A comparison between wolves, *Canis lupus*, and dogs, *Canis familiaris*, in showing behaviour towards humans

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Both human and nonhuman primates use imperative pointing to request a desired object from another individual. Gaze alternation often accompanies such pointing gestures, and in species that have no hands this can in itself function as imperative pointing. Dogs have exceptional skills in communicating with humans. The early development of these skills is suggested to have been facilitated by domestication. Adult wolves socialized with humans can use human-provided information to find food in various situations, but it is unclear whether they would use gaze alternation to show their human partner a target location they cannot reach on their own. In our experiment, we tested wolves and dogs in a task where they could indicate an out-of-reach food location to one of two human partners. One partner reacted in a cooperative way and gave the food hidden in the indicated location to the subject whereas the other responded in a competitive way and ate the food herself. Our results suggest that wolves, as well as dogs, use 'showing' behaviours to indicate a food location to a human partner, and that both can adjust their communication to the cooperativeness of their human partners, showing more indicating signals in the presence of the cooperative partner than in the presence of the competitive one. We conclude that wolves and dogs, both kept in packs under the same conditions, can use humans as cooperative partners, and point imperatively in order to receive a desired out-of-reach object. It seems that intensive socialization with humans enables both wolves and dogs to communicate cooperatively about a food location with humans, most probably relying on skills that evolved to promote social coordination within their packs.

At about 12 months of age, children start to point in order to communicate with their caregivers (Bates, Camaioni, & Volterra, 1975; Blake, O'Rourke, & Borzellino, 1994). Children use declarative pointing when they want an adult to share attention/feelings with them about an interesting event or object, and they use imperative pointing when they want an adult to do something for them, such as giving them a desired object (Bates et al., 1975; Camaioni, 1993). Imperative pointing has been described not only in humans, but also in captive chimpanzees, *Pan troglodytes* (e.g. Leavens & Hopkins, 1998; Leavens, Hopkins, & Bard, 1996; Leavens, Hopkins, & Thomas, 2004), orang-utans, *Pongo pygmaeus*, gorillas,

Gorilla gorilla, and bonobos, *Pan paniscus* (for review see Leavens & Hopkins, 1999) when interacting with humans. In most cases, pointing occurred towards objects or food items that were out of reach of the animals but that could be reached by the familiar humans with whom the animals were interacting. Therefore, it is usually assumed that the animals point in order to get their human partners to give these desired objects to them. Pointing in children (e.g. Bruinsma, Koegel, & Kern Koegel, 2004) as well as in nonhuman primates is often accompanied by gaze alternation (e.g. Anderson, Kuwahata, & Fujita, 2007; Leavens & Hopkins, 1998). Accordingly, it has been argued that in species that have no hands, gaze alternation and other behaviours combining attention-attracting and directional components can have a similar function as pointing (Harding & Golinkoff, 1979; Leavens & Hopkins, 1998; Leavens, Russell, & Hopkins, 2005). For instance, various studies have shown that dogs readily alternate their gaze between the

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reward location and humans when a desired food item or toy is out of their reach (Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato Previde, 2009; Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005; Passalacqua et al., 2011; Virányi, Topál, Miklósi, & Csányi, 2006).

Dogs have also proved to be exceptionally skilled in communication with humans in several other paradigms, including reading human communicative gestures such as pointing and gaze cues (Miklósi, Polgárdi, Topál, & Csányi, 1998; Téglás, Gergely, Kupán, Miklósi, & Topál, 2012), or taking humans' attentional states into account (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004; Virányi, Topál, Gácsi, Miklósi, & Csányi, 2004). Dogs were the first animals to be domesticated, and as such, have shared a common environment with humans for more than 10 000 years (Freedman et al., 2014; Pang et al., 2009; Savolainen, Zhang, Luo, Lundeberg, & Leitner, 2002), for a longer time than any other species. Based on these findings, it has been suggested that the domestication of dogs has facilitated their cooperation and communication with humans (Cooper et al., 2003; Hare, Brown, Williamson, & Tomasello, 2002; Miklósi et al., 2003). This hypothesis is supported by comparative studies showing that, at the age of 3–4 months, dogs outperform hand-raised wolves in following human pointing in object choice tasks (Gácsi et al., 2009; Hare & Tomasello, 2005; Miklósi et al., 2003; Miklósi, Topál, & Csányi, 2004; Virányi et al., 2008). At an adult age, however, hand-raised wolves can also use human-provided information, showing that domestication might have affected the speed of development of such skills rather than the skills themselves (Gácsi et al., 2009; Udell, Dorey, & Wynne, 2008; Virányi et al., 2008). Therefore, it is crucial to compare wolves and dogs that are raised and kept under identical conditions in order to exclude the interpretation that differential experience, rather than differences in genetic predisposition, explains their behavioural differences.

