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„Reading human facial expressions by free-ranging dogs and pet dogs – a comparative study“

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Abstract

Domestic dogs (*Canis familiaris*) have been shown to discriminate and emotionally understand human facial expressions. To what extent the experience with humans contributes to the development of such socio-cognitive abilities with humans has remained an open question. In this study, we investigated the influence of the dogs' experience with humans on their ability to read human facial expressions by comparing the responses of free-ranging dogs in Morocco and pet dogs in Vienna in a facial expression recognition task. An experimenter demonstrated one of three facial expressions (happy, angry, neutral) to the dogs while eating some food, which was 'accidentally' dropped later during the task. Different behavioural responses by the dogs, including eating food, gazing style, proximity to experimenter, and tail wagging, were recorded and coded for analysis. This identified one statistically significant interaction between dog group and facial expression condition: pet dogs tested in outdoor areas ate the dropped food more likely than free-ranging dogs in the happy or neutral conditions. Further, we found that all dog groups responded with more gaze aversions to the angry condition than to the happy or neutral conditions. This result suggests that all dogs understood the value of an angry facial expression. Irrespective of the facial expression condition, we additionally observed that free-ranging dogs generally wagged their tails more often than pet dogs, and they preferred to stay further away from the experimenter. Our findings suggest that experience with humans is not a determining factor for dogs to show human emotion reading skills but also, that human facial expressions in our specific study setting does not elicit a major behavioural change. These findings advance insight into the complexity of heterospecific emotion recognition studies and provide a solid basis for future research about the human-dog relationship.

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1 Introduction

1.1 Facial expressions as a measure of intent and emotion in mammals

The display of facial expressions is an important means of communication in humans (*Homo sapiens*) (1). Facial expressions provide information about physical sensations and emotional states and intentions of an individual (2). Not only for humans but in fact for most social living mammals, they represent a meaningful component of a behavioural repertoire allowing readers to adapt their behaviour accordingly (3). There is increasing evidence that most mammals can use visual cues from faces for correct emotion recognition in others (1), most probably through involvement of face-processing areas in the temporal cortex (reviewed in Tate et al., 2006). The ability to receive and process signals from other faces is not only relevant for conspecific social interactions but also seems to be present in heterospecific (individuals of different species) communications. The correct discrimination of facial expressions in a heterospecific individual is challenging as expressions and their corresponding meaning vary between species and context. Nevertheless, such heterospecific interactions have frequently been documented, for example when it comes to mutualistic interactions or predator-prey interactions (4–7). So far, little is known about the evolutionary and ontogenetical development underlying such heterospecific communication abilities. A promising species pair to study the background and development of heterospecific relationship and facial emotion recognition are domestic dogs (*Canis familiaris*) and humans. This particular pair represents an interesting match for heterospecific investigations because firstly, dogs often live in close relationship with humans and are dependent on humans for food supply and survival, secondly, humans display many diverse facial expressions and use them constantly in their non-verbal communication (3), and lastly, a wealth of data shows that dogs excel at reading human behavioural cues (4).

1.2 Dogs understand human facial expressions

Many studies have demonstrated that domestic dogs pay attention to cues from human faces, including the ability to discriminate familiar and unfamiliar humans based on visual facial features (4,8). A growing body of evidence indicates that dogs also have an ability to interpret and differentiate human facial expressions. Very recently, a functional magnetic resonance imaging (fMRI) study on neural processing in dogs provided evidence for a brain network that is sensitive to familiarity and emotional content in human faces. Brain areas responsible for reward (Caudate, Hippocampus and Amygdala) were activated in dogs when presented with familiar or emotionally salient faces (9). Consistent with these findings, one study recorded the behaviour of dogs in a two-choice task after they had observed humans directing emotional facial expression towards two identical objects. The dogs in this study could distinguish between a fearful and a happy facial expression; they preferentially chose to examine an object that the human directed a happy rather than a fearful or neutral expression to, and thus, refer the correct emotional message from a facial expression to specific objects. Another nice demonstration that dogs emotionally categorize facial expression was provided by Müller et al. in 2015. In their experiment, dogs could only succeed in a task upon accurately discriminating the different emotional contents of expressions. In the training phase, dogs had to discriminate happy and angry faces on pictures showing only either the upper or lower part of the face. In the test phase, the dogs were then presented again with happy and angry faces, but this time showing a different part of the face and/or a different person than in the training phase. The dog's ability in accurately discriminating the correct emotion was statistically significant. This result indicates that the dogs must have used the emotional expression rather than simple facial cues they remembered to solve this task, which again is in line with findings from other studies (10,11).

As outlined above, there is ample evidence for domestic dogs having an ability to discriminate human facial expressions and attribute the correct emotional valence to it. This raises the question of the origin of such an impressive skill. Answers can be found by studying the ontogenetic and evolutionary development of this ability.

1.3 The role of domestication and experience on dogs' social abilities

A wealth of research has been done on the relationship between social abilities of dogs and their experience with humans (e.g., different dog breeds, puppies, free-ranging dogs), including also the comparison of dogs with their closest relatives, the wolves (*Canis lupus*), to assess the influence of domestication and individual experience on behavioural characteristics. Consequently, many theories have been put forward to explain why dogs show social skills with humans. Back in 2002, Hare et al. postulated and tested three different hypotheses. The canid generalization hypothesis suggests that canids are generally very flexible and perform equally well when it comes to utilizing social information, a trait that is crucial for living together with conspecifics but also for hunting prey. The human exposure theory on the other hand, postulates that dogs have learned their skills in their ontogenies. The extent and quality of experience with humans will have an influence on the task performance. Finally, the last hypothesis emphasizes that domestication imposed a selection pressure for specific social cognition and communication skills with humans. The authors tested these hypotheses with dogs, dog puppies and wolves in an object choice task, including human social cues, and a food-finding game. Results from the study provide strong evidence in support of the domestication hypothesis; dogs performed better than wolves in using social cues from humans to find hidden food in an object, and the performance of the puppies matched the performance of older dogs (12).

The results of several studies, however, conducted at the Wolf Science Center (WSC) in Ernstbrunn, Austria, challenge the domestication hypothesis and suggest another explanation, formulated in the Canine Cooperation Hypothesis (13). According to this hypothesis, wolf-wolf cooperation constitutes the basis for dog-human cooperation and social understanding, with no need for further selection for social attentiveness and tolerance during the domestication process. In addition, similarities in sociability and cooperativeness between humans and wolves may have favoured the evolution of dog. The Canine Cooperation Hypothesis does not exclude a role of experience per se, meaning that higher experience may lead to more enhanced socio-cognitive abilities with humans.

To further dissect the role of experience and life history with humans, comparative studies with free-ranging dogs can be informative. Free-ranging dogs make up around 80% of the total world dog population (14,15). They differ from pet dogs in terms of freedom to move and to reproduce (free-breeding) (16). Pet dogs are mostly pure-breeds and therefore represent a genetically distinct, more inbred population compared to free-ranging dogs, which resemble more closely an ancient dog population (17). Free-ranging dogs mostly forage solitarily, while they are highly dependent on human for food supply (e.g., from refuses) (18). Although they do not have a close relationship with an owner, free-ranging dogs are still in constant interaction with both familiar and unfamiliar humans, receiving both positive and negative behavioural feedbacks. Understanding human intention and emotions is also to their benefit, as it allows them to prevent negative and dangerous encounters. Recently, it was reported that free-ranging dogs in India could follow complex pointing cues in a two-way object-choice task. They were able to follow distal pointing cues to locate hidden food reward (17). Another study with Indian free-ranging dogs tested their responsiveness when confronted with human gestures. The task included a social cue phase where one of the four gestures (friendly cue, low impact threatening, high impact threatening, neutral cue) was performed, followed by a food provisioning phase. Higher levels of approach and higher duration of human proximity was detected in the friendly cue condition, emphasizing the importance of positive social communication from humans to encourage the dogs to approach. Generally, dogs approached the experimenter more often in the food provision phase than in the social cue phase, which underlines the dependency of free-ranging dogs on humans for sustenance (19). Importantly, another study comparing the response to human pointing gestures (leading to food reward) in different age groups (puppies, juveniles, adults) in the same population of free-ranging dogs, showed that puppies were in fact the most responsive to human gestures. Unlike juvenile and adult dogs, puppies showed the highest ability to follow dynamic proximal pointing and showed less general avoidance of humans. On the other hand, the authors reported that only adult dogs adjusted their behaviour according to their experience with the reliability of the experimenter. These findings indicate a role of ontogeny in the development of social cognition skills, showing a certain plasticity that allows experience to modulate it (20). Considering avoidance of humans, Brubaker et al. (2019) observed that free-ranging dogs (when compared to pet dogs and shelter dogs) spent less time in proximity to the experimenter and differed in their gazing behaviour. When the experimenter was in an attentive state (making eye contact with the dog), free-ranging dogs looked at them significantly more than when the experimenter was in an inattentive state (turned away from the dog). This led to conclusion that free-ranging dogs might be primarily interested in obtaining food from humans and once the human does not indicate interest in the dog anymore, they lose interest quickly (21).

