of human communicative cues (i.e. pointing) is only a product of the more ancient split between wolf and dog, or whether it has been further enhanced by a more recent selection on working dogs, Wobber et al. (2009) compared more versus less wolf-like breeds, which could also be classified as either working with humans or not. Results showed that 'cooperative' breeds used social cues more skilfully, regardless of the breed's genetic closeness to wolves. Similarly, Gàcsi et al. (2009b) showed that dogs of breeds selected for work in contact with humans were significantly more successful in using human pointing gestures than both the independent working breeds and mongrels, confirming the importance of the selection for work type in shaping dogs' understanding of human communicative cues.

However, the grouping of breeds based on their 'working role' can be problematic for a number of reasons. It has been shown that recent selection, with its emphasis on physical as opposed to temperament traits has significantly affected the breed's typical behaviour (Svartberg 2006); thus one cannot be sure that dogs today mirror the 'cooperative' versus 'independent' working roles they were originally selected for. Besides, it is not always clear on what basis a breed should be considered a 'cooperative worker'. Wobber et al. (2009) included sled dogs as a cooperative working breed, whereas Gàcsi et al. (2009b) included them in the independent working breeds.

Another difficulty in studying breed differences is that it has been shown that both the comprehension and production of communicative cues in dogs is influenced by their environment and life experiences. Shelter dogs are not as skilled as pet dogs in pointing comprehension (Udell et al. 2010; but see also Hare et al. 2010), and both are surpassed by trained retrievers (McKinley & Sambrook 2000). Moreover, dogs kept outside the house have been shown to use gazing behaviour less than those kept in the house for companionship in a problem-solving task (Topál et al. 1997), whereas agility- and search-and-rescue-trained dogs are more prone to use gazing as a communicative cue than untrained pet dogs (Marshall-Pescini et al. 2009) and there is evidence that this behaviour is modulated by learning (Bentosela et al. 2008, 2009; Jakovcevic et al. 2010). Despite these caveats, the comparison between breeds remains an important tool in understanding the potential genetic influence on dogs' communicative abilities. To our knowledge, apart from the study by Jakovcevic et al. (2010) showing differences between three breeds in the acquisition and extinction of gazing at humans, studies on the spontaneous production by the dog of communicative cues towards humans (as opposed to the correct interpretation/comprehension of human cues by dogs) are lacking. Furthermore, a number of studies have looked at the comprehension of communicative cues in dogs at early stages of their development (Agnetta et al. 2000; Riedel et al. 2008; Gàcsi et al. 2009a), but nothing is known about the development of human-directed communicative cues, such as gazing.

In the current study we analysed the potential influence of breed groups and development (age and experience) on human-directed gazing behaviour with a simplified version of the 'unsolvable task' used to compare wolves and dogs by Miklósi et al. (2003). Given the results of this previous study, we predicted that more wolf-like (primitive) breeds would be less prone to use human-directed gazing behaviour than other breed groups. Furthermore, according to previous findings showing the effects of life experiences on the expression of human-directed gazing behaviour, we expected adult dogs to show this behaviour more than younger dogs.

METHODS

Breed Groups

Given that the major canine organizations (American Kennel Club, AKC, and Federation Cynologique Internationale, FCI) propose different classifications of breeds based on various criteria (function, morphology, geographical origin), we decided to adopt the genetic clustering based on relatedness among breeds and to the wolf outlined by Parker et al. (2004). According to this classification we considered the following three groups: Primitive, Hunting/Herding and Molossoid (i.e. mastiff-type dogs). It is worth noting that there is a major overlap between the clustering outlined by Parker et al. (2004) used here and the categories defined by the FCI, since breeds in our Primitive group are all included in FCI Group 5; most breeds (apart from the German shepherd and the bull terrier) in our Molossoid group are included in FCI Group 2, and all breeds in our Hunting/Herding group are included in FCI Group1 and Group 8, respectively.

Age Groups

To gain more insight into the development of human-directed gazing behaviour we considered three age groups differing in the amount of experience with humans and with sufficiently developed motivation and motor skills to accomplish the task: 2-month-old pups tested prior to entering the owner's home to reduce the potential influence of life experiences; 4.5-month-old and adult dogs, both kept as pets but with different amounts of experience in interacting with people.

Subjects

Two-month-old puppies

Overall, 167 puppies (84 males and 83 females) were tested at the age of 2 months (range 60–70 days, mean = 61.2 days), before adoption. Pups were recruited from registered dog breeders, avoiding house-raised puppies. The rationale for this decision was that standardizing the life of the pups in homes would be more difficult than in pens. Registered breeders were selected on the basis of the following criteria regarding the social and physical environment in which the pups were raised. (1) Puppies had to spend most of the day with their mother and littermates. (2) Puppies had to live in pens (not in the breeder's home). (3) Puppies had to have, as a minimum, two daily interactions with humans (and no more than four). (4) Puppies underwent enrichment sessions, which had to include interactions with familiar and unfamiliar humans (including manipulation and play, etc.), unfamiliar dogs and novel objects. Twenty-five breeders met these criteria and were thus included in the study (i.e. two breeders per selected breed). We chose more than one breeder for each breed to avoid the risk of testing specific blood lines and to homogenize the sample.