Besides the pointing studies, it has been shown that hand-raised, captive wolves can also adjust their behaviour to the attentional state of humans to a certain extent, as they beg for food preferentially from a human who is oriented towards them rather than from someone whose back is turned to them (Udell, Dorey, & Wynne, 2011). Moreover, wolves can follow human gaze into distant space by the age of 14 weeks (Range & Virányi, 2011) and can find hidden food based on a human demonstration in a local enhancement task (Range & Virányi, 2013). Therefore, it seems that wolves have the necessary social attentiveness and can (or at least can learn to) benefit from information provided by humans (Range & Virányi, 2015). Accordingly, since extensive individual socialization by humans seems to lead to social competences in wolves comparable to those of dogs, it is difficult to assess whether and in what way domestication has impacted these skills in dogs. Even less is known about the origins of dog–human communication in the opposite direction: when dogs/wolves provide information to humans, for example, during 'showing'.

Miklósi, Polgárdi, Topál, and Csányi (2000) defined 'showing' as a communicative behaviour consisting of a directional component referring to an external target and an attention-getting component that attracts the receiver's attention to the sender. In their experiment, the behaviour of the dogs was recorded after they had observed the hiding of a piece of food or a favourite toy in a place that they could not access themselves. Miklósi et al. (2000) found that after the hiding, when both reward and owner were present at the same time the dogs looked more frequently at their owner and the baited location than when only the hidden target or the owner was in the room. Importantly, gaze alternation between the target location and owner occurred only when both the reward and the owner were present. Nor did the dogs show gaze alternation between an empty food location and the owner, or between the door

(through which the owner had left) and the target location. Consequently, Miklósi et al. (2000) argued that dogs, similarly to other animal species, might be able to engage in functionally referential communication. It can still be questioned, however, to what extent the sophisticated use of gaze alternation and other showing behaviours reflects the association that dogs (and potentially human-raised wolves) have formed during life-long experiences involving food and their owners, for example, a dog may have the learned expectation that if food is out of reach the human present will give it to the dog. In order to exclude this simple explanation, we improved the showing paradigm by testing the animals with two familiar partners playing either a cooperative or a competitive role during the experiment. If showing behaviours reflect the communicative intention of the subjects, they should occur more often with the cooperative partner than with the competitive one, despite the fact that both partners have regularly worked with the subjects and are therefore already associated with donating food to a similar extent before the test starts.

To date, only one study has addressed the question of whether wolves show humans where an out-of-reach food item can be found. Kubinyi, Virányi, and Miklósi (2007) mentioned an unpublished study by Virányi, Gasci et al. (2006), Virányi, Topal et al. (2006) comparing the showing behaviour of 1-year-old wolves and dogs using the paradigm developed by Miklósi et al. (2000). They reported that both wolves and dogs indicated a food location to a human partner by alternating their gaze between the food location and the human. However, the wolves did so less often than the dogs. These results may suggest that domestication has facilitated the development of this kind of communication with a human partner in dogs. Alternatively, however, in this previous study the dogs and wolves might have gathered different experiences with humans in such situations by the age of testing (1 year), since the dogs were kept as pets whereas the wolves, at the age of 2–4 months, were moved back to the farm where they were born. Therefore, currently no data are available that compare the showing behaviour of dogs and wolves raised and kept under identical conditions.

Using a modified version of Miklósi et al. (2000) paradigm in the present study, we investigated whether identically raised and kept adult wolves and dogs exhibit similar showing behaviour in the presence of food and a human. Importantly, we compared whether wolves and dogs differentiated between a cooperative and a competitive human partner in their showing behaviour in order to exclude the interpretation that their behaviour reflects a general food–human association. The domestication hypothesis as outlined above would suggest that dogs outperform wolves. Alternatively, however, we may hypothesize that wolves have the necessary social attentiveness and can therefore communicate with humans in a similar way to dogs if they are raised and kept close to humans, predicting that wolves and dogs perform in a similar way.