Noteworthy are experiments performed by Martina Lazzaroni (Domestication Lab at the University of Veterinary Medicine Vienna) in her doctoral thesis (22). These comparative studies between dog and wolf packs at the WSC, pet dogs in Vienna, Austria, and free-ranging dogs in Morocco indicated that life experience does not play a major role in the interaction of dogs with humans. Also, the behaviour of free-ranging dogs in these studies showed that dogs need less human socialization than wolves to develop human social interaction skills. Domestication seems to be more relevant than a dogs' life experience when it comes to their social interactions with humans (16,23,24). This interpretation, emphasizing the role of domestication over the role of experience, is in line with the findings of a very recent study from Salomons et al. (2021). Dog and wolf puppies between 5 and 18 weeks old were compared in different temperament and cognitive tasks, whereby wolf puppies received more intense human socialization than dog puppies. The results of this study revealed that dog puppies showed higher human social interaction skills (e.g., making eye contact, using human gestures correctly) and are more attracted (e.g., more likely to approach) to humans. The authors conclude that domestication enhanced cooperative-communication abilities with humans through selection for attraction towards humans, which altered social maturation (25).

As evident from the research summarized above, the respective roles of domestication and experience in dogs' high socio-cognitive abilities with humans is an ongoing scientific discussion that required further studies to fill critical knowledge gaps. Towards this end, this study took the approach of comparing the behaviour of dogs from distinct populations, differing in their experience with human socialization, to assess the influence of individual experience on dog's socio-cognitive skills with humans.

1.4 Research aims and motivation

This study aimed at the exploration of the role of dog's experience with humans in their development of skills to read human facial expressions. To this end, we investigated (i) whether free-ranging dogs from a population in Morocco match pet dogs' ability from Vienna to read human facial expressions and (ii) whether both dogs populations can interpret facial expression by adaptive behavioural responses. Recent literature (see Introduction) suggests that dogs' ability to accurately read and respond to human facial expression is independent of the extent of their human exposure and, hence, that even free-ranging dogs are supplied with the basic cognitive skills needed to read human emotions and intents. If true, this would predict that free-ranging dogs can discriminate human facial expressions as skillfully as pet dogs and that both groups will show equal responses by adaptation of their behaviour. Such responses can be reflected in their motivation to eat food, their tendency to approach the experimenter (proximity), their gazing style and their tail wagging (taken as a proxy for positive arousal). The following specific behavioural patterns could be predicted:

1. Free-ranging dogs and pet dogs will eat all available food more likely when the experimenter displays a happy face than and an angry or neutral face.
2. Free-ranging dogs and pet dogs will make more gaze aversions when facing an experimenter displaying an angry face than when displaying a happy or neutral face.
3. Free-ranging dogs and pet dogs spend more time in proximity to an experimenter displaying a happy face than to the same experimenter showing an angry or neutral face. Additionally, free-ranging dogs will stay less in proximity to the experimenter than pet dogs, independent of the emotion displayed.
4. Free-ranging dogs and pet dogs will make longer eye contact with the experimenter in the happy condition than in the angry or neutral condition. Additionally, free-ranging dogs will generally make less eye contact with the experimenter than pet dogs.
5. Free-ranging dogs and pet dogs wag their tails for a longer duration when facing an experimenter displaying a happy face than when displaying an angry or neutral face.

We tested these predictions in an experimental approach designed to include a facial expression task with free-ranging dogs living in Morocco and pet dogs living in Vienna. Free-ranging dogs were tested in the streets or at the beaches. To create similar conditions and integrate comparable environmental effects by the test settings in both groups, pet dogs were also tested outdoors, either in dog areas (more distraction) or in private gardens (less distraction). During the task, an experimenter demonstrated one of three facial expressions (happy, angry, neutral) to the dogs, while eating food. The food was then 'accidentally' dropped during the task. The behaviour of the dog was video recorded for further analysis with respect to the dog's proximity to the experimenter, its attention, its attitude towards the experimenter and whether it approached and ate the dropped food.

2 Methods

2.1 Ethical statement

Ethical approval for this study was obtained from 'Ethik und Tierschutzkommission' of the University of Veterinary Medicine (Protocol number: ETK-05/11/2018 and ETK-16/01/2019). Informed consent was obtained by all owners of the pet dogs prior to testing. The authorization to test the free-ranging dogs was provided by the municipality of Taghazout (Morocco).

2.2 Subjects and study area

Free-ranging dogs (Frd): The study area for the free-ranging dogs was focused on Taghazout in Morocco. Around two million dogs live in Morocco, most of them are freely moving around and can be considered as free-ranging dogs (26). Some dogs are not entirely free but can still be regarded "free-ranging" since the Moroccan concept of owning a pet dog (95% of the resident people claim to own at least one dog) differs a lot from the more Western concept. Dogs are hardly ever under strict human care meaning that they don't receive veterinary care and treatments, nor do they live inside the house of the owner. Consequently, the big majority of dogs in Morocco are left to themself and free to reproduce ("free-breeding"). The population used in this study lives within 0.5 km^2 of the center of the town of Taghazout. Free-ranging dogs spend a lot of time scavenging on human garbage produced by the local people or touristic activities (restaurants, hotels etc.) and even eat human feces. Besides, locals and tourists feed dogs directly, sometimes on a regular basis at specific locations. This pattern of food supply has the effect that solitary dogs roam around, moving from one spot to another looking for food. Taghazout is known to have a positive attitude and high tolerance to dogs. Free-ranging dogs in general vary a lot in their characteristics (e.g., acting shy or friendly with people), yet a peculiarity of Taghazout dogs is that most of them are extremely friendly. Preliminary results show that 73% of dog-initiated and 80% of human-initiated (locals and tourists) interactions happen on a positive and friendly basis. This circumstances facilitates conducting tests with this population, as not many of them are shy or aggressive but mostly relaxed due to repeated positive human experience (22).

In this study, a total of 72 free-ranging dogs were tested. Three female experimenters (JG, LB, RD) travelled by car to look for free-ranging dogs in their natural environment in the municipality of Taghazout. Particular attention was paid on choosing dogs that were solitary to avoid interference by conspecifics and, on including only adult dogs (appearing to be over 1 year of age). Dogs were tested either in the streets or at the beaches of Taghazout.

Pet dogs (Pd): The study area for the pet dogs was focused on Vienna and the Wolf Science Center in Ernstbrunn, Austria; a few dogs were additionally tested in Baselland, Switzerland. All pet dogs tested were not familiar with the experimenter. Two groups of pet dogs were tested in different environments. In the first group of pet dogs (PdA), 64 mixed-breed dogs (34 females; 30 males; age: 62 adult dogs (>1year old) and two juvenile dogs) were tested in outdoor areas such as dog parks of Vienna or in a testing enclosure at the Wolf Science Center. Three female experimenters (JS, ML, RD) recruited the dogs by approaching owners in outdoor areas and asking if they want to participate spontaneously with their dog.

To optimize the experimental setting and to control for distraction from the surrounding, a second group of mixed-breed pet dogs (PdG) was tested for a follow-up study in gardens of the owners. Two female experimenters (JS, RD) tested a total of 53 pet dogs (33 females; 20 males; age: adult dogs only (<1 year old)). The dogs were recruited by an online announcement and by directly contacting them over the data base of dog owners of the Clever Dog Lab (University of Veterinary Medicine of Vienna). In this case, the owners were told to not feed their dogs within two hours before their appointment of the experiment to keep the dogs food motivated.

2.3 Testing procedure

The testing procedure (Figure 1) was slightly different for the pet dogs and free-ranging dogs since it had to be adjusted to the different environments.

Free-ranging dogs (Frd): The experimenters located solitary dogs while moving around the village with a car. Once a suitable dog was located, one helper got out of the car and approached the dog to get its attention. Meanwhile the experimenter set up the testing scene, which contains a chair and a tripod with a video camera within a two-meter distance. Even though the aim was to have as few outside influences as possible, it was not possible to test the dogs in a complete distraction-free area. If the dog's attention was on the experimenter during eating and facial expression phase, it was considered as a success. Two helpers were responsible for recording the experiment with the camera and distracting other dogs or possible factors that might disturb the course of the experiment, while the experimenter run the trial.