Four-and-a-half-month-old dogs

A total of 54 dogs (27 males, 27 females) of the same three breed groups were tested at 4.5 months (range 119–165 days, mean = 133 days).

Adults

A total of 172 adult dogs (74 males, 98 females) were recruited through advertisements in local dog magazines, parks, vet clinics, breed specialists, web forums, etc. (age range 1–12 years, mean $\pm$ SD = 4.43 $\pm$ 3.03 years). All dogs lived as pets and had no specific training experience; none of the owners reported practising any particular activity with their dogs.

Apparatus

The apparatus and procedure were the same as in Marshall-Pescini et al. (2009); the procedure for 2-month-old puppies was slightly different because for adult and 4.5-month-old dogs the experimenter and owner were present, while with the 2-month-old pups only the experimenter was present during the test. The apparatus consisted of a transparent 15 $\times$ 15 cm lid-less plastic container (commercial Tupperware), placed upside down over a few titbits of food on a 35 $\times$ 60 cm wooden board. The container, with holes on the top, could be either moved off the platform or overturned to obtain the food or it could be securely screwed to the board so the food could not be reached (Fig. 1). The apparatus was the same for all age categories.

Procedure

Puppies were tested at their breeders in a quiet, 5 $\times$ 5 m outdoor area, temporarily fenced off, using a portable 'puppy pen' covered by a dimming net (to avoid distraction from the outside), while for 4.5-month-old and adult dogs testing was carried out in a secluded outdoor enclosure (also with dimming net and approximately 25 m^2) at the University of Milan or Parma. Breeders and owners were asked not to feed their dogs for at least 4 h prior to testing. The task used was a modified version of the unsolvable task (Miklósi et al. 2003), made easier so as to be feasible also to 2-month-old puppies. The test consisted of three consecutive solvable trials in which dogs could obtain the food by manipulating the container, immediately followed by an unsolvable trial in which the container was fixed onto the wooden board and thus obtaining the food became impossible. In the standard procedure (Marshall-Pescini et al. 2009) both the experimenter and the owner were present during the test; however, in the present study the breeders could not guarantee their presence systematically during the test, as it was time consuming. Thus for 2-month-old puppies we decided to run the test only with the experimenter present.

When testing the 2-month-old puppies, the experimenter knelt down on the ground 50 cm from the wooden board on which the container was placed (Fig. 1a). In the solvable trials the experimenter held the puppies close to her while placing some food (four large pieces of Frolic) under the container. She then released the puppy and allowed it to move freely around the test area.

For the 4.5-month-old and adult dogs the owner and the experimenter were present, standing 50 cm back from the wooden board on either side (Fig. 1b), and the owner kept the dog between his legs (or just in front) while the experimenter placed food under the container. The dogs were then released to move freely around the area.

For all dogs the solvable trials were interrupted after a maximum of 1 min or as soon as the dog obtained the food, after which a new solvable trial started. A total of three solvable trials were presented. Only dogs that succeeded at least twice in obtaining the food in the solvable trials were tested in the unsolvable one. This criterion was set to ensure that all dogs (whatever the age) learned the task before going on to the unsolvable test. We did not vary the number of solvable trials presented since we wanted to avoid multiple failures in the potentially solvable trials, which could lead to frustration and a decrease in motivation in the unsolvable one. Furthermore, preliminary testing of 2-month-old puppies showed that if they were unable to solve the task within the first three trials their interest in the apparatus rapidly decreased making multiple presentations useless. Finally, we wanted to avoid having subjects with different numbers of trials prior to the impossible one, since this could affect the attention/interest in the most relevant part of the test.

In the unsolvable trial the apparatus was identical but the container was screwed to the board, so the food could not be reached even if it was clearly visible inside. The experimenter squatted down next to the container, placing a hand over it and lightly tapping it; then the same procedure was followed as in the

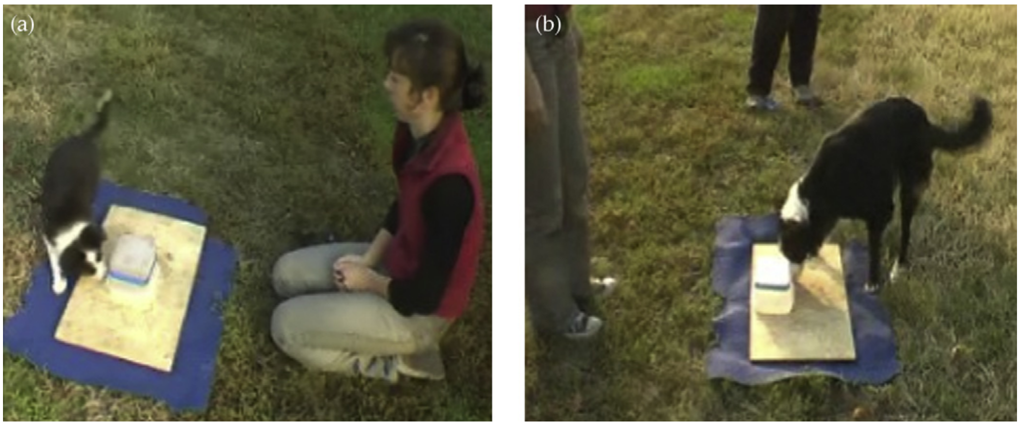

Figure 1. Experimental set-up and apparatus: (a) 2-month-old puppies, (b) adults and 4.5-month-old dogs.