METHODS

We tested 13 (male/female: 7/6) adult dogs and eight (male/female: 5/3) adult timber wolves in this experiment. The subjects were between 1.5 and 3.5 years of age when being tested (dogs: mean = 2.35 years; wolves: mean = 2.33 years). All subjects that participated in this study were born in captive facilities (all the dogs arrived from four different shelters in Hungary, three wolves came from a zoo in Austria, one from Switzerland and four from the U.S.A.). All dog and wolf puppies were separated from their mothers within the first 10 days of life and were hand-raised and socialized in the same way at the Wolf Science Center (WSC). For details see Range and Virányi (2014). The subjects grew up in peer groups with 20–24 h of daily contact with humans in their first 5

months, when they were then introduced to packs of older animals (founded by four dogs and three wolves, respectively). At the time of this study, the dogs lived in four packs, and the wolves in two different packs, in large enclosures (2000−8000 m^2) at the Game Park Ernstbrunn, Austria, where they remained after participating in this study. According to their dietary needs, the dogs were fed every day with dry food or meat mixed with dry food, while the wolves were fed every third day with carcasses. Water was available for all subjects ad libitum. Since puppyhood, all subjects had participated regularly in different cognitive behavioural tests and had been trained on a daily basis. The training consisted of obedience training, including commands such as sit, down, roll over, or touch, and was conducted either in the test building or in the test enclosure in physical separation from the pack. Accordingly, the subjects were used to being separated from their pack to work with familiar humans.

General Experimental Set-up

The experiment took place at the Wolf Science Center in a large test room (9 × 5.37 m and 2.56 m high at the lowest point). On three sides of the test room three boxes (plastic flower pots, 10 cm in diameter) were hanging on a chain from the ceiling close to the wall. The boxes served as hiding places during the experiment. The chain was used to adjust the height of the boxes so that the humans could take out a piece of food and the wolves were unable to reach them when jumping up. To ensure a relaxed test environment, three persons who were familiar to the wolves and dogs were involved in this experiment (hand raisers or trainers with almost daily contact, who had regularly rewarded them with food during various interactions and tasks). The experimenter hid the food for the subjects. The other two persons were assigned the roles of 'cooperative partner', who always rewarded the subjects, and 'competitive partner', who always ate the food herself/himself.

The whole experiment extended over at least 3 days (Fig. 1). On the first day, each animal started with a prefeeding session followed by its first training session. After a break of at least 3 min a second training session was conducted, followed by a preference test in order to check whether the subjects differentiated between the cooperative and competitive partners. On the second day, each subject again had a prefeeding session, followed by a training session and a preference test. If in the preference test a subject reached the criterion of choosing the cooperative partner in at least three out of four trials, the animal received its first test session. Subjects that did not reach that criterion in the preference test

received an additional preference test after a break of at least 3 min. If the subject still did not reach the criterion, the procedure of the second day was repeated, after a break of at least 24 h. On the third test day, when an animal had been successful on day 2, it started again with a preference test, in which it had to reach the same criterion, followed by a second test session. In cases where an animal did not reach the criterion in the preference test, that animal repeated the third day after a break of at least 24 h. (Details of the prefeeding, training, preference test and test sessions are given below.) Between the training and test sessions, all three humans involved in the test went on working with the subjects in accordance with the every day routines of the WSC, that is, regardless of their role in the experiment. Therefore, outside the test situation the humans were all associated with food to a similar extent.

Prefeeding

The prefeeding phase aimed at teaching the subjects that the three boxes could contain food and that humans (exemplified by the experimenter) could provide them with this out-of-reach reward. All subjects already had experience with this procedure since they had participated in another test using the same equipment and baiting procedure. During the prefeeding, the experimenter first showed a piece of sausage to the animal and then put it into one of the boxes, while making sure that the animal paid attention to the hiding procedure by calling the animal's name if it did not watch what she was doing. Then she baited the second and third boxes in the same way. The order of baiting the boxes was randomized across subjects and within subjects and across trials. After the baiting, the experimenter stood in the middle of the test room and addressed the animal, asking it to show her the food. If the animal looked at any of the boxes, the experimenter went there and rewarded the animal with its content. Then she addressed the animal again until all three boxes were empty. If the animal looked at an empty food location the experimenter verbally responded that the food location was empty without approaching the box, and asked the animal to show another one. If, however, an animal insisted and repeatedly indicated the same empty food location, the experimenter went there and presented the empty box to the animal by showing an empty hand after reaching into the box. If an animal did not look at the boxes when being asked, the experimenter approached a box randomly and touched the box waiting until the animal looked at it. Then she provided the reward.

Training

The prefeeding phase was followed by a training session on both days 1 and 2, in which the subjects were introduced to the roles of the other two humans participating in this test. In the case of the wolves, two female humans played these roles, while in the case of the dogs, a female and a male took them on. These two human partners had been chosen so that they were of similar age, and had both worked with the animal in the same situations to the same intensity and thus had a similar relationship with it. One of the two persons was assigned the role of the cooperative partner who always rewarded the subjects, whereas the other one, the competitive partner, always ate the food herself/himself. The role assignment to one person or the other was semirandomized so that a certain person was the cooperative partner for half of the male and half of the female subjects, while for the other half that person was the competitive partner.