The starting position was with the experimenter sitting on the chair and holding a piece of sausage with a cracker. On her lap there was a bag of extra sausages and crackers. The helper that distracted the subject dog from the very beginning would now bring the subject over to the set-up. The trial began when the dog was focused on the experimenter. The experimenter ate the cracker for 5 seconds, looking down at the food. Then, she made eye contact with the dog for 5 seconds with one of three facial expressions: happy, angry, or neutral (Figure 2). The happy facial expression included a smile, the angry expression included a frown and a furrowed brow, and the neutral would exhibit a straight mouth with no other movement. After the facial expression, the experimenter dropped the gaze and ate again. These alternating phases between eating and showing a facial expression were repeated three times, with eating as the last action before the experimenter "accidentally" dropped the food on the ground. If the dog looked away or got too distracted during the experiment, the experimenter would cough or rustle the bag in her lap to regain its attention. The experimenter only dropped the food when she was sure that the dog was attentive to her. After dropping the food, the experimenter made the same facial expression for again 5 seconds when having eye contact with the dog and alternated with looking away from the dog between each facial expression. This was regardless of whether the dog had yet approached to eat the food on the ground. After the third and final expression, the experimenter stood up, walked about 1-2m away from the dog in between the chair and camera, and faced away from the set-up for one minute. During the standing time, the experimenter did not make any movements and ignored the dog if it approached. The trial ended after this phase. LB tested 27 dogs, RD tested 25 dogs and JG tested 20 dogs.

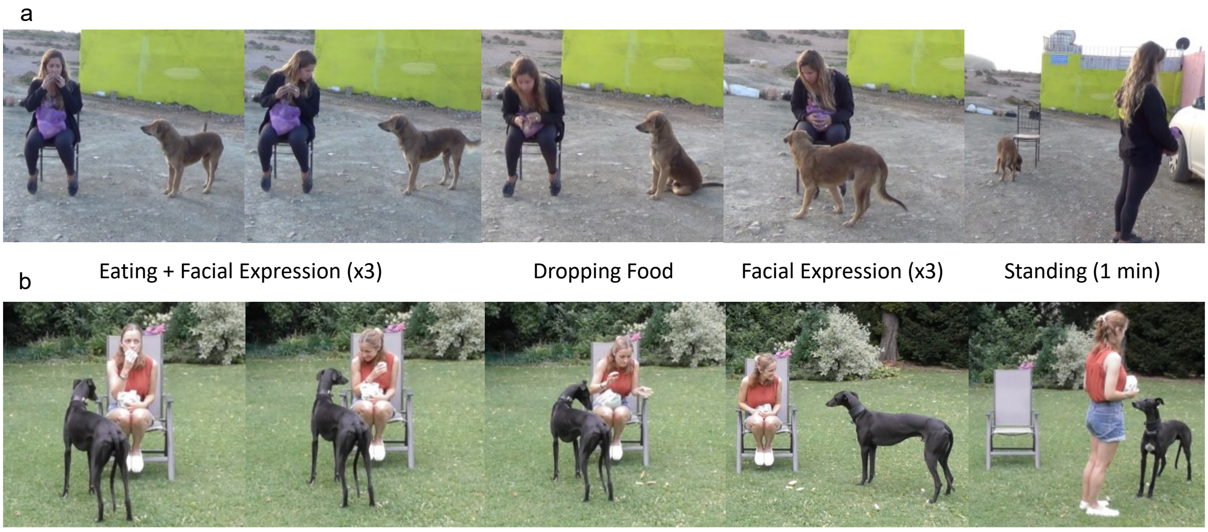

Figure 1. Test set up and procedure with free-ranging dogs (a) and pet dogs (b). In both cases, the experimenter sat on a chair and ate sausage and biscuit. Then she paused eating and made eye contact while making one of three facial expressions (happy (b), angry (a), neutral). The procedure of eating (for 5 seconds) which is followed by making the facial expression (for 5 seconds) was repeated three times. After that, the experimenter drops the food and then alternated again between looking away from the dog and making the facial expression for three times. Then she stood up and faced away from the set up for one minute. After the standing time, the experiment ended. Sometimes, the owners of pet dogs were present and sat on a second chair 2-3m to the side of the experimenter, facing away from the experiment (not seen in this Figure).

a b c

Figure 2. Examples of the experimenter expressing a happy (a), angry (b) and neutral (c) facial expression.

Pet dogs (Pd): The first group of pet dogs (PdA) was tested in outdoor areas in Austria. Three female experimenters (JS, ML, RD) were involved. If the owner of the pet dog was present during the experiment (for example when a dog was very dependent on the owner's presence in order to be calm and focused or, there was no possibility for the owner to go elsewhere), they were told to sit on a second chair (facing away from the experiment set up) reading a newspaper, ignoring the dog no matter what it was doing throughout the whole experiment. The experimenter ignored the dog while explaining the experiment to the owner and during setting up the experiment. The trial began when the dog was focused on the experimenter. The remaining process of the experiment is the same as described for the free-ranging dogs. JS tested 39 dogs, ML and RD tested each 12 dogs.

The second group of pet dogs (PdG) were tested with the same procedure, but this time in the owner's garden with fewer distractions. Two experimenters (JS, RD) were involved in the experiments. JS tested 43 dogs and RD tested 10 dogs.

Each session was videotaped by a video camera (Panasonic HD-Camcorder HC-W580). The three conditions performed were counterbalanced among the experimenters.

2.4 Data analysis and statistics

All videos were coded using Solomon coder® (developed by András Péter, Dept. of Ethology, Budapest, solomon.andraspeter.com). The coding started when the experimenter began eating while sitting on the chair and it ended after 60 seconds of standing time of the experimenter. See Table 1 for definitions of the coded behaviour. Additionally, free-ranging dogs were classified into two body condition groups, using the scale of the WSAVA Global Nutrition Committee (wsava.org, 05.01.22): under ideal (thin dogs) and ideal/over ideal (normal to fat dogs) body condition.

The videos from the free-ranging dogs were coded by LB and JG. Inter-observer reliability was carried out between three experimenters (LB, JG, ML), each coding the same 10 videos out of 72 videos (Intra-class correlation coefficient: Eating available food ICC = 1; Gaze aversion ICC = 0.8; Proximity ICC = 0.97; Looking at experimenter ICC = 0.86; Tail wagging ICC = 0.97). The videos from the pet dogs (PdA and PdG) were coded by JS. Inter-observer reliability was carried out between two experimenters (JS, ML), each coding the same 20 videos out of 117 videos (Intra-class correlation coefficient: Eating available food ICC = 0.806; Gaze aversion ICC = 0.826; Proximity ICC = 0.974; Looking at experimenter ICC = 0.876; Tail wagging ICC = 0.849).

Behaviour	Description
Eating available food (frequency)	The subject eats the whole sausage and the biscuit.
Gaze aversion (frequency)	The subject has eye contact with the experimenter and then looks away.
Proximity (duration)	The subject is within one dog body length distance of the experimenter.
Looking at experimenter (duration)	The subject's head is oriented towards the experimenter's face.
Tail wagging (duration)	The subject wags the tail from side to side.

Table 1. Description of the coded behaviour.

Statistical analyses were run in R (version 4.0.2 (27)). We used Generalized Linear Mixed Models (GLMM (28)) with beta error distribution and logit link function (29,30), using the function glmmTMB of the equally named package (version 1.0.0 (31)) for models of the coded variables 'Proximity', 'Tail wagging' and 'Looking at experimenter' (see table 1). We used Generalized Linear Mixed Models (GLMM (28)) with a negative Poisson distribution using the function glmer.nb for the model 'Gaze aversion' and with a binomial distribution using the function glmer of the package lme4 for the model 'Eat available food' (32). Collinearity of predictors, assessed by applying the function vif of the R package car (33) appeared not to be an issue (34). Overdispersion appeared not to be an issue (range of dispersion parameters 0.936-1.124). We determined model stability by dropping levels of the random effects one at a time and comparing the estimates derived from models fitted on the respective subsets with those obtained for the full data set. This revealed the model to be of moderate stability for models 'Looking at experimenter', 'Gaze aversion' and 'Eat available food' but of poor stability for all the other models. We obtained confidence intervals of model estimates by means of a parameteric bootstrap (N=1,000 bootstraps; function simulate of the package glmmTMB) for all models. For all models, to keep type I error rate at the nominal level of 5% (35,36) we included all theoretically identifiable random slopes components (condition, sex and body condition within experimenter ID). P-values for the individual effects were based on likelihood ratio tests comparing the full model with the respective reduced models lacking the model predictors (R function 'anova') (37).

Eating available food model: We tested whether the probability of eating all available food or not differed between groups and between conditions. To this end, we ran a GLMM with a binomial distribution, including group (PdA, PdG, FrD), condition (happy, angry, neutral) and their interaction as fixed effects, the identity of the experimenter as random factor. We also added in the model sex and body condition to control for their effect. We compared the full model with a null model lacking the predictors group, condition, and their interaction. We tested post-hoc comparisons using the function emmeans of the equally named package (versions 1.7.0).

Gaze aversion model: We tested whether the frequency of gaze aversions differed between groups and between conditions. To this end, we ran a GLMM with a negative poisson distribution, including group (PdA, PdG, FrD), condition (happy, angry, neutral) and their interaction as fixed effects, the identity of the experimenter as random factor. We included the test duration (log transformed) as an offset term. We also added in the model sex and body condition to control for their effect. We first tested the significance of the interaction by comparing the full model with an identical reduced model lacking the interaction between group and condition and since this comparison did not result significant for all three models, we compared the full model with a null model lacking the predictors group, condition, and their interaction.