solvable trials with dogs having 1 min to attempt to overturn the container or do anything else within the enclosed area. In the case of puppies the experimenter remained crouched down for 1 min ignoring the pup, while in the case of 4.5-month-old and adults the experimenter and owner remained standing silently at the two sides of the wooden board, looking in front and ignoring the dog.

All trials were videorecorded using a wide angle video camera positioned on a tripod located in the test area.

This research complies with the current Italian laws on animal welfare.

Data Analysis

Digital video footage was taken for all trials and the Solomon Coder (beta 091110, copyright 2006–2008 by András Péter, developed at ELTE TTK Department of Ethology, Budapest, Hungary) was used to record the dogs' behaviour during testing. Based on previous studies (Marshall-Pescini et al. 2009), the following mutually exclusive behavioural categories were scored: (1) Gazing at the person (i.e. owner–experimenter): the dog does not approach the person, but from a stationary position turns/lifts its head towards the person (duration and latency); (2) Gazing at the container: the dog from a stationary position turns/lifts its head towards the container (duration and latency); (3) Interaction with the person (owner–experimenter): the dog approaches and establishes physical contact with the person, e.g. rubbing, nosing, licking, pawing a hand or leg or jumping up (duration and latency); (4) Interaction with the container: any behaviour involving the dog being physically in contact with the container (duration and latency); and (5) Other: any other behaviour exhibited by the dog (duration). Furthermore, in the unsolvable trial, the dogs' two-way Gaze alternation behaviour between person and container (and vice versa) within 2 s was calculated. Finally, in the three solvable trials the latency to success was recorded.

In terms of duration the categories Gazing at the person and Interaction with the person were the sum of the respective behaviours towards owner and experimenter; in terms of latency, we measured the amount of time from the beginning of the trial to the dog gazing at either the owner or the experimenter, whichever happened first. The latter thus gave a measure of the inclination to gaze at the person regardless of his/her identity.

A random selection of trials (20%) was coded by a second observer and interobserver reliability on the duration of behaviours was calculated using Spearman correlations (Gazing at the person: $r_S = 0.88$, $N = 33$, $P < 0.001$; Gazing at the container: $r_S = 0.65$, $N = 33$, $P < 0.001$; Interaction with the person: $r_S = 0.65$, $N = 33$, $P < 0.001$; Interaction with the container: $r_S = 0.92$, $N = 33$, $P < 0.001$).

As 2-month-old puppies were tested only with the experimenter, we could not compare them directly with 4.5-month-old and adult dogs. Thus, breed group differences were investigated at 2 months old, whereas age and breed group comparisons were carried out with 4.5-month-old and adult dogs.

To test the effect of breed grouping (based on Parker et al. 2004) and sex on the behaviours shown above we used generalized linear models (GLM). Since the sex effect was not significant this variable was not included in the final model. The behavioural categories were considered response variables while the breed grouping was included as the independent factor. According to the distribution of the response variable, the negative binomial error structure and log link function were used, while to test differences in success solving the task we used the logistic regression (i.e. GLM with binomial error structure and log link function; Crawley 2007). For puppies to overcome the possible pseudoreplication that may arise from the autocorrelation of individuals coming from the same litter (Pinheiro & Bates 2000) the analyses were carried out using generalized mixed effect models (GLMM, with negative binomial error) with litter as a random factor. The response variable, independent factor and error structure were fitted as for adult dogs. GLMs were fitted with R (Cran-R, R Foundation for Statistical Computing, http://cran.r-project.org/), while GLMMs were performed using Genstat 6th edition (Genstat, VSN International, Hemel Hempstead, U.K.) using the IRREML library.