During the training, the subjects were held on a leash by the experimenter on one side of the test room. Approximately 3 m away from the animal, a bowl with six pieces of sausage was placed in the middle of the test room. On the opposite side of the bowl, in the two corners of the test room, the two partners were waiting (their positions were counterbalanced across subjects). In a
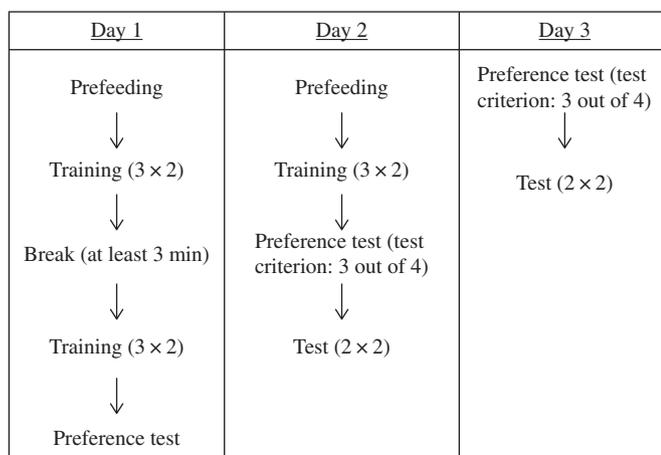
Day 1	Day 2	Day 3
Prefeeding	Prefeeding	Preference test (test criterion: 3 out of 4)
↓	↓	↓
Training (3 × 2)	Training (3 × 2)	Test (2 × 2)
↓	↓	
Break (at least 3 min)	Preference test (test criterion: 3 out of 4)	
↓	↓	
Training (3 × 2)	Test (2 × 2)	
↓		
Preference test		

Figure 1. Experimental procedure.

predetermined order, the two partners went to the bowl three times each, called the animal's name, took a piece of sausage out, and either ate it or gave it to the animal. For half of the subjects, the cooperative partner started; for the others, the competitive partner approached the bowl first. The cooperative partner always went to the subject, holding the sausage in her/his hand and offered it to the animal. The competitive partner, however, demonstratively ate the sausage, making sure that the animal observed the action, then went to the animal and presented her/his empty hand. In this way, both partners appeared and could be associated with food to the same extent.

Preference test

The preference test was conducted to assess whether the animals learned the role of the two partners in a context different from our showing test. During the preference test, the subject was held by the experimenter by its collar on one side of the test room, while on the opposite side the two partners were waiting 3 m apart, at an equal distance (4–5 m) from the animal. Both partners presented simultaneously a piece of sausage on their open palm to the animal. At that moment the experimenter released the subject to make a choice. If it went to the cooperative partner, it was allowed to eat the sausage; but if it went to the competitive partner, the person ate the sausage herself/himself just before the subject would have reached it. After each choice, the experimenter called the subject back. A total of four trials were conducted. The positions of the cooperative and competitive partners were predetermined and semirandomized with the stipulation that neither of them remained on the same side more than twice in a row.

Test

While the two partners were absent, the experimenter presented a piece of sausage to the subject and hid it in one of the three potential food locations. Subsequently, she left the test room through the door, behind which the two partners were waiting (Fig. 2). Afterwards, one of the two partners, who did not know in which of the three boxes the experimenter had hidden the food, entered, closed the door and sat down on a chair equidistant to the three hiding places. The partner was passive but observed the subject attentively for 1 min. After this, she/he stood up and went to the box that she/he thought the subject had indicated during that minute. If she/he found the sausage and was the cooperative partner, she/he gave it to the subject; if she/he was the competitive partner, she/he ate the sausage. If the subject had indicated an empty box, the partner showed the

empty box after checking it. Following this, the partner left the test room. The subjects were tested twice with the cooperative partner and twice with the competitive partner, with the stipulation that the same partner did not show up consecutively in the first two trials.

Behavioural Coding

The experiment was videotaped with a digital video camera (Sony HDR-CX320). From the video recordings of the test sessions, during the 1 min when the partner was passive, we analysed how often a subject looked at the food location or at an empty box, for how long and how often it watched the human partner, how often a subject went to a human partner and for how long it was in close proximity to her/him (within reaching distance of the partner's hand). Furthermore, we counted how often gaze alternation occurred between one of the boxes and the partner. Gaze alternation was defined as looking at the partner's face and then directly (continuous head movement without interruption) to one of the boxes or vice versa. Additionally, we analysed other showing behaviours including: (1) going to the partner (close proximity) and looking at her/him, followed by going to one of the three boxes and looking at it; (2) going to the partner (close proximity), touching her/him with the nose or looking at her/him (not necessarily with eye contact) and then looking at one of the three boxes; (3) looking at the partner (into the face from any distance) and then going to one of the boxes and looking at that.