Proximity, Tail wagging and Looking at experimenter models: In models 'Proximity', 'Tail wagging' and 'Looking at experimenter' we tested whether the proportion of time individuals spent in proximity with the experimenter, or tail wagged at the experimenter, or looked at the experimenter differed between groups and between conditions. To this end we ran three GLMMs (Proximity model, Tail wagging model and Looking at experimenter model) including group (PdA, PdG, FrD), condition (happy, angry, neutral) and their interaction as fixed effects. We also added sex (male or female) and body condition (thin or normal) into the models to control for their effects and included the identity of the experimenter (experimenter ID) as a random factor. We first tested the significance of the interaction by comparing the full model with an identical reduced model lacking the interaction between group and condition and since this comparison did not result in significance for all three models, we compared the full model with a null model lacking the predictors group, condition, and their interaction.

3 Results

Observations on 'Eating available food': We tested whether the probability to eat all available food dropped by the experimenter depends on the displayed facial expression and is different between dog groups. Overall, the full model was highly significant as compared to the null model (full-null model comparison: χ^2 = 36.735, *df* = 8, $p < 0.001$). Specifically, dog groups differed in their probability to eat all available food and and the influence of facial expression (interaction between group and condition: χ^2 = 11.948, *df* = 4, *p* = 0.017) (Figure 3); pet dogs ate all available food more likely than free-ranging dogs (Frd-PdA: *z* = -5.011, $p < 0.001$; Frd-PdG: *z* = -3.861, $p < 0.001$). Within each dog group, there were no statistically significant differences apparent between facial expression conditions. For the happy and the neutral expression, however, we found differences between groups; pet dogs in dog areas (PdA) ate all the available food more likely than free-ranging dogs (Frd) in the happy condition (post-hoc comparison: *z* = 3.314, *p* = 0.01), and in the neutral condition (post-hoc comparison: *z* = 3.983, $p < 0.001$).

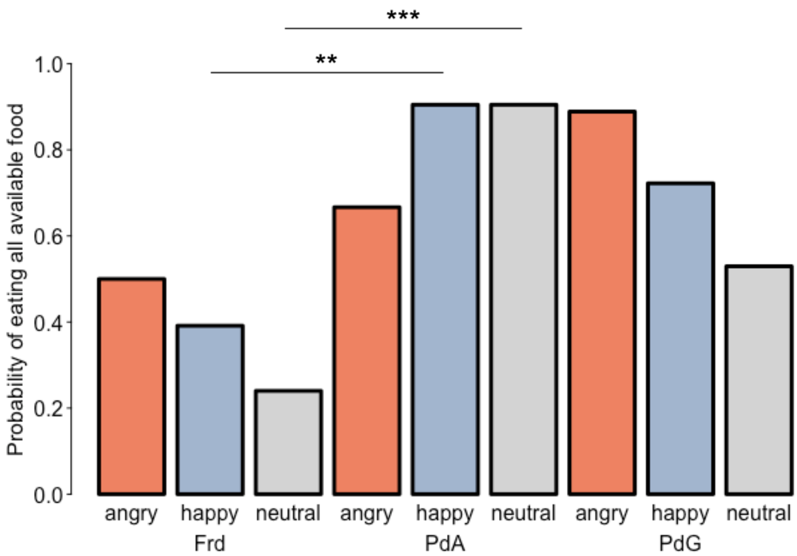

Figure 3. Barplots showing the probability of eating all available food (sausage and biscuit) depending on the facial expression (angry, happy, neutral) of the experimenter for free-ranging dogs (Frd, N=72), pet dogs tested in outdoor areas (PdA, N=64) and pet dogs tested in gardens (PdG, N=53). *, *p*-values ≤ 0.01; **, *p*-values ≤ 0.001; *.**

Observations on 'Gaze aversion': We tested whether the frequency of gaze aversion by dogs depends on the dog group and/or the displayed facial expression. Generally, we found that pet dogs tested in private gardens (PdG) and free-ranging dogs (Frd) performed more gaze aversions than pet dogs tested in dog areas (PdA) (PdG-PdA: *z* = 3.269, *p* = 0.001; Frd-PdA: *z* = -4.404, $p < 0.001$), whereas no difference was apparent between pet dogs tested in gardens and free-ranging dogs (*z* = -1.185, *p* = 0.236) (Figure 4). However, all groups responded similarly to facial expressions (interaction between group and condition was not significant, full-reduced model comparison: $\chi^2 = 5.500$, $df = 4$, $p = 0.240$), averting gaze more frequently in the angry than in the happy condition ($z = -2.956$, $p = 0.003$) and showing a tendency to more frequent gaze aversion in the angry compared to the neutral condition ($z = -1.909$, $p = 0.056$). We did not find differences between the neutral and the happy condition ($z = 1.081$, $p = 0.279$). See supplementary material Table 4a and Table 4b.

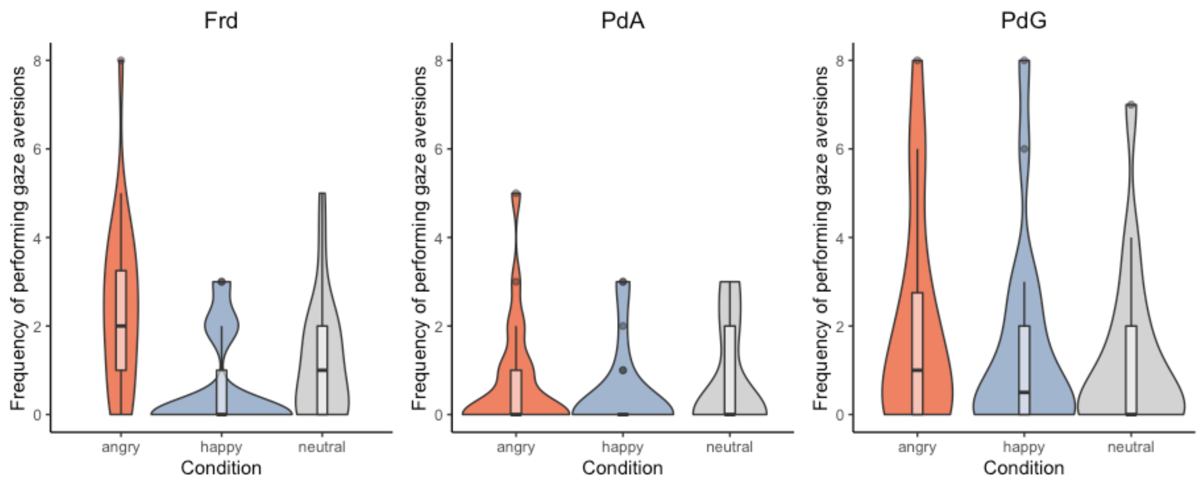

Figure 4. Violin plots with inlaid boxplots demonstrating median, first and third quartile of frequency of gaze aversion during the experiment for free-ranging dogs (Frd, N=72), pet dogs tested in outdoor areas (PdA, N=64) and pet dogs tested in gardens (PdG, N=53) and in dependence of the facial expression displayed (angry, happy, neutral). Violin plots outline the kernel probability density whereby the width of the shaded area indicates the proportion of data for each location.

Observations on 'Proximity': We tested whether the duration of staying in proximity to the experimenter depends on the dog group and/or the displayed facial expression. We found that pet dogs in gardens and in outdoor areas remained in proximity to the experimenter for longer time periods than free-ranging dogs (PdA-Frd: $z = 5.770$, $p < 0.001$; PdG-Frd: $z = 5.808$, $p < 0.001$), irrespective of the facial expressions displayed (interaction between group and condition was not significant, full-reduced model comparison: $\chi^2 = 5.722$, df = 4, p = 0.221) (Figure 5). There were no differences in the time spent in proximity to the experimenter between the two groups of pet dogs ($z = 0.341$, $p = 0.733$). Notably, dogs with a body condition classified as "thin", present only in the group of free-ranging dogs, stayed in proximity with the experimenter significantly longer than subjects classified as having a "normal" body condition ($z = 2.425$, $p = 0.015$). We did not find differences between facial conditions in the time spent in proximity to the experimenter (angry-happy: $z = -0.784$, $p = 0.433$; angry-neutral: $z = -0.971$, $p = 0.332$; happy-neutral: $z = -0.490$, $p = 0.624$). See supplementary material Table 1a and Table 1b.