RESULTS

Two-month-old Puppies

Of the 167 puppies tested, only 97 solved the possible task twice thus gaining access to the unsolvable trial (Table 1). More

Table 1
Number of dogs tested in the study and that successfully passed at least two solvable trials

	Breeds	Tested	Successful
Two-month-old			
Primitive	Akita inu	15	9 (3)
N=48	Alaskan malamute	19	11 (3)
(M=25; F=23)	Samoyed	3	1 (1)
	Siberian husky	11	4 (2)
Hunting/Herding	Australian shepherd	29	18 (3)
N=80	Border collie	18	12 (3)
(M=39; F=41)	Golden retriever	18	7 (3)
	Labrador retriever	15	13 (2)
Molossoid	American Staffordshire	1	1 (1)
N=39	Boxer	13	4 (2)
(M=20; F=19)	Bull terrier	5	4 (1)
	German shepherd	10	6 (2)
	Rottweiler	10	7 (2)
Total		167	97
Four-and-a-half-month-old			
Primitive	Akita inu	1	1
N=8	Alaskan malamute	2	2
(M=5; F=4)	Siberian husky	5	4
Hunting/Herding	Australian shepherd	7	6
N=24	Border collie	3	3
(M=11; F=13)	Golden retriever	4	3
	Labrador retriever	10	7
Molossoid	American Staffordshire	3	3
N=22	Boxer	9	7
(M=11; F=11)	German shepherd	6	6
	Bull terrier	2	2
	Rottweiler	2	2
Total		54	46
Adults			
Primitive	Akita inu	10	8
N=61	Alaskan malamute	17	13
(M=23; F=38)	Basenji	12	7
	Siberian husky	13	7
	Samoyed	3	2
	Shiba inu	6	1
Hunting/Herding	Australian shepherd	9	4
N=56	Beagle	3	3
(M=26; F=30)	Border collie	7	7
	Breton	1	1
	Golden retriever	16	8
	Labrador retriever	11	9
	Flat-coated retriever	2	2
	Dachshund	7	7
Molossoid	American Staffordshire	7	7
N=55	Bernese mountain dog	12	4
(M=25; F=30)	Boxer	10	9
	German Shepherd	14	7
	Bull terrier	2	2
	Rottweiler	10	8
Total		172	116

M = male, F = female. For the 2-month-old puppies the number of litters tested for each breed is reported in parentheses.

Table 2
Mean ± SE and statistical results for breed group differences in 2-month-old puppies

Unsolvable trial	Primitive	Hunting/Herding	Molossoid	*df*	Wald χ^2 test	*P*
Gazing at the person (L)	46.42±3.17	42.19±3.20	34.49±5.50	2	2.39	0.303
Gazing at the container (L)	50.08±3.46	54.73±1.80	51.00±3.72	2	1.57	0.456
Interaction with the person (L)	38.92±4.78	41.50±2.88	35.78±4.72	2	1.49	0.475
Interaction with container (L)	0.06±0.04	0.75±0.51	2.38±1.61	2	1.65	0.439
Gazing at the person (D)	0.91±0.25	0.75±0.20	1.62±0.46	2	4.05	0.132
Gazing at the container (D)	0.29±0.10	0.3±0.10	0.92±0.60	2	2.08	0.353
Interaction with person (D)	5.5±2.04	7.41±1.67	10.54±2.79	2	3.03	0.220
Interaction with the container (D)	50.36±5.98	43.03±3.42	40.75±5.25	2	1.41	0.494

L indicates latency and D indicates duration of each behaviour.

specifically, 25 puppies (52%) from the Primitive group, 50 (62.5%) from the Hunting/Herding group and 22 (56.4 %) from the Molossoid group solved the tasks, a difference that was not significant (Wald $\chi^2 = 1.54$, $P = 0.470$).

No breed group difference emerged in the latency to success in the first trial and in any other behaviour in the first trial (mean ± SE: Primitive: 26.16 ± 4.61 s; Hunting/Herding: 33.21 ± 3.03 s; Molossoid: 33.61 ± 4.69 s; Wald $\chi^2 = 1.85$, $P = 0.392$).

In the unsolvable trial, 14 Primitive dogs (56%), 22 Hunting/Herding dogs (44%) and 13 Molossoid dogs (59%) looked at the researcher at least once but no statistically significant difference emerged in this behaviour (Wald $\chi^2 = 1.27$, $P = 0.529$). There was also no effect in the latency and in the duration of any variable observed (Table 2). Finally, only four puppies (one from the Primitive, two from the Hunting/Herding and one from the Molossoid group) at this age showed gaze alternation behaviours, which did not allow us to carry out statistical analyses.

Given the lack of breed group differences, puppies were considered as a single group and between-trial analyses were carried out to assess gazing and interacting behaviour towards the experimenter. The latency to gaze at the person was lower in the unsolvable trial compared to the other three solvable trials (mean solvable trial: 50.16 s; unsolvable trial: 41.53 s; Wald $\chi^2 = 8.53$, $P = 0.004$) and the duration of gazing at the person was higher in the unsolvable trial than the three solvable trials (mean solvable trial: 0.49 s; unsolvable trial: 0.99 s; Wald $\chi^2 = 66.63$, $P < 0.001$).

Four-and-a-half-month-old and Adult Dogs

Of the 172 adult dogs tested, 116 solved the task twice thus gaining access to the unsolvable trial. More specifically, 38 dogs (62.3%) from the Primitive group, 41 (73.2%) from the Hunting/Herding group and 37 (67.2%) from the Molossoid group solved the tasks, a difference that was not significant (Deviance = 1.5981, *df* = 2, $P = 0.45$; Table 1).