For the statistical analysis we pooled these behaviours with gaze alternations. These results are reported as 'showing behaviours'.

Of the videos, 27% were analysed by a second coder who was blind to the test condition, the hiding location and the purpose of the test, and interobserver reliability was tested by calculating Spearman's rank correlations. Correlations (rho) were generally high: frequency looking at partner: 0.81; time looking at partner: 0.75; frequency of looking at the food location: 0.81; frequency of looking at an empty location: 0.78; frequency of going to the human partner: 0.80; time spent in close proximity to human partner: 0.76; showing behaviour: food location: 0.75; empty location: 0.75.

Statistical Analysis

We calculated generalized linear mixed-effects models to investigate the influence of the cooperativeness of the partner, species, test day and the sex of the test subject on the occurrence and frequency of different behaviours. The individual and the trial were included in the model as random factors. For analyses of whether or not showing behaviour occurred, a model with binomial distributions was calculated. For analyses of the frequencies, models with Poisson distributions were used. Durations were analysed with a linear mixed-effect model using the same fixed and random factors as described above. To get a normal distribution of the residuals, we used a square-root transformation for the duration of looking at the partner and a log transformation for the duration of being in close proximity to the partner. The analyses were done with the program R 2.15.2 (R Core Team, 2012).

Ethical Note

No special permission for use of subjects (wolves and dogs) in such sociocognitive studies is required in Austria (Tierversuchsgesetz 2012 e TVG 2012). The relevant committee that allows research without special permissions regarding animals is the
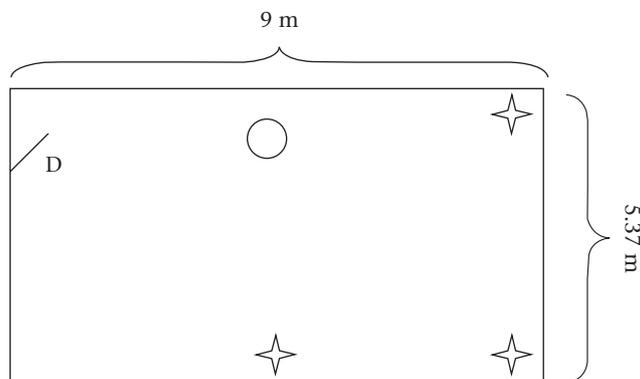

Figure 2. Outline of the test room. The potential food locations hanging from the ceiling are marked with stars, and the circle marks the position of a chair. The humans enter and leave the room through a door (D).

RESULTS

Showing Behaviour

The likelihood that a subject showed the food location to the human partner during the test was influenced by the role of the partner (GLMM: $F_{1,141} = 7.730$, $P = 0.006$) with more subjects showing the food location to the cooperative than to the competitive partner (Fig. 3). This result was the same for both species (GLMM: species∗partner: $F_{1,139} = 1.42$, $P = 0.24$), and this difference was obvious on both test days (GLMM: partner∗test day: $F_{1,140} = 1.85$, $P = 0.18$). Still, overall the subjects were more likely to indicate the food location during the first than during the second day (GLMM: $F_{1,144} = 9.350$, $P = 0.003$). Furthermore, in general, the likelihood of showing the food location to the human partner, independent of her/his cooperativeness, was not influenced by sex or species (GLMM: sex: $F_{1,18} = 0.37$, $P = 0.55$; species: $F_{1,19} = 0.59$, $P = 0.45$). The likelihood that a subject indicated an empty food location was not affected by the partner's role (GLMM: $F_{1,143} = 0.68$, $P = 0.40$) or by species, test day, or sex (GLMM: species: $F_{1,19} = 0.90$, $P = 0.40$; day: $F_{1,145} = 1.82$, $P = 0.20$; sex: $F_{1,18} = 1.13$, $P = 0.30$).

Looking at a Potential Food Location

Analysing the number of looks to the location where the food was hidden, we found that the subjects looked more often at the food location on the first test day than on the second (GLMM: $F_{1,144} = 5.850$, $P = 0.020$). Furthermore, we found a tendency for a difference between wolves and dogs (GLMM: $F_{1,19} = 4.130$, $P = 0.060$) with wolves looking more often at the food location than the dogs. However, we found no influence of the role of the partner present during the test (GLMM: $F_{1,143} = 0.79$, $P = 0.38$), and this did not differ between the two species (GLMM: species∗partner: $F_{1,142} = 2.51$, $P = 0.12$), or test days (GLMM: day∗partner: $F_{1,141} = 0.43$, $P = 0.51$). Furthermore, sex of the subjects did not influence the number of looks to the food location (GLMM: $F_{1,18} = 0.31$, $P = 0.58$).