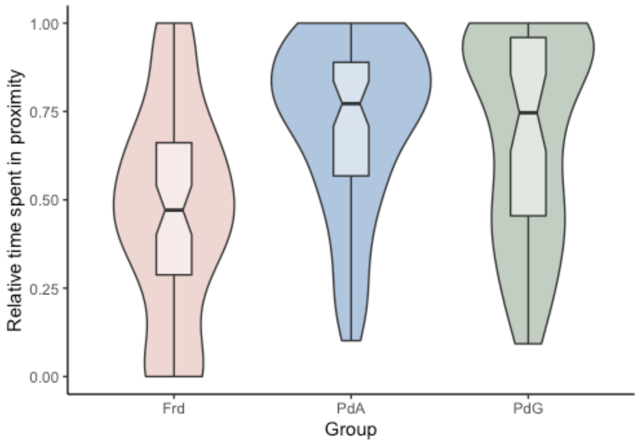

Figure 5. Violin plots with inlaid boxplots demonstrating median, first and third quartile and minimum and maximum of relative time (proportion duration of proximity/total duration of experiment) spent in proximity to the experimenter for free-ranging dogs (Frd, N=72), pet dogs tested in outdoor areas (PdA, N=64) and pet dogs tested in gardens (PdG, N=53). Violin plots outline the kernel probability density with the width of the shaded area indicating the proportion of data at each location.

Obervations on 'Looking at experimenter': We tested whether the duration of looking at the experimenter (the dog's head is oriented towards the experimenter's face) depends on the dog group and/or the displayed facial expression. We found that, overall, pet dogs tested in gardens (PdG) and free-ranging dogs (Frd) looked at the experimenter for longer than pet dogs tested in dog areas (PdA) (PdG-PdA: z = 3.837, p < 0.001; Frd-PdA: z = -2.813, p = 0.005), irrespective of facial condition displayed (interaction between group and condition was not significant, full-reduced model comparison: χ^2= 5.580, df = 4, p = 0.233) (Figure 6). Pet dogs tested in gardens and free-ranging dogs showed no difference in the mean duration of looking at the experimenter (z = 1.115, p = 0.265), and neither facial condition made a difference in the duration of looking at the experimenter (angry-happy: z = -0.915, p = 0.360; angry-neutral: z = -0.482, p = 0.630; happy-neutral: z = 0.351, p = 0.725). See supplementary material Table 3a and Table 3b.

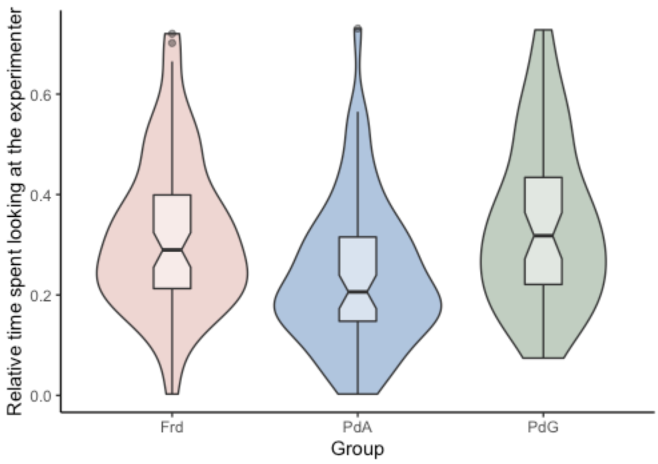

Figure 6. Violin plots with inlaid boxplots demonstrating median, first and third quartile and minimum and maximum of relative time spent looking at the experimenter (proportion duration of looking/total duration of experiment) between free-ranging dogs (Frd, N=72), pet dogs tested in outdoor areas (PdA, N=64) and pet dogs tested in gardens (PdG, N=53). Violin plots outline the kernel probability density whereby the width of the shaded area indicates the proportion of data for each location.

Observations on 'Tail wagging': We tested whether the duration of tail wagging depends on the dog group and/or the displayed facial expression. We found that free-ranging dogs wagged their tails at the experimenter for longer than both groups of pet dogs (PdA-Frd: $z = -3.302$, $p < 0.001$; PdG-Frd: $z = -3.896$, $p < 0.001$), irrespective of the facial condition displayed (interaction between group and condition was not significant, full-reduced model comparison: $\chi^2 = 6.133$, $df = 4$, $p = 0.189$) (Figure 7). We found no differences in the duration of tail wagging between the two groups of pet dogs ($z = -0.765$, $p = 0.444$), and no differences in tail wagging were observed between facial conditions in all groups (angry-happy: $z = -0.351$, $p = 0.725$; angry-neutral: $z = 0.049$, $p = 0.960$; happy-neutral: $z = -0.397$, $p = 0.691$). See supplementary material Table 2a and Table 2b.

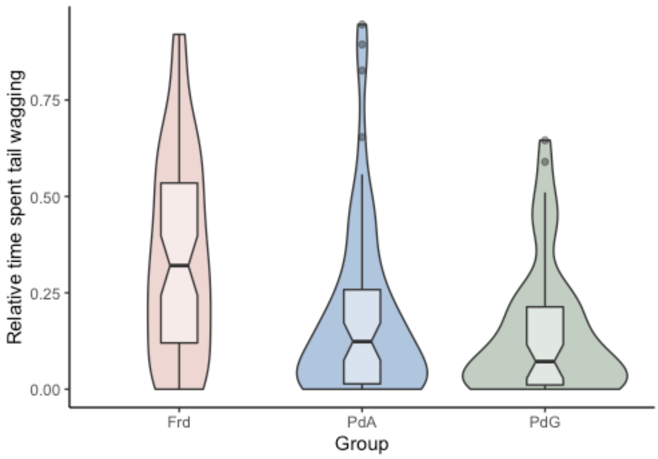

Figure 7. Violin plots with inlaid boxplots demonstrating median, first and third quartile and minimum and maximum of relative time (proportion duration of tail wagging/experiment duration) spent tail wagging for free-ranging dogs (Frd, N=72), pet dogs tested in outdoor areas (PdA, N=64) and pet dogs tested in gardens (PdG, N=53). Violin plots outline the kernel probability density whereby the width of the shaded area indicates the proportion of data for each location.

4 Discussion

In this study, we investigated the role of dogs' experience with humans in the development of the ability to read human behavioural cues. To this end, we compared free-ranging dogs from Morocco with pet dogs from Vienna for their ability to understand human facial expressions. Overall, the results obtained suggest that dogs are able to distinguish between different human facial expressions although, in the tests performed, they not always behave according to the message the human experimenter intended to give with a specific facial expression. Interestingly, we did not find major differences in the ability to discriminate between different human facial expressions between poorly socialized free-ranging dogs and highly socialized pet dogs. This indicates that the extent of past exposure to human beings does not impact on the behaviour of dogs confronted with an angry, happy, or neutral human facial expression. Alternatively, it may be more relevant for free-ranging dogs to pay attention to human communication cues because the outcome of an encounter might be more dire; they may be able to learn more quickly about human behaviour with less human exposure needed than pet dogs.

In our study, the facial expression performed by the experimenter had an influence on the likelihood to eat the food and on the frequency of gaze aversion. We found a statistically significant interaction between the type of facial expression and dogs' group in their eating behaviour; when confronted with a happy and neutral facial expression, pet dogs in dog areas ate the dropped food more likely than free-ranging dogs (Frd). Here, the difference between dog groups seems to be mainly driven by a generally higher tendency of pet dogs in outdoor areas to eat all food, rather by an effect of the facial expression. It is also possible that the distracting situation led to a higher focus on eating the food due to potential food competition by other dogs than focusing on the experimenter's communication. Overall, the observations on eating all available food were unexpected and not in accordance with our prediction that both dog groups will eat the food more likely in the happy facial condition; within the group of pet dogs in gardens and free-ranging dogs, we could even notice an inverse pattern with dogs eating all available food with a higher probability when confronted with an angry condition than with a happy condition or a neutral condition (Figure 3). The inverse pattern could be explained by the happy condition leading to further expectations by the dogs, such as a positive interaction (e.g., cuddling or playing with a toy) that might follow, distracting the dogs from eating the food. Other explanations for why the eating-all-food behaviour did not match our prediction could be (i) a misinterpretation by the dog of the message (angry: "Stay away, this is my food") intended by the facial expression in the testing situation, (ii) the dogs not caring about the angry emotional state of the human during the experiment, (iii) a human facial expression on its own being a too low-impact communication to impress dogs in general, or (iv) the duration of the performed facial expression being too short to elicit a behavioural change. Supporting the possibility iv, a study from Call et al. 2003 demonstrated that dogs that were presented with food and told to “leave it”, ate the food more often when the commanding human was in an inattentive state (e.g. having their eyes closed or facing away) than when facing the dogs and tracking them with their eyes (38). Hence, if the facial expression in our experiment was presented for longer or even permanently, the dogs might have eaten the food less likely in the angry facial condition. In addition, stimuli such as the neutral facial expression might be confusing for dogs as they are most likely less used to encountering humans showing neutral emotions towards them. This may cause uncertainty about what the human counterpart intends to communicate and how to properly adapt to it. Free-ranging dogs might also be used to very positive behaviour from tourists in Taghazout, so they may have ignored or averted from the angry expression but paid more attention to the experimenter when she expressed a familiar (happy or neutral) expression deviating the focus from the food. Regarding free-ranging dogs, the independence of the eating-all-food behaviour on facial expression was an unexpected result and not in line with a former study with Indian free-ranging dogs. In this study, the authors showed that free-ranging dogs had higher motivation to approach the food in a friendly condition than in a neutral or angry one (19). This discrepancy might be explained by the difference in methodology; the study with Indian free-ranging dogs measured the latency to approach and start to eat the food, whereas our test set up only allowed to measure the likelihood of eating all dropped food.