Of the 54 4.5-month-old dogs, 46 successfully solved the task twice thus gaining access to the unsolvable trial: seven (87.5%) from the Primitive group, 19 (79.1%) from the Hunting/Herding group and 20 (90.9 %) from the Molossoid group (Table 1). Adult dogs were significantly slower than young dogs in obtaining the reward with no breed group differences emerging (mean latency to success: 4.5-month-old: 20.97 ± 3.04 s; adults: 28.67 ± 2.13 s; Table 3).

In the unsolvable trial, considering the latency to gaze at the person, adult dogs gazed at the person significantly sooner than young dogs (mean latency to gaze at the person: 4.5-month-old: 37.3 ± 3.67 s; adults: 24.02 ± 1.95 s) but no breed group differences emerged, nor any interaction between age and breed groups (Fig. 2). In the latency to gaze at the container there was a significant difference between groups with adult dogs gazing at the bowl sooner than young dogs but no breed group effect emerged (mean latency to gaze at the container: 4.5-month-old: 53.72 ± 2.06 s; adults: 42.3 ± 1.92 s; Table 3).

Regarding the latency to interact with the person no difference emerged for either age or breed group (mean latency: 4.5-month-old: 46.8 ± 2.78 s; adults: 41.4 ± 2.08 s) whereas we found a difference in the latency to interact with the container (mean latency to interact with the container: 4.5-month-old: 1.58 ± 1.31 s; adults: 0.26 ± 0.09 s; Primitive: 0.27 ± 0.19 s; Hunting/Herding: 0.24 ± 0.09 s: Molossoid: 1.34 ± 1.06 s; adults:

Table 3
Statistical results of breed and age group differences in 4.5-month-old and adult dogs

	df	Deviance	*P*
First solvable trial			
Success L			
Breed group	2	1.446	0.485
Age	1	3.906	0.048
Breed group*Age	2	6.461	**0.039**
Unsolvable trial			
Gazing at the person L			
Breed group	2	3.420	0.180
Age	1	10.230	**0.001**
Breed group*Age	2	3.037	0.218
Gazing at the container L			
Breed group	2	0.391	0.822
Age	1	7.807	**0.005**
Breed group*Age	2	4.175	0.123
Interaction with the person L			
Breed group	2	1.229	0.540
Age	1	0.957	0.327
Breed group*Age	2	0.363	0.833
Interaction with the container L			
Breed group	2	7.702	**0.021**
Age	1	4.909	**0.026**
Breed group*Age	2	2.376	0.304
Gaze alternation person - container			
Breed group	2	0.219	0.896
Age	1	13.738	**<0.001**
Breed group*Age	2	1.081	0.582
Gazing at the person D			
Breeds group	2	19.455	**<0.001**
Age	1	15.039	**<0.001**
Breeds*Age	2	0.784	0.6756
Gazing at the container D			
Breed group	2	1.994	0.368
Age	1	16.873	**<0.001**
Breed group*Age	2	1.327	0.515
Interaction with the person D			
Breed group	2	4.296	0.116
Age	1	0.516	0.472
Breed group*Age	2	5.838	0.053
Interaction with the container D			
Breed group	2	2.794	0.247
Age	1	15.920	**<0.001**
Breed group*Age	2	0.135	0.934

Latency (L) to success in the first solvable trial is reported, as well as the latency (L) and duration (D) of each behaviour in the unsolvable trial. Significant results are shown in bold. Means ± SE are reported in the text.

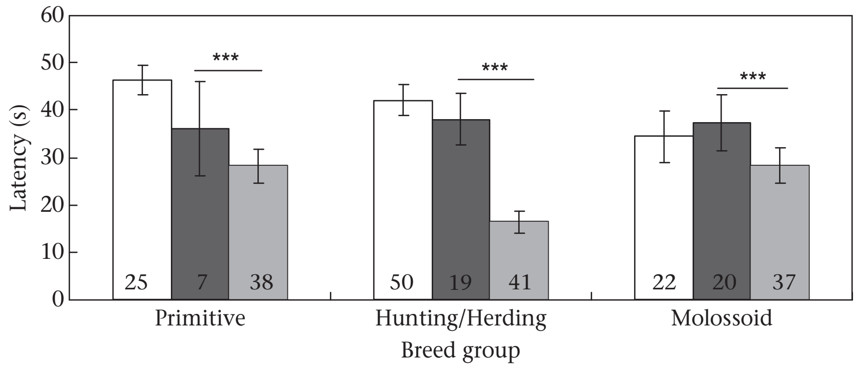

Figure 2. Mean ± SE latency (s) to gazing at the person in the unsolvable trial for 2-month-old (white bars), 4.5-month-old (dark grey bars) and adult (pale grey bars) dogs in each breed group. $***P \leq 0.001$. Two-month-old puppies were not statistically compared with the other two age groups and are thus included only for visual comparison. Sample sizes are indicated in each bar.