When analysing the number of looks to an empty food location, we found a species difference (GLMM: $F_{1,19} = 5.250$, $P = 0.030$), whereby wolves looked more often at an empty food location than dogs. However, the role of the human partner did not influence this behaviour (GLMM: partner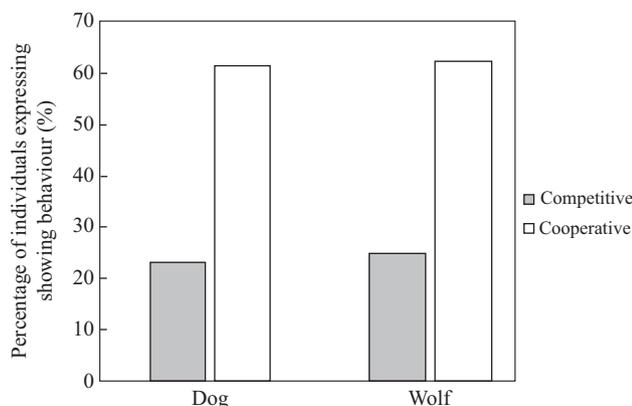: $F_{1,143} = 0.02$, $P = 0.90$), either in wolves or in dogs (GLMM: partner∗species: $F_{1,142} = 1.20$, $P = 0.27$). Furthermore, for both wolves and dogs, we found a tendency to look more often at an empty food location during the first than during the second test day (GLMM: $F_{1,145} = 3.240$, $P = 0.070$), but we found no influence of sex of the subject (GLMM: $F_{1,18} = 0.09$, $P = 0.77$).

In line with the previous results, wolves in general looked more often at any potential food location than dogs (GLMM: $F_{1,19} = 7.010$, $P = 0.016$), and all subjects did so more on the first than on the second test day (GLMM: $F_{1,144} = 9.390$, $P = 0.003$). However, we found no influence of sex of subject or partner present on the frequency of looking at a potential food location (GLMM: human partner: $F_{1,143} = 0.52$, $P = 0.47$; sex: $F_{1,18} = 0.29$, $P = 0.60$).

Contact with Human Partner

Regarding contact with the human partners, we found that the dogs looked more often, and for longer, at the human's face than the wolves (frequency: GLMM: $F_{1,19} = 4.670$, $P = 0.040$; duration: LME: $F_{1,19} = 10.300$, $P = 0.005$) and the dogs also went more often to their human partner than the wolves (GLMM: $F_{1,18} = 15.800$, $P < 0.001$). However, we found no influence of the role of the partner, sex of subject or test day on any of these variables (frequency of looking at human: frequency: GLMM: partner: $F_{1,143} = 0.37$, $P = 0.54$; sex: $F_{1,18} = 2.75$, $P = 0.11$; test day: $F_{1,144} = 2.51$, $P = 0.12$; duration of looking at human: LME: partner: $F_{1,141} = 2.96$, $P = 0.09$; sex: $F_{1,18} = 1.84$, $P = 0.19$; test day: $F_{1,143} = 2.08$, $P = 0.15$; going to partner: GLMM: partner: $F_{1,140} = 1.85$, $P = 0.20$; test day: $F_{1,2} = 0.13$, $P = 0.80$; sex: $F_{1,17} = 2.45$, $P = 0.10$).

Moreover, analysing how long a subject was in close contact with the human partner (if this behaviour occurred), we found an interaction between species and partner (LME: $F_{1,92} = 4.220$, $P = 0.040$; Fig. 4). When the cooperative partner was present, we found no difference between wolves and dogs (LME: $F_{1,23} = 1.92$, $P = 0.20$). However, when tested with the competitive partner, wolves spent less time with the human than dogs did (LME: $F_{1,17} = 5.510$, $P = 0.030$). Neither test day nor sex of subject influenced the time the subject spent next to the human partner (LME: test day: $F_{1,2} = 0.21$, $P = 0.69$; sex: $F_{1,15} = 1.97$, $P = 0.18$).
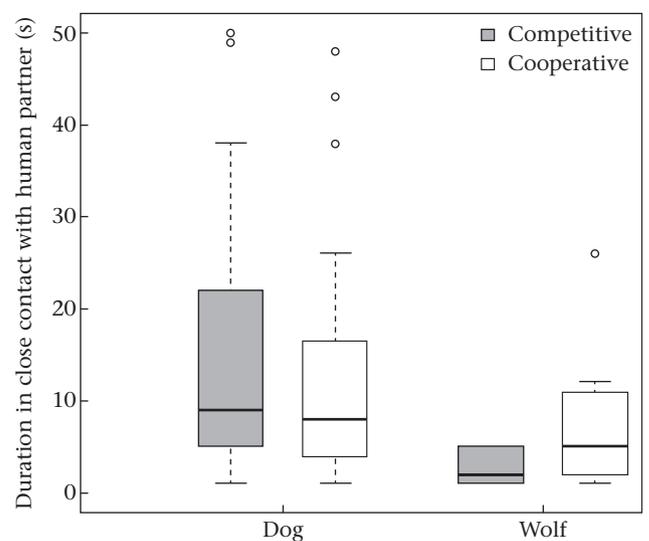
Figure 3. Percentage of subjects engaging in showing behaviour in the presence of the cooperative and the competitive partner.