Our data suggest that the human facial expression had an influence on the frequency of gaze aversions in dogs. All three dog groups responded with significantly more gaze aversions in the angry condition than in the happy condition and the same showed as a tendency between the angry and the neutral condition. Breaking eye contact by gaze aversion is a possible indicator of subordination and avoidance of interaction in dogs (39), and it can further indicate that a situation is stressful for dogs (40). Gaze aversion is generally considered as a submissive behavioural pattern (41,42). Our results provide the strongest evidence for the free-ranging dogs having equal abilities to pet dogs in distinguishing between facial expressions and to interpret the emotional valence of an angry expression. Similar results were obtained in another study that investigated how dogs decode human behavioural cues with different emotional intents (friendly, moderately agonistic, ambivalent) in playful and non-playful situations. This experimental set-up involved the tracking of the frequency of gaze aversion when an experimenter approached the dog, holding eye contact in the three emotional conditions. In this setting, dogs made more gaze aversions in non-playful situations when the experimenter approached them with a threatening behaviour than with a friendly behaviour, particularly when the experimenter was unfamiliar to the dog (39).

The condition of the facial expression had no influence neither within nor between dog groups in all other behavioural tests, i.e., proximity to the experimenter, looking at the experimenter and tail wagging. Neither free-ranging dogs nor pet dogs chose to stay further away in the angry condition when compared to the happy or neutral conditions. Notably, a previous study with Indian free-ranging dogs reported that dogs stayed in proximity longer under a friendly human cue condition than under a low-, high impact threating or neutral cue condition (19). Possible reasons for this discrepancy between the observation might be again that (i) the stimuli of the facial expression in our setting were of too low-impact or have not been displayed long enough, (ii) the stimuli were misread or (iii) simply not of a high enough importance to override the dog's high motivation to remain close to the experimenter to get food. Regarding the tail wagging behaviour, dogs wagged their tails in the angry condition for as long as in the happy or neutral conditions, challenging our assumption that tail wagging is related to positive arousal, unless an angry expression can elicit a positive signal in dogs. It was previously shown that dogs perform asymmetric tail wagging as a reaction to different emotive stimuli (43). In 2013, Siniscalchi et al. demonstrated that dogs not only show left-or right-biased wagging but are also sensitive to these expressions by other dogs. Amazingly, dogs watching videos of other dogs wagging their tails displayed a more anxious behaviour with a higher heart rate when the dog wagged its tail more prominently to the left side (44). It was concluded that dogs receive left-biased tail-wagging as a stress signal and a right-biased wagging a relaxing signal. In line with this, another study overserved that dogs show left-biased tail wagging when faced with a stimulus that elicits a withdrawal response, such as the encounter with a foreign dog in an agonistic state (43). Siniscalchi et al. (2013) suggested that dogs use asymmetric tail wagging as a signal for impending danger in the environment (44). Hence, tail wagging is not simply used as an indicator for positive arousal but also as a communicative behaviour, with the preferential direction of tail wagging indicating the state of another animal. Also, the height at which the tail is held is an important sign of the emotional state with a low tail position being associated with anxiety and nervousness (45). The signature of tail wagging seems to be very complex and dependent on multiple variables, including posture or vocalization (45,46). Very recently, findings by Pedretti et al. (Pedretti – personal communication) reinforced the concept of tail wagging being a communicative behaviour (here towards humans). They demonstrated that dogs performed more tail wagging in a frustrating situation (getting no reward) when a human social partner was present, than when a human social partner was absent in the same frustrating situation and in a positive anticipation (getting reward) situation. It was concluded that tail wagging behaviour has an important communicative component and is not just an arousal indicator since it is influenced by the presence of an audience. Tail wagging in our experiment could thus have been used by dogs to communicate different intents and emotions to the experimenter (e.g., soothing the experimenter that shows an angry expression) by adjusting the height of the tail and showing side-biased tail wagging. We did not analyze the lateralization of the tail wagging, which might very well explain why dogs from all groups wagged their tail as much in the happy condition as well as in the angry or neutral condition; we might have missed that in the happy condition the tail wagging was more to the right side whereas in the angry condition in might have been more to the right side.

Whilst free-ranging dogs and pet dogs showed very similar and in general low behavioural responses to facial expressions in our tests, we did find differences in responses between the dog groups, however independent of facial expression. We found that pet dogs ate all available food more likely than free-ranging dogs. A possible explanation was proposed in a study by Brubaker et al. (21), saying that free-ranging dogs loose interest and get bored when not receiving clear signals, intentions or attention from humans. The set-up of our experiment might indeed have evoked such a reaction. Moreover, the very high motivation to eat the food of pet dogs tested in outside areas or in gardens (discussed above) suggests that pet dogs are generally less inhibited by humans than free-ranging dogs. The assumption of free-ranging dogs feeling more inhibited by humans is also reflected in the result from the analysis of the dog's proximity to the experimenter, showing that free-ranging dogs remained at higher distance to the experimenter than pet dogs throughout the experiments. The preference of free-ranging dogs to stay in greater distance to humans during an experiment has been observed previously. Brubaker et al. (2019) investigated the responses of Indian free-ranging dogs, shelter, and pet dogs to a human in three attentional state conditions; the human making eye contact (attentive state), the human turned away (inattentive state) and human exiting the testing area. Regardless of the human attentional state, Indian free-ranging dogs spent overall less time in proximity (within arms length of the experimenter) than shelter and pet dogs, consistent with the result of our study. Yet, the presence of a potential food source seems to have an impact on the dog's motivation to approach a human. Bhattacharjee et al. (2018) reported that free-ranging dogs approached the experimenter more often in a food provision phase than in the social phase of the experiment, in agreement with the dogs' dependency on humans for sustenance. This notion is supported in our observation that dogs classified as "thin" preferred to stay in closer proximity to the experimenter than dogs with a "normal" body type. Overall, our observations from measuring the proximity are in line with published work and support the idea that free-ranging dogs tend to be more vigilant than pet dogs when encountering humans and thus, prefer to observe the situation within safe distance. This behaviour is most likely the results of individual life experiences and can vary between individuals due to former negative and positive human encounters. Nevertheless, most dogs from all groups spent at least some time in proximity to the experimenter, which supports the concept that dogs, regardless of their socialization experience, share an overall interest and willingness in being close with a human (22), even if it is only to catch food. Another difference found between dog groups is that pet dogs tested in outdoor areas showed overall less gaze aversions than pet dogs tested in gardens and free-ranging dogs. Similalry, our result from the “looking” behaviour shows that pet dogs tested in outdoor areas looked less at the experimenter during the test than free-ranging dogs and pet dogs tested in gardens. Both findings are in line with each other and emphasize again (see discussion of the “eating-all-food” behaviour) the importance of the testing area. We attribute these differences to the fact that dogs in outdoor areas were more distracted by the surrounding and thus, less focused on the experimenter. Finally, our study revealed one last difference between dog groups; free-ranging dogs spent more time tail wagging than both groups of pet dogs. As discussed, tail wagging behaviour could have an important communicative component and, in this sense, it would be interesting to examine if free-ranging dogs and pet-dogs showed different left- or right-bias preferences in the experiment, signaling different emotions and intentions in the test situation. For free-ranging dogs, for instance, it might be more important to signal positive intentions to prevent negative encounters with humans.

To follow up on this study, investigation of the height and direction of tail wagging seems to be a promising new approach. In particular, when analyzing facial expression recognition, tail wagging might represent a meaningful reaction of a dog, allowing it to fine-tune responses to distinct human emotional stimuli. Also, the current study as well as future studies could benefit from controlling for other factors. To be emphasized is the familiarity of the experimenter as it had shown effects in previous studies; dogs performed worse in a task of referring the right emotional message from a facial expression when the performer was unfamiliar (47). Yet, familiarity did not seem to be important in other studies (11) (48). Secondly, to effect of dog breeding should be considered, it is likely that dogs that were bred with a purpose to closely interact and cooperate with humans (e.g., shepherd dogs) react differently in a human interaction task than dogs that were bred to work independently from humans (e.g., herd guardian dogs) (4). We noticed that dogs overall showed high individual variance in their reactions; we had dogs that were quiet and preferred higher proximity versus dogs that wagged their tail and acted very boisterous even before the experiment started. This might be explained by the individuality of every single dog which might also be influenced by differences in characters of specific dog breeds. A way to control for individual variability would be to test the same dog in all three conditions. However, this would require a very carefully designed experiment to minimize learning effects. Testing different age groups of dogs is a further possibility to address the influence of human experience on the development of dogs’ social abilities; it would be interesting to see if dog puppies react differently in a human facial expression interpretation test than adult dogs. Also, future work should take into account differences in the motivation to eat food as well as individual life history of free-ranging or pet dogs tested (e.g., origin, human exposure). All considered, follow-up studies should consider the shortcomings from this study as mentioned and aim to resolve them with an adapted study design (stratify certain traits, increase sample sizes to control for inter-individual variance) that will generate more differentiating and statistically robust results.