Primitive: 0.1 ± 0.06 s; Hunting/Herding: 0.25 ± 0.12 s; Molossoid: 0.44 ± 0.26 s) with adult dogs interacting sooner than young dogs, and Hunting/Herding dogs interacting sooner than the other two groups both at 4.5 months and as adults (Table 3).

There was a significant difference in the duration of gazing at the person as a function of both breed group and age but there was no interaction between these two variables (mean for gazing at the person: 4.5-month-old: Primitive: 2.96 ± 1.02 s; Hunting/Herding: 3.76 ± 0.94 s; Molossoid: 2.01 ± 0.64 s; adults: Primitive: 5.72 ± 1.11 s; Hunting/Herding: 11.06 ± 1.63 s; Molossoid: 4.15 ± 0.84 s) with adult dogs spending more time gazing at the person than 4.5-month-old dogs and Hunting/Herding dogs spending more time gazing at the person than the other two breed groups, in both the young and adult groups (Tukey test: Primitive versus Hunting/Herding: $df = 103$, $P = 0.036$; Hunting/Herding versus Molossoid: $df = 117$, $P < 0.001$; Primitive versus Molossoid: $df = 102$, $P = 0.087$; Fig. 3). Also, in the duration of gazing at the container an age difference emerged, with adults looking at the container more than 4.5-month-old dogs (mean: 4.5-month-old: 0.4 ± 0.17 s; adults: 1.71 ± 0.32 s; Table 3).

Considering the duration of the interaction with the person, neither age nor breed group alone showed a significant effect but their interaction was significant: adult dogs in the Hunting/Herding group interacted less than the other two groups, whereas in the young group, dogs in the Hunting/Herding group interacted for longer than dogs in the Molossoid and Primitive groups (mean for interacting with person: 4.5-month-old: Primitive: 1.65 ± 0.83 s; Hunting/Herding: 4.40 ± 1.68 s; Molossoid: 3.54 ± 2.02 s; adults: Primitive: 5.84 ± 1.20 s; Hunting/Herding: 46 ± 0.35 s; Molossoid: 4.49 ± 1.15 s; Table 3).

The duration of the interaction with the container showed young dogs interacting for significantly longer than adults (mean: 4.5-month-old: 50 ± 4.3 s; adults: 30.5 ± 2.42 s). Regarding gaze alternation between person and container, adult dogs carried out this behaviour significantly more than young dogs (mean: 4.5-month-old: 0.11 ± 0.05; adults: 0.75 ± 0.13) but no breed group differences were found (Table 3).

DISCUSSION

The aim of the current study was to explore the potential effects of breed grouping and development (age and experience) on dogs' human-directed communicative behaviour (i.e. gazing) in an unsolvable task. We found that adult dogs in the Hunting/Herding group gazed at humans for longer periods than those in the Primitive and Molossoid groups when the task became unsolvable. The same pattern of results emerged when comparing the gazing behaviour of the different breed groups at 4.5 months. These results indicate an effect of the breed group on the dogs' gazing behaviour; however, our original hypothesis was only partially supported since

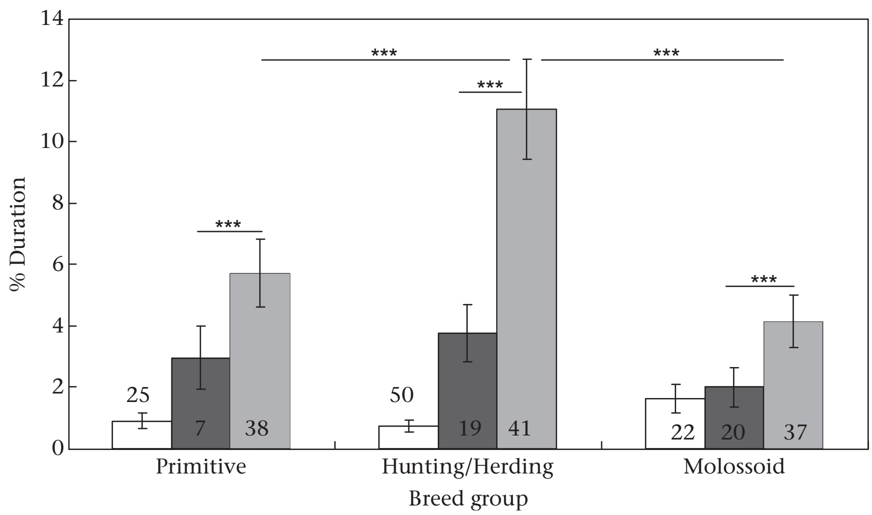

Figure 3. Mean ± SE percentage duration of gazing at the person in the unsolvable trial for 2-month-old (white bars), 4.5-month-old (dark grey bars) and adult (pale grey bars) dogs in each breed group. $***P \leq 0.001$. Two-month-old puppies were not statistically compared with the other two age groups and are thus included only for visual comparison. Sample sizes are indicated in/above each bar.

we expected that dogs in the Primitive group, owing to their closer genetic relatedness to wolves, would use human-directed gazing behaviour less than those in the other two groups. On the contrary, dogs in the Primitive and Molossoid breed groups did not differ in their gazing behaviour; rather, it was dogs in the Hunting/Herding group that looked at the humans more. This suggests that the selection for 'cooperative' work with humans (since this group was substantially made up of dogs selected for work such as herding and retrieving) may have had a greater influence on the dogs' communicative behaviour towards humans than their genetic relatedness to wolves.