Figure 4. Time the subjects spent in close proximity to the human partner, if they did so. The top, middle and lower horizontal lines show the 75th, 50th and 25th percentiles, respectively. The whiskers mark the main body of the data, and the circles the outliers.

DISCUSSION

Our results demonstrate that the showing behaviour to human partners of both wolves and dogs was very similar. Dogs and wolves not only showed the food location to their human partners similarly often but they also adjusted their showing behaviour to the cooperativeness of their human partner to the same degree from the first test day, in being more likely to show the food location in the presence of the cooperative partner than in the presence of the competitive partner. Importantly, wolves and dogs differentiated between the two different partners only in their showing behaviour but not in the likelihood of simply looking at a food or empty location.

Virányi, Gasci et al. (2006), Virányi, Topal et al. (2006) showed that wolves indicate a food location in a similar paradigm, but they found that wolves did so less than dogs. The difference between the two studies seems to result from the different performance of the dogs tested in the two studies. In our study all subjects were hand-raised, and therefore intensively socialized with humans but the dogs as well as the wolves were integrated into packs at the age of 4–5 months, where they mainly interacted with conspecifics. In contrast, in the previous study, while the wolves were integrated into packs at the age of 2–4 months, the dogs were kept as pets until the study was conducted at the age of 1 year. Interestingly, our pack dogs showed fewer gaze alternations and other food-indicating signals than pet dogs that had been tested with the same set-up by the same experimenter (Heberlein, Turner, & Virányi, 2016). This difference is comparable to the difference between the wolves and dogs described by Virányi, Gasci et al. (2006), Virányi, Topal et al. (2006); see Kubinyi et al. (2007), suggesting that the differences in showing behaviour between wolves and dogs may not originate from domestication but rather from their different experiences, which seem to affect the showing behaviour of dogs in a similar way.

Dogs and wolves adjusted their showing behaviour to the cooperativeness of the partner, with more food-indicating signals in the presence of the cooperative partner than with the competitive partner. Differentiating between cooperative and competitive individuals has been demonstrated also in ravens, *Corvus corax*, where the birds adjusted their caching behaviour to their previous experiences with the human participants and prevented only the competitive human from finding their caches (Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007). Importantly, however, only the showing behaviour of the subjects was adjusted to the role of the human partner; looking at the food location (without looking at or contacting the partner) did not depend on the cooperativeness of the human partner. The same results have been found in pet dogs, where it is argued that looking at the food location in itself is not a signal intended to communicate the food location to the human partner (Heberlein et al., 2016).

Both human partners had a similar relationship with the subjects and were associated to a similar extent with food before the experiment started. Moreover, outside the test situation both partners continued to reward the subjects to a similar extent. Only in the context of the experiment did the subjects experience that one person (the cooperative partner) gave them food, while the other person (the competitive partner) ate the food herself/himself. During the training this included getting food 'for free' from the cooperative partner, while during the preference test the subjects got the food when choosing to go to the cooperative partner but not when going to the competitive one. Therefore, the subjects might have associated food with the cooperative partner more than with the competitive partner, but we can exclude that a food association with the two partners was learned in the context of showing behaviour. Except during prefeeding, showing behaviour itself was not specifically reinforced during any step of the experiment. Importantly, during prefeeding a third person, who was not one of the later partners, reinforced the subjects' behaviour, looking at the food location (not necessarily showing, but this might be involved). Therefore, the subjects might have learned to associate getting food with looking at the food location, and showing the location to a human partner, but this learning process was not linked to either of their two later partners. During the actual test, if an animal engaged in showing behaviour right before the test was over, the cooperative partner would have rewarded it some seconds later, which might have allowed reinforcement of showing behaviour and consequent associative learning. The chance of such reinforcement, however, was low since in most cases the animals indicated the food location near the beginning of the test. Even if associative learning had influenced the occurrence of showing behaviour, it could not fully explain the observed differentiation between the two partners, since the animals differentiated between them from the beginning onwards and therefore proved to be flexible in the use of showing behaviour. However, this flexibility was somewhat limited in comparison to that of pet dogs tested in the same way, which not only showed a food location more often to the cooperative partner than to the competitive partner, but also showed an empty food location more often to the competitive than to the cooperative partner, in a way that could mislead the competitive partner searching for the food. In the current experiment, we found no such misleading behaviours, either in the dogs or in the wolves. This difference between the two studies can potentially be explained by the fact that we tested the wolves and dogs with two familiar humans who had close working relationships with the subjects, while in the pet dog study either two completely unfamiliar persons were used or a somewhat familiar person (known from joint walks) played the role of the competitive partner and an unfamiliar one was the cooperative partner. The lack of a working relationship between the competitive partner and the pet dogs may explain the higher propensity to show an empty food location. Such active interactions have also been found to influence other behaviours (e.g. attention) of dogs towards familiar persons (Horn, Range, & Huber, 2013).