Finally, what are the implications of our findings with regard to the main questions whether free-ranging dogs perform as well as pet dogs in understanding human facial expressions or, more generally, whether human experience is a relevant factor for dogs to develop their complex social human interaction skills. Considering gaze aversion results, our study would support the theory that human exposure is a minor factor in the development of social skills with humans. Also, the fact that all three dog groups behaved in similar and overall consistent patterns (except for pet dogs tested in outdoor areas eating more food in all conditions) supports the idea that the level of experience with humans does not fundamentally alter the social behaviour of dogs towards humans. Importantly, human facial expressions in our specific experimental design could not elicit significant behavioural adaptions to the expressed emotions in all three dog groups. Yet, we found behavioural differences between dog groups that were independent of the emotional expression condition. These can probably be routed in individual life experience, such as that free-ranging dogs prefer to stay at higher distance and that they wagged their tails more often. This might indicate that free-ranging dog are indeed very careful and attentive when it comes to human encounters. An important point here is that our population of free-ranging dogs are known to be very friendly and Taghazout, the city around where the dogs live, is known to be very tolerant to dogs. These dogs thus might have experienced a lot of friendly interactions with humans (22) and therefore be more trusting and less sensitive when encountering humans. It would be interesting to conduct the same experiment with another free-ranging dog population more used to negative interactions. Also, free-ranging dogs are known to be very food-motivated and to run tasks more willingly when food is involved (19). To perform a facial expression task with a stimulus other than food (e.g., social cuddling) would also be very interesting. In this sense, the current study provides a lot of starting points to further investigate on behavioural differences between dog populations.

In conclusion, the domestication process generated a remarkably high sociability in dogs and yet, it is known from multiple comparative studies that even the dogs' ancestors, the wolves, show social attentiveness towards humans (complex forms of wolf-human communication and cooperation). Wolves pay as much attention to human partners as dogs do and even outperform dogs in learning by observation. This supports the Canine Cooperation Hypothesis; the wolf-wolf cooperation needed to live in a wolf pack constituted the basis for human-dog cooperation without further selection needed (13). A study showed that dog puppies (7 to 24 weeks) are able to find hidden food in an object choice paradigm based on human social interaction cues (49), indicating that the amount of experience with humans does not seem to be crucial and that such skills might be congenital. The same is reflected in studies with free-ranging dogs to which results of our study add a valuable contribution. We conclude that free-ranging dogs from Morocco behave very similarly to pet dogs in Vienna in a facial expression task. This might either indicate that being able to read human facial expressions might be a congenital trait with only little to no influence of experience, or, alternatively, that dogs with less human exposure developed quicker skills to learn human communication as a consequence of a selection pressure coming from less but still important encounters with humans with potential negative outcome for survival. However, facial expressions in our study did not generally show a high impact on other behavioural patterns such as "eating-all-food", "proximity to the experimenter", "tail wagging" or "looking at the experimenter". Irrespective of the facial expression response, our data also indicates that free-ranging dogs differ in their way to approach humans and how they communicate with tail wagging as discussed. The results of this thesis may not all be conclusive by themselves, but they advance our insight into the complexity of the behavioural aspects of the human-dog relationship and, thereby, provide a solid basis for the conceptual refinement in future studies on the dogs' extremely high human social interactions skills.

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Appendix

Supplementary material

Reported for all the statistical models are in the following the estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum estimates derived after excluding individuals one at a time.

Table 1a_Proximity. [a] Dummy coded with free-ranging dog being the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category; [e] Not indicated because having a limited interpretation; [f] The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Term	**Estimate**	**SE**	***z* or χ^2**	***P***	**Lower CI**	**Upper CI**	**Min**	**Max**
Intercept	-0.148	0.245		NI[e]	-0.639	0.321	-0.306	0.210
Group(PdA)[a]	1.013	0.348		NI[e]	0.346	1.739	0.612	1.299
Group(PdG)[a]	0.879	0.362		NI[e]	0.132	1.600	0.481	1.142
Condition(happy)[b]	-0.683	0.335		NI[e]	-1.440	-0.002	-1.207	-0.458
Condition(neutral)[b]	-0.285	0.325		NI[e]	-0.924	0.360	-0.774	-0.010
Sex(m)[c]	0.048	0.173	0.280	0.780	-0.273	0.427	-0.043	0.127
Body condition (thin)[d]	0.867	0.329	2.635	0.008	0.236	1.507	0.646	1.100
Group(PdA)*Condition(happy)	0.695	0.487	5.722	0.221[f]	-0.258	1.729	0.123	1.337
Group(PdA)*Condition(neutral)	0.127	0.479			-0.866	1.065	-0.177	0.595
Group(PdG)*Condition(happy)	1.190	0.505			0.236	2.307	0.806	1.837
Group(PdG)*Condition(neutral)	0.155	0.506			-0.840	1.187	-0.859	0.877

Table 1b_Proximity. Results of the model lacking the interaction between group and condition (the full-reduced model comparison between the initial model including the interaction- see Table 1a- and a null model lacking the predictors group, condition and

their interaction was significant: χ^2=36.88, *df*=8, *P*<0.001). [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category. The difference between PdA and PdG was estimated as 0.073±0.214, *z*=0.341, *P*=0.733. The difference between happy and neutral was estimated as 0.100±0.204, *z*=-0.490, *P*=0.624.

Term	**Estimate**	**SE**	***z***	***P***
Intercept	-0.316	0.209	-1.514	0.130
Group(PdA)[a]	1.262	0.219	5.770	<0.001
Group(PdG)[a]	1.323	0.228	5.808	<0.001
Condition(happy)[b]	-0.223	0.284	-0.784	0.433
Condition(neutral) [b]	-0.199	0.205	-0.971	0.332
Sex(m)[c]	0.049	0.168	0.289	0.773
Body condition (thin)[d]	0.836	0.345	2.425	0.015

Table 2a_Tail wagging. [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category; [e] Not indicated because having a limited interpretation; [f] The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Term	**Estimate**	**SE**	***z* or χ^2**	***P***	**Lower CI**	**Upper CI**	**Min**	**Max**
Intercept	-0.610	0.229		NI[e]	-1.078	-0.131	-0.717	-0.518
Group(PdA)[a]	-1.066	0.336		NI[e]	-1.706	-0.478	-1.241	-0.789
Group(PdG)[a]	-0.742	0.355		NI[e]	-1.458	-0.075	-1.038	-0.630
Condition(happy)[b]	-0.494	0.309		NI[e]	-1.143	0.159	-0.555	-0.431
Condition(neutral)[b]	-0.044	0.324		NI[e]	-0.697	0.584	-0.326	0.150
Sex(m)[c]	-0.059	0.165	-0.356	0.722	-0.388	0.281	-0.275	0.031
Body condition (thin)[d]	0.280	0.302	0.926	0.354	-0.313	0.876	0.158	0.380
Group(PdA)*Condition(happy)	1.029	0.453	6.133	0.189[f]	0.129	1.935	0.792	1.113

Group(PdA)*Condition(neutral)	0.330	0.505			-0.652	1.325	-0.536	0.708
Group(PdG)*Condition(happy)	0.242	0.465			-0.740	1.202	0.116	0.448
Group(PdG)*Condition(neutral)	-0.357	0.608			-1.400	0.602	-0.591	0.002

Table 2b_Tail wagging. Results of the model lacking the interaction between group and condition (the full-reduced model comparison between the initial model including the interaction- see Table 2a- and a null model lacking the predictors group, condition and their interaction was significant: χ^2=21.1, *df*=8, *P*=0.006). [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category. The difference between PdA and PdG was estimated as 0.152±0.199, *z*=-0.765, *P*=0.444. The difference between happy and neutral was estimated as 0.076±0.192, *z*=-0.397, *P*=0.691.