Recent results by Gàcsi et al. (2009b) have similarly highlighted the importance of selection for cooperative work in dogs' interspecific communicative abilities. In this study, dogs belonging to cooperative working breeds showed a better performance in comprehending the human pointing gesture than dogs selected for more independent kinds of work. Taken together these results would support the view of a genetic component to interspecific communicative abilities, which may have indeed been modified by domestication (as the wolf–dog comparisons suggest), but which has also undergone a subsequent selection process, probably as one feature among others that are considered to make up a successfully cooperative working breed. Fox (1971, pp. 203–204) suggested that: 'Selection appears to influence the threshold of certain behaviour patterns. A response component of a given trait is more easily released by an adequate stimulus in one breed than in another, and this lowered threshold greatly facilitates trainability to bring out and shape the innate capacities of the animal and its reaction to appropriate stimuli'. This might be the case in our study since breed group differences in human-directed gazing behaviour started appearing at 4.5 months, once the dogs had entered the human home, and thus were exposed to the appropriate social environment/stimulus for its emergence. Further studies would be needed to investigate this aspect.

The second aim of this study was to examine potential age group differences in the use of gazing towards humans. Looking at the results of the comparisons between the adults and the 4.5-month-old dogs, it emerges that although breed group differences can be found at both ages, the adults gazed towards the humans for longer periods and sooner than 4.5-month-old dogs in all breed groups. Moreover, adults also used gaze alternation between humans and the container more often than 4.5-month-old dogs. Adults looked for longer periods not only at the humans but also at the container, whereas the 4.5-month-old dogs manipulated the container for longer periods. These results suggest that although 4.5-month-olds do look at the person when the task becomes unsolvable, they also persist for longer than adults in attempting to solve it. Adult dogs not only look at the person for longer but also use gaze alternation, considered to be a better indicator of intentional communication since it carries a referential component to the object on which action should be taken (Miklósi et al. 2000).

At 2 months, the gazing behaviour was present equally in all three breed groups; however, we found that puppies looked at humans sooner and for longer periods in the unsolvable trial compared to the three solvable trials. This finding possibly indicates that the gazing carried a request-like meaning as has been found in other studies with adult dogs (Miklósi et al. 2000, 2003, 2004; Marshall-Pescini et al. 2009). Results suggest that similarly to the comprehension of human communicative cues (e.g. the pointing gesture), which appears at a very young age (Riedel et al. 2008; Gàcsi et al. 2009a), the use of human-directed gazing behaviour may also be present from a very young age. Compared to the other two age groups, the time spent gazing at the human in the unsolvable trial at 2 months was extremely short, just as the time spent gazing at the person was shorter in 4.5-month-olds than in adult dogs. The same tendency was found in the frequency of gaze alternation: in the group of 2-month-old puppies only four individuals showed this behaviour, whereas in the other two age groups it was increasingly common.

Thus, whereas dogs' comprehension of human communicative cues appears early, does not improve with age and seems to require very limited early learning to develop fully (Gàcsi et al. 2009a), our results suggest that the production of human-directed gazing behaviour improves with age, undergoing a learning process based on positive rewarded human interactions during the first months of a dog's life.

In summary, our results suggest that although the domestication process has shaped the emergence of human-directed gazing behaviour (Miklósi et al. 2003), the subsequent selection for cooperative working traits may have had a strong influence on its occurrence. The fact that this behaviour increased with the age of the subjects suggests that an appropriate human environment might be necessary for the development and learning of this behaviour.

Acknowledgments

This research was supported by funds from PRIN 2006 to Emanuela Prato-Previde and to Paola Valsecchi, by a Hungarian–Italian exchange (Hungarian Research Fund T049615) to G.L. and C.P., by a doctoral grant from the University of Milan to C.P. and a doctoral grant to S.B. from the University of Parma. We thank Nicola Ferrari for his help in statistical analysis and Isabella Merola for her invaluable help in data collection. Finally, we thank all the owners, breeders and dogs that participated as volunteers.

References

Agnetta, B., Hare, B. & Tomasello, M. 2000. Cues to food location that domestic dogs of different ages do and do not use. *Animal Cognition*, **3**, 107–112.

Bentosela, M., Barrera, G., Jakovcevic, A., Elgier, A. M. & Mustaca, A. E. 2008. Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). *Behavioural Processes*, **78**, 464–469.

Bentosela, M., Jakovcevic, A., Elgier, A. M., Mustaca, A. M. & Papini, M. 2009. Incentive contrast in domestic dogs (*Canis familiaris*). *Journal of Comparative Psychology*, **123**, 125–130.

Crawley, M. J. 2007. *The R Book*. Chichester: J. Wiley.