While in this study the showing behaviour of dogs and wolves was rather comparable, we also found some characteristic differences in the behaviour of the two species. First of all, independent of the human partner present, the wolves looked more often at the three food hiding places than the dogs, whereas the dogs looked at the humans and approached them more often than the wolves. This might reflect a higher food motivation in wolves than in dogs. Miklósi et al. (2003) proposed that higher attraction of wolves to food resources may also partly explain why wolves look at their human partners later and less often in an unsolvable task than dogs. Independently from this difference, both wolves and dogs looked more often at any food location and displayed more showing behaviour on the first test day than on the second. This might indicate that the general arousal and/or motivation of the subjects induced by the novel test situation decreased from the first to the second test day. One reason for this might be that the subjects did not get rewarded immediately when indicating a food location but had to wait for a minute for the human partner to stand up and to go to one of the food hiding places. Alternatively, we can exclude a bad representation of the food location, since they are precise in their showing behaviour. Furthermore, Fiset and Plourde (2013) showed that dogs as well as grey wolves understand object permanence at least in a visual displacement task.

In addition to their different food motivation, the different gazing pattern of dogs and wolves (the dogs focusing less on food locations but more on humans than the wolves) could also reflect a difference in their human-directed behaviour. Miklósi et al. (2003,

2005) suggested that dogs might have been selected for higher dependency on humans and, in particular, to look into their faces more often in comparison to wolves, which allows for better communication (Miklósi et al., 2003). This explanation is supported by findings indicating that dogs remain attached to their owners longer than wolves, who may have such a close bond to their human caretaker only at very young ages even after extensive human socialization (Hall, Lord, Arnold, Wynne, & Udell, 2015; Topál et al., 2005). Topál et al. (2005) found that young dogs but not young wolves showed a preference for their owner over an unfamiliar human, which does not imply, however, that the wolves do not recognize their human caregivers. In contrast, Kubinyi et al. (2007) described that in their greeting behaviour wolves show a preference for their human raisers even in comparison to other familiar humans. Rather, it has been argued that the preference of dogs for their owner in the attachment study reflects a dependent relationship with her/him which has been suggested to be similar to the mother–infant bond in humans (Prato Previde, Custance, Spiezio, & Sabatini, 2003; Topál et al., 2005; Topál, Miklósi, Csányi, & Dóka, 1998). Since the subjects had a close relationship with both the cooperative and the competitive partner, the higher dependency of dogs on them may also explain why in our experiment the dogs not only looked at their human partners more often than the wolves but also went to them more often and were less discriminative regarding with whom they stayed in contact. The wolves stayed for a shorter duration in close proximity to the competitive partner than the dogs, whose lower selectivity may indicate a stronger influence of their long-term relationship with their trainer in comparison to wolves.

To sum up, in spite of potentially higher food motivation in wolves and higher dependency on humans in dogs, both dogs and wolves engage in showing behaviour to indicate a food location to a cooperative but not to a competitive human partner. Based on this flexibility, dogs as well as wolves appear to be able to engage in functionally referential communication with humans. Importantly, dogs and wolves raised under the same conditions and kept similarly in packs in a game park setting do not differ in their showing behaviour; but both use such behaviours less often than pet dogs living in human families, suggesting that closeness to humans and different experiences with them can strongly influence the showing behaviour of dogs. Further research has to investigate whether wolves with even more experience would communicate a food location to their human partners as intensively as pet dogs if they lived similarly close to humans.

Acknowledgments

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