Term	**Estimate**	**SE**	***z***	***P***
Intercept	-0.701	0.189	-3.715	<0.001
Group(PdA)[a]	-0.642	0.194	-3.302	<0.001
Group(PdG)[a]	-0.794	0.204	-3.896	<0.001
Condition(happy)[b]	-0.067	0.191	-0.351	0.725
Condition(neutral) [b]	0.009	0.187	0.049	0.960
Sex(m)[c]	-0.151	0.158	-0.958	0.338
Body condition (thin)[d]	0.208	0.295	0.704	0.481

Table 3a_Looking. [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category; [e] Not indicated because having a limited interpretation; [f] The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Term	**Estimate**	**SE**	***z* or χ^2**	***P***	**Lower CI**	**Upper CI**	**Min**	**Max**
Intercept	-0.639	0.148		NI[e]	-0.944	-0.367	-0.665	-0.589

Group(PdA)[a]	-0.589	0.221		NI[e]	-1.039	-0.157	-0.636	-0.476
Group(PdG)[a]	-0.052	0.218		NI[e]	-0.488	0.352	-0.363	0.046
Condition(happy)[b]	-0.493	0.210		NI[e]	-0.888	-0.116	-0.653	-0.322
Condition(neutral)[b]	-0.096	0.196		NI[e]	-0.489	0.272	-0.196	0.002
Sex(m)[c]	-0.002	0.110	-0.015	0.988	-0.215	0.225	-0.091	0.054
Body condition (thin)[d]	0.249	0.200	1.28	0.212	-0.138	0.643	0.047	0.484
Group(PdA)*Condition(happy)	0.653	0.312	5.580	0.233[f]	0.076	1.270	0.496	0.813
Group(PdA)*Condition(neutral)	0.059	0.307			-0.555	0.692	-0.096	0.183
Group(PdG)*Condition(happy)	0.608	0.310			0.034	1.225	0.413	0.781
Group(PdG)*Condition(neutral)	0.062	0.307			-0.579	0.676	-0.036	0.193

Table 3b_Looking. Results of the model lacking the interaction between group and condition (the full-reduced model comparison between the initial model including the interaction- see Table 3a- and a null model lacking the predictors group, condition and their interaction was significant: χ^2=22.349, *df*=8, *P*= 0.004). [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category. The difference between PdA and PdG was estimated as 0.521±0.135, *z*= 3.837, *P*<0.001. The difference between happy and neutral was estimated as 0.045± 0.131, *z*= 0.351, *P*=0.725.

Term	**Estimate**	**SE**	***z***	***P***
Intercept	-0.734	0.131	-5.605	<0.001
Group(PdA)[a]	-0.377	0.134	-2.813	0.005
Group(PdG)[a]	0.150	0.134	1.115	0.265
Condition(happy)[b]	-0.165	0.181	-0.915	0.360
Condition(neutral) [b]	-0.061	0.126	-0.482	0.630

Sex(m)[c]	-0.005	0.107	-0.048	0.962
Body condition (thin)[d]	0.177	0.207	0.857	0.391

Table 4a_Gaze aversion. [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category; [e] Not indicated because having a limited interpretation; [f] The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Term	**Estimate**	**SE**	***z* or χ^2**	***P***	**Lower CI**	**Upper CI**	**Min**	**Max**
Intercept	-3.652	0.296		NI[e]	-4.321	-3.161	-3.980	-3.404
Group(PdA)[a]	-1.849	0.451		NI[e]	-2.876	-0.990	-2.199	-1.527
Group(PdG)[a]	-0.800	0.419		NI[e]	-1.676	0.092	-1.146	-0.469
Condition(happy)[b]	-1.546	0.443		NI[e]	-2.643	-0.716	-1.928	-0.996
Condition(neutral)[b]	-0.814	0.393		NI[e]	-1.641	-0.054	-0.925	-0.732
Sex(m)[c]	0.049	0.223	0.219	0.827	-0.446	0.489	-0.129	0.148
Body condition (thin)[d]	-0.312	0.481	-0.650	0.516	-1.506	0.480	-0.923	-0.020
Group(PdA)*Condition(happy)	1.114	0.690	5.500	0.240[f]	-0.339	2.684	0.563	1.742
Group(PdA)*Condition(neutral)	0.834	0.631			-0.486	2.201	0.140	1.173
Group(PdG)*Condition(happy)	1.234	0.625			-0.029	2.658	0.678	1.457
Group(PdG)*Condition(neutral)	0.350	0.606			-0.957	1.669	-0.082	0.530

Table 4b_Gaze aversion. Results of the model lacking the interaction between group and condition (the full-reduced model comparison between the initial model including the interaction- see Table 4a- and a null model lacking the predictors group, condition and their interaction was highly significant: χ^2=30.306, *df*=8, *P*<0.001). [a] Dummy coded with free-ranging dog as the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d]

Dummy coded with body condition normal as the reference category. The difference between PdA and PdG was estimated as 0.943±0.288, *z*=3.269, *P*=0.001. The difference between happy and neutral was estimated as 0.309±0.287, *z*= 1.081, *P*=0.279.

Term	Estimate	SE	*z*	*P*
Intercept	-3.934	0.245	-16.031	<0.001
Group(PdA)[a]	-1.266	0.287	-4.404	<0.001
Group(PdG)[a]	-0.323	0.272	-1.185	0.236
Condition(happy)[b]	-0.809	0.274	-2.956	0.003
Condition(neutral) [b]	-0.499	0.261	-1.909	0.056
Sex(m)[c]	0.031	0.222	0.142	0.887
Body condition (thin)[d]	-0.282	0.483	-0.585	0.558

Table 5_Eating all food. [a] Dummy coded with free-ranging dog being the reference category; [b] Dummy coded with condition angry as the reference category; [c] Dummy coded with female as the reference category; [d] Dummy coded with body condition normal as the reference category; [e] Not indicated because having a limited interpretation; [f] The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Term	Estimate	SE	*z* or χ^2	*P*	Lower CI	Upper CI	Min	Max
Intercept	-0.162	0.439		NI[e]	-1.126	0.718	-0.737	0.691
Group(PdA)[a]	0.759	0.637		NI[e]	-0.515	2.288	0.035	1.348
Group(PdG)[a]	2.226	0.865		NI[e]	0.891	11.548	1.394	18.810
Condition(happy)[b]	-0.601	0.614		NI[e]	-1.993	0.650	-1.592	0.069
Condition(neutral)[b]	-1.186	0.629		NI[e]	-2.774	-0.073	-1.542	-0.637
Sex(m)[c]	0.145	0.359	0.404	0.686	-0.587	0.957	-0.050	0.587
Body condition (thin)[d]	0.696	0.601	1.158	0.247	-0.673	2.358	0.111	0.942
Group(PdA)*Condition(happy)	2.189	1.076	36.735	<0.001 [f]	0.214	12.852	1.514	3.141
Group(PdA)*Condition(neutral)	2.793	1.092			0.816	13.398	2.237	3.716
Group(PdG)*Condition(happy)	-0.586	1.107			-10.131	1.803	-1.248	0.638

Group(PdG)*Condition(neutral)	-0.829	1.095			-10.217	1.351	-18.187	-0.052

Deutsche Zusammenfassung

Hunde (*Canis familiaris*) besitzen nicht nur die Kompetenz, unterschiedliche Gesichtsausdrücke beim Menschen zu unterscheiden, sondern sind außerdem fähig, ihnen die entsprechende Emotion korrekt zuzuordnen. In der Wissenschaft wird schon lange darüber diskutiert, inwiefern Domestikation und individuelle Erfahrung an der Entstehung einer solch komplexen sozial-kognitiven Fähigkeit eine Rolle spielen. Ein möglicher Ansatz, den Ursprung dieses zwischenartlichen Verständnisses zu erforschen, ist, Hunde mit unterschiedlichen Erfahrungen im Umgang mit Menschen miteinander zu vergleichen. In vorliegender Studie wurden freilebende Hunde in Marokko mit in Wien lebenden Haushunden in einem Experiment zur Erkennung von menschlichen Gesichtsausdrücken miteinander verglichen. Der Versuch, im Freien abgehalten, verlief folgendermaßen: Die Experimentatorin aß etwas, spielte dem Hund einen von drei Gesichtsausdrücken (fröhlich, wütend, neutral) vor und ließ anschließend ihr Essen absichtlich fallen. Unsere Resultate zeigten, dass Haushunde, die in Parks getestet wurden, das Essen sowohl unter fröhlicher als auch neutraler Kondition eher wegfraßen als freilebende Hunde. Zudem wandten, unabhängig von Gruppenzugehörigkeit, die Hunde ihren Blick am häufigsten bei einem wütenden Gesichtsausdruck von der Person ab; alle Hunde interpretierten also die Bedeutung dieses Gesichtsausdruckes richtig. Auch stellten wir fest, dass die freilebenden Hunde allgemein mehr mit ihrem Schwanz wedelten und auch größere Distanz zur Experimentatorin bevorzugten als Haustierhunde. Unsere Studie lässt uns schlussfolgern, dass Erfahrung mit Menschen allein nicht entscheidend ist für Hunde, Emotionen vom menschlichen Gesicht ablesen zu können. Allerdings können wir auch feststellen, dass in der von uns gewählten Versuchsanordnung allein durch den gewählten Gesichtsausdruck keine größere Verhaltensänderung bei den Hunden hervorzurufen ist.