Dorey, N. R., Udell, M. & Wynne, C. D. L. 2010. When do domestic dogs (*Canis familiaris*) start to understanding human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, **79**, 37–41.

Fox, M. W. 1971. *Behaviour of Wolves, Dogs and Related Canids*. New York: Jonathan Cape.

Frank, H. & Frank, M. G. 1982. Comparison of problem-solving performance in six-week-old wolves and dogs. *Animal Behaviour*, **30**, 95–98.

Frank, H. & Frank, M. G. 1985. Comparative manipulation-test performance in ten week old wolves (*Canis lupus*) and Alaskan malamutes (*Canis familiaris*): a Piagetian interpretation. *Journal of Comparative Psychology*, **99**, 266–276.

Gàcsi, M., Gyori, B., Virány, Z., Kubinyi, E., Range, F., Belényi, B. & Miklósi, Á 2009a. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. *PLoS ONE*, **4**, e6584.

Gàcsi, M., McGreevy, P., Kara, E. & Miklósi, Á 2009b. Effects of selection for cooperation and attention in dogs. *Behavioural Brain Function*, **5**, 31.

Hare, B. & Tomasello, M. 2005. Human-like social skills in dogs? *Trends in Cognitive Science*, **9**, 439–444.

Hare, B., Brown, M., Williamson, C. & Tomasello, M. 2002. 'The domestication of social cognition in dogs.'. *Science*, **298**, 1634–1636.

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R. & Trut, L. 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, **15**, 226–230.

Hare, B., Rosati, A., Kaminski, J., Brauer, J., Call, J. & Tomasello, M. 2010. The domestication hypothesis for dogs' skills with human communication: a response to Udell et al. (2008) and Wynne et al. (2008). *Animal Behaviour*, **79**, e1–e6.

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.

McKinley, J. & Sambrook, T. 2000. Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, **3**, 13–22.

Maros, K., Gácsi, M. & Miklósi, Á 2008. Comprehension of human pointing gestures in horses (*Equus caballus*). *Animal Cognition*, **11**, 457–476.

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 task. *Behavioural Processes*, **78**, 449–454.

Miklósi, Á & Soproni, K. 2006. A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, **9**, 81–93.

Miklósi, Á, Polgárdi, R., Topál, J. & Csányi, V. 1998. Use of experimenter-given cues in dogs. *Animal Cognition*, **1**, 113–121.

Miklósi, Á, Polgárdi, R., Topál, J. & Csányi, V. 2000. Intentional behaviour in dog-human communication: an experimental analysis of 'showing' behaviour in the dog. *Animal Cognition*, **3**, 159–166.

Miklósi, Á, Kubinyi, E., Topál, J., Gacsi, M., Virányi, Z. & Csányi, V. 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, **13**, 763–766.

Miklósi, Á, Topál, J. & Csányi, V. 2004. Comparative social cognition: what can dogs teach us? *Animal Behaviour*, **67**, 995–1004.

Parker, H. G., Kim, L. V., Sutter, N. B., Carlson, S., Lorentzen, T. D., Malek, T. B., Johnson, G. S., DeFrance, H. B., Ostrander, E. A. & Kruglyak, L. 2004. Genetic structure of the purebred domestic dog. *Science*, **304**, 1160–1164.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed Effects Models in S and S-Plus*. New York: Springer.

Pongrácz, P., Miyake, T., Vida, V. & Csányi, V. 2005. The pet dog's 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.

Proops, L. & McComb, K. 2010. Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition*, **13**, 197–205.

Riedel, K., Schumann, K., Kaminski, J., Call, J. & Tomasello, M. 2008. The early ontogeny of human-dog communication. *Animal Behaviour*, **75**, 1003–1014.

Scott, J. P. & Fuller, J. L. 1965. *Genetics and the Social Behavior of the Dog*. Chicago: University of Chicago Press.

Serpell, J. A. & Hsu, Y. 2005. Effects of breed, sex, and neuter status on trainability in dogs. *Anthrozoos*, **18**, 196–207.

Smith, B. S. & Litchfield, C. A. 2010. Dingoes (*Canis dingo*) can use human social cues to locate hidden food. *Animal Behaviour*, **13**, 367–376.

Soproni, K., Miklósi, Á, Topál, J. & Csányi, V. 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*, **115**, 122–126.

Svartberg, K. 2006. Breed-typical behavior in dogs historical remnants or recent constructs? *Applied Animal Behaviour Science*, **96**, 293–313.

Topál, J., Miklósi, A. & Csányi, V. 1997. Dog-human relationship affects problem solving behaviour in the dogs. *Anthrozoos*, **10**, 214–224.

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

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

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belenyi, B., Ujfalussy, D. & Miklósi, Á 2008. Comprehension of human pointing gestures in young reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, **11**, 373–387.

Wilsson, E. & Sundgren, P. 1997. The use of a behaviour test for the selection of dogs for service and breeding, I: method for testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. *Applied Animal Behaviour Science*, **53**, 279–295.